The Evolution of Mammalian Hearing

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Abstract. In amphibians, reptiles and birds, the ears are internally coupled either through the mouth or through an interaural canal, an arrangement that makes the ears directional and enhances localization cues. In the evolution of mammals, however, the two ears became isolated. Having lost the directionality of coupled ears, mammals evolved both the ability to hear sounds well above 10 kHz and external ears. This allowed them to use two high-frequency cues for localizing: the difference in the intensity of a sound at the two ears, and the directionality induced by the pinnae (another mammalian invention). Because the magnitude of the high-frequency locus cues depends on the size of the head and pinnae relative to the wavelength of the sound, smaller mammals hear higher frequencies than larger mammals in order to use these cues. Localization acuity, however, is related not to the magnitude of the locus cues available to an animal, but to the accuracy needed to direct the eyes to a sound source. The result is that mammals with relatively narrow fields of best vision (e.g., humans and cats) require more accurate localization acuity to direct their gaze than do animals with broad fields of best vision (e.g., gerbils and cattle). So why did mammals give up the directional advantage of coupled ears? We suggest that mammals, because they breathe continuously, needed to isolate their ears from their mouth to prevent breathing sounds from masking external sounds. Amphibians and reptiles do not require such isolation because they are intermittent breathers. Birds, which, like mammals, are continuous breathers, isolated their ears from their mouth by evolving a canal that connects their ears through the skull, allowing them to retain the advantages of coupled ears.

INTRODUCTION

There were three major anatomical developments in the evolution of the mammalian ear. One was the evolution of the three-boned middle ear. The second was the development of external ears (pinnae). The third, less recognized, was the acoustic isolation of the two ears.

In non-mammalian tetrapods (amphibians, reptiles, and birds), sound not only reaches the external surface of the tympanic membrane, but then passes through the head to the internal surface of the opposite tympanic membrane. In amphibians and most reptiles, sound travels between the ears through the mouth (buccal cavity); in birds and crocodilians, it travels through an interaural canal. This arrangement makes the ear act as a pressure-difference receiver, enhancing the directionality of sound.[1,2] But the ears of mammals are isolated from each other, which may have forced mammals to develop other mechanisms for localizing sound. This, in turn led to the development of two additional anatomical structures. We propose the following scenario.

First, along with the isolation of the two ears, mammals evolved the three-boned middle ear enabling them to hear higher frequencies than non-mammalian tetrapods, that is, above 10 kHz. Although it is often stated that the development of high-frequency hearing allowed early mammals to communicate at frequencies inaudible to non-mammalian predators and to detect the high frequencies produced by insect prey,[3] evidence indicates that high-frequency hearing is primarily driven by the need to localize sound.

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FIGURE 1. The smaller an animalÕs functional head size, the higher it must hear in order to use pinnae cues and/or the binaural intensity-difference locus cue. The stars represent cetaceans and pinnipeds whose hearing was determined underwater. The filled circles are bats; the eight bats shown here that use laryngeal echolocation hear slightly higher than predicted by their functional head size.[4] The triangles are subterranean rodents that have relinquished the ability to localize brief sounds and therefore do not hear high frequencies. (Modified from Heffner and Heffner, 2016[5] [copyright AIP]. For references to individual audiograms see Koay et al., 1998[6] and Heffner et al., 2014[7]; for the killer whale, see Branstetter et al., 2017

FIGURE 2. Retinal ganglion cell isodensity contours for the cat, Norway rat, and cattle. The region of best vision is defined as the 75% isodensity contour. Note small area of best vision for

Some Mammals Do Not Use All Available Locus Cues

As previously noted, mammals have three potential sound-localization cues: binaural time differences, binaural intensity differences, and pinna cues. Some mammals use all three cues and early in the history of the discipline this was assumed to be universal. However, there are other mammals that use only one or the other of the binaural cues, and the subterranean rodents, being unable to localize sound, apparently donÕt use any of the cues.

The ability to use the two binaural locus cues can be demonstrated by determining the ability of an animal to localize pure tones. In this test, the animals are trained to localize tones presented from loudspeakers located in front of them at a fixed angle of separation, typically ±30¼. Because low-frequency pure tones can bend around an animalÕs head with little or no attenuation, they must be localized with the binaural time cue (referred to in the case of pure tones as the binaural phase cue). At higher frequencies, pure tones cannot be localized using the phase cue because successive cycles arrive two quickly for the nervous system to match the arrival of the same cycle at the two ears, at which point the phase cue becomes ambiguous and tones must be localized using the binaural intensity difference cue.

The ability of an animal to use pinna cues can be demonstrated by determining its ability to perform a front-back discrimination using noise bursts with speakers symmetrically centered on the interaural line so that there are no binaural time or intensity differences between the front and back locations. Animals that use pinna cues are able to localize high-frequency noise, but not low

FIGURE 4. Many mammals use both binaural time and intensity difference cues (on the left). However, some use only one the other cue (on right). Of the mammals that use only one cue, those with functional interaural distances larger than 400 µs use only the binaural time cue whereas those with interaural distances smaller than 200 µs use only binaural intensity cue. However, in both cases, there are similar-sized species that retain use of both cues (Modified from Heffner and Heffner, 2016[5] [copyright AIP]).

The question is whether these changes gave mammals better sound-localization acuity than amphibians, reptiles, and birds, or whether it was just to compensate for the loss of the pressure-difference receiver mechanism.

So far, no one has been able to train amphibians or reptiles to respond reliably to sound so we know little about their behavioral hearing abilities. Although birds easily learn to respond to sound, minimum audible angles have been determined for only six species. A seventh species, the barn owl, has been tested by training it to orient to the source of a sound, which shows it to have a threshold of 3-5¼. Just how that threshold compares to minimum audible angle is not known, but it indicates that accurate sound localization does not necessarily require hearing frequencies well above 10 kHz.

Finally, we turn to the evolutionary question and ask why the two ears of mammals became isolated. One possibility is that because mammals are continuous breathers, they isolated their ears from their mouth cavity to

SUMMARY

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