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SHORT COMMUNICATION

Otto Gleich · Robert J. Dooling · Geoffrey A. Manley

Audiogram, body mass, and basilar papilla length: correlations in birds and predictions for extinct archosaurs

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Abstract The inner ear in the group of archosaurs (birds, crocodilians, and extinct dinosaurs) shows a high degree of structural similarity, enabling predictions of their function in extinct species based on relationships among similar variables in living birds. Behavioral audiograms and morphological data on the length of the auditory sensory epithelium (the basilar papilla) are available for many avian species. By bringing different data sets together, we show that body mass and the size of the basilar papilla are significantly correlated, and the most sensitive frequency in a given species is inversely related to the body mass and the length of the basilar papilla. We also demonstrate that the frequency of best hearing is correlated with the high-frequency limit of hearing. Small species with a short basilar papilla hear higher frequencies compared with larger species with a longer basilar papilla. Based on the regression analysis of two significant correlations in living archosaurs (best audiogram frequency vs body mass and best audiogram frequency vs papillar length), we suggest that hearing in large dinosaurs was restricted to low frequencies with a high-frequency limit below 3 kHz.

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O. Gleich (✉)
ENT Department, University of Regensburg,
Franz-Josef-Strauß-Allee 11,
93042 Regensburg, Germany
e-mail: otto.gleich@klinik.uni-regensburg.de
Tel.: +49-941-9449426
Fax: +49-941-9449424

R. J. Dooling
Department of Psychology,
University of Maryland,
College Park, MD 20742, USA

G. A. Manley
Lehrstuhl für Zoologie,
Technische Universität München,
Lichtenbergstr. 4,
85747 Garching, Germany

Introduction

The dimensions of the auditory sensory epithelium are related to the hearing range in vertebrates [16]. The present study provides an analysis within the group of archosaurs comparing new data on cochlear dimensions in fossil *Archaeopteryx* [3] and in two dinosaur species [9, 19] with data from *Caiman* and from extant avian species. Birds are highly vocal animals, and consequently, there are considerable data sets available on avian hearing from behavioral as well as anatomical and physiological techniques [8]. Here, we compare the frequency of best hearing and a measure of the high-frequency limit of hearing derived from behaviorally determined audiograms of many avian species with morphological parameters (body mass and the length of the basilar papilla) and use the resulting correlations to predict the functional characteristics of the hearing organs of some extinct relatives.

Methods

Behavioral audiograms for a number of bird species were taken from publications that are listed in Fay [4] and Dooling ([2]; for detailed references of audiogram data, see S1). These data form the basis for our comparison of hearing in a total of 37 species. For each species, the raw audiogram data points [threshold in decibel sound pressure level (dB SPL) and frequency in kilohertz] were used to calculate a best-fit third-order polynomial in 100-Hz frequency steps for the range of frequencies for which thresholds had been measured. From these functions, we determined the frequency of best hearing (i.e., the frequency with the lowest threshold) and the high-frequency limit of hearing (defined as the point on the high-frequency side of the audiogram where threshold rises to ≥30 dB above the lowest threshold, corresponding to the highest frequency represented on the basilar papilla; [9]).

Direct measurements of the length of the basilar papilla were obtained for 19 bird species and for *Caiman crocodilus* from a number of publications (see S1 for a complete list of

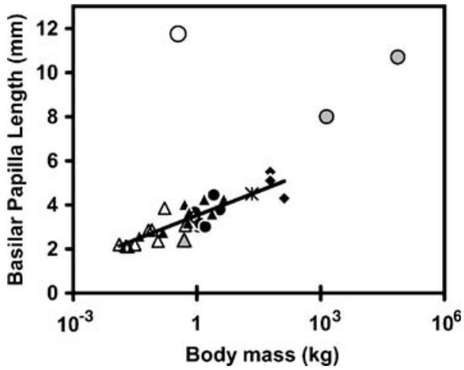

Fig. 1 Basilar papilla length as a function of body mass for 35 species. Separate symbols identify groups of birds according to phylogenetic relationships [5, 18]. These groups are Palaeognathae (N=4, *filled diamonds*), the tinamou (*filled square*), waterbirds (N=7, *filled circles*), primitive land birds (N=7, *filled triangles*), and advanced land birds. The latter are further subdivided into songbirds (N=9, *open triangles*) and two groups of birds of prey representing Falconiformes (buzzard, *open diamond*) and Strigiformes (the barn owl, *open circle*). In addition, a representative of Crocodylia (*Caiman*, *star*), *Archaeopteryx* (*gray triangle*), and two dinosaur species (*gray circles*) are shown. The regression line shows the best-fit function determined for 30 extant bird species, excluding the barn owl [$y=0.3186\ln(x)+3.5228$, $r=0.87$, $p<0.001$). This function also provides a fair representation for the *Caiman* (*star*), *Archaeopteryx* (*gray triangle*), and the two dinosaur species (*gray circles*), while the barn owl (*open circle*) deviates substantially from the distribution of all other archosaurs

references). Measurements of the length of the basilar papilla obtained using different methods were adjusted to represent the length of the basilar papilla in the living state [7, 8]. The length of the entire cochlear duct was determined for an additional 12 bird species from pairs of stereo photographs of the labyrinth published by Gray [10]. For the extinct archosaurs, the total length of the cochlear duct was derived from the available figures in the publications describing the inner ears of *Allosaurus fragilis* [19], *Brachiosaurus brancai* [9], and *Archaeopteryx lithographica* [3]. Based on previous work on birds, the length of the basilar papilla was then estimated as two thirds of the total cochlear duct length, with the rest being occupied by the lagenar macula.

For a number of species, body mass had been recorded during previous experimental work or was published in the literature on basilar papilla dimensions. An estimate of the body mass for *B. brancai* was provided by Gunga et al. [11]. For additional species, various other sources and ornithological web sites were used to obtain an estimate of body mass (see S1 for a complete list of references). A table listing all data used for the present analysis, including common and scientific names, as well as relevant references is provided in S1.

Results

Measurements and estimates of the basilar papillar length were available in 31 bird species, in the *Caiman* as a representative of crocodilian archosaurs, in two dinosaur species, and in *Archaeopteryx*. Figure 1 shows a plot of papillar length as a function of body mass for 35 archosaur species. The barn owl (open circle) clearly deviates from the pattern shown by birds and other extant (*Caiman*) and extinct representatives of archosaurs (*Archaeopteryx* and dinosaurs).

The basic hearing capability of a given species is defined by the audiogram [1]. One quantitative measure that can be derived from the audiogram is the most sensitive (best) frequency. Figure 2a shows the correlation between body mass and the frequency of best hearing for 37 species. Groups of birds are coded as in Fig. 1 according to phylogenetic relationships, with additional owl species indicated by crosses. Many owl species deviate considerably from the distribution of the other birds, especially the barn owl (open circle), for which it has been shown that a number of morphological gradients in the basilar papilla differ strongly from the "normal" avian pattern [6, 9, 13]. This correlates with the highly specialized use of hearing by barn owls [14]. Although there are no comparable data showing morphological or physiological specializations of

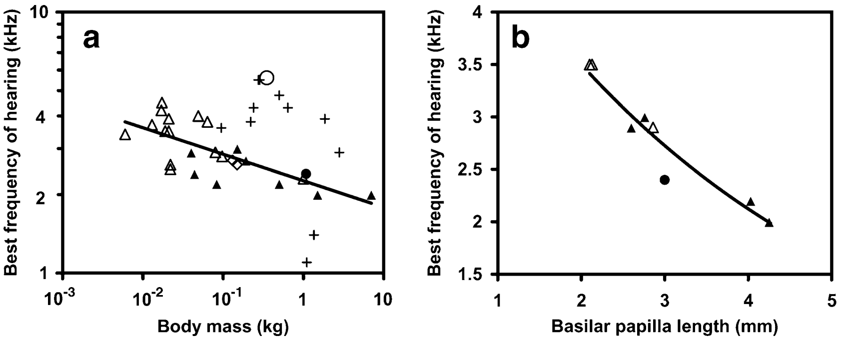

Fig. 2 **a** The frequency of best hearing as a function of body mass for 37 species. Symbols represent different bird groups as in Fig. 1, with additional owls coded by *crosses*. With the exception of owls, birds of different phylogenetic groups show a systematic relationship between body mass and the best audiogram frequency as indicated by the regression line calculated for the data from 25 species excluding owls ($y=2.2582x^{-0.1016}$, $r=0.74$, $p<0.001$). The barn owl (*open circle*) and many other owls (*crosses*) clearly deviate from the distribution shown by the other birds. **b** The frequency of best hearing as a function of the length of the basilar papilla. Symbols represent different bird groups as in previous figures. The *regression line* ($y=5.7705e^{-0.25x}$, $r=0.96$, $p<0.001$) shows a significant correlation between the length of the basilar papilla and the frequency of best hearing

the inner ear in other owl species, this figure suggests that they may also show varying degrees of specialization. The owl data were therefore excluded from further consideration in this analysis. The best-fit function (excluding owl data) shows an inverse relationship between the best audiogram frequency and body mass; small birds hear better at higher frequencies than do large birds.

While behavioral audiograms are available for 37 bird species, and data on the length of the basilar papilla are available for 35 archosaur species, both sets of data are known for only nine bird species: canary, zebra finch, and starling as representatives of songbirds; budgerigar, pigeon, chicken, and quail as representatives of primitive land birds; the mallard duck as a representative of waterbirds; and the highly specialized barn owl. Figure 2b shows the relationship between the most sensitive audiogram frequency and the length of the basilar papilla, excluding the data point of the barn owl (11.75 mm basilar papilla length and a best audiogram frequency of 5.6 kHz) that would be far off the highly correlated distribution of data points from the other eight bird species. This figure demonstrates that species with a long basilar papilla have the most sensitive frequency of hearing at lower frequencies than do species with a short basilar papilla.

The frequency of best hearing and the high-frequency limit of hearing were derived for 22 species (excluding owls). These data are shown in Fig. 3 along with a regression line. The high degree of correlation between both audiogram parameters indicates that the most sensitive frequency of the audiogram is also strongly predictive of the upper limit of hearing.

Using the regressions illustrated in Figs. 2 and 3, we can make predictions concerning the best frequency and the high-frequency limit of hearing for species where body mass and/or the length of the basilar papilla is known. For the emu, based on an average adult body mass of 60 kg and a 5.5-mm-long basilar papilla, the predicted frequency of best hearing would be ~1.5 kHz with a corresponding high-frequency limit of hearing of ~3.8 kHz. While no behavioral audiogram is available for the emu, this prediction is in very good agreement with an "audiogram" based on physiological recordings from a large number of auditory nerve fibers of emu chicks (see Fig. 2a in [17]). For *Archaeopteryx*, where body mass (0.486 g) and the size of the basilar papilla (2.4 mm) are within the range of living birds, these correlations predict a best frequency of hearing of 2.4–3.2 kHz and a high-frequency limit of 5.5–6.9 kHz. For the large dinosaurs (body mass 1.4 and 75 tons; basilar papilla 8.0 to 10.7 mm), the extrapolation of the regression analyses suggests lower frequencies of best hearing (0.7–1.5 kHz) and a high-frequency limit of hearing below 3 kHz (1.8–3.0 kHz).

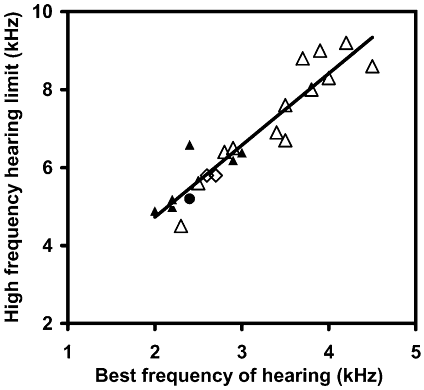

Fig. 3 The upper frequency limit of hearing as a function of the frequency of best hearing. Symbols represent different avian groups as in previous figures. The regression line was calculated for 22 species (y=1.8436x+1.0426, r=0.94, p<0.001)

Discussion

At first glance, it appears logical that small birds can fit only small basilar papillae into their heads, and as the size of a species increases, it can also accommodate longer basilar papillae. However, a closer look at Fig. 1 demonstrates that body mass varies between 6 g and 75 tons, while the length of the basilar papilla varies only between 2.1 and 11.75 mm. Since the barn owl (body mass 350 g) has an almost 12-mm-long basilar papilla, a value more than three times as long as that expected for a species of comparable body size (Fig. 1), it is not clear why space constrictions would limit the size of the basilar papilla to 5.5 mm in the emu or in other large archosaurs.

From a theoretical point of view, one might expect that an extended high-frequency hearing range might be advantageous for birds to use interaural intensity cues to more accurately localize sound sources [12]. However, the present data show that, with the exception of highly specialized birds such as the barn owl, extending the high-frequency hearing range was not an important evolutionary pressure. Instead, the data suggest that the length of the basilar papilla determines the high-frequency hearing limit of a given species (Fig. 2b). The mechanisms that form the basis for this inverse relationship are not obvious. The comparison of morphological gradients across a range of bird species showed fairly similar patterns in the base of the basilar papilla despite the fact that frequencies that are mapped to the base of the basilar papilla vary between these species [9]. The only species that showed highly specialized modifications of the basilar papilla for high-frequency hearing up to the limit imposed by the single ossicle columella ear [15] was the barn owl. In contrast to other species, the elongation of the basilar papilla in the barn owl extended the high-frequency hearing range.

The two correlations between the best audiogram frequency and body mass (Fig. 2a) on the one hand and between the best audiogram frequency and the length of the basilar papilla (Fig. 2b) on the other may be used to predict limited high-frequency hearing in the large archosaurs. That these extinct archosaur species do roughly conform to the typical relationship between body mass and papillar length (Fig. 1) supports the view that these estimates of high-frequency hearing are realistic. However, without knowing the audiograms of extinct dinosaurs, the possibility that they developed unique specializations cannot of course be excluded. The observation that the predicted best frequency of hearing in the emu, one of the largest living archosaurs, was in excellent agreement with an "audiogram" derived from recordings of auditory nerve fibers [17] provides further support for the validity of this analysis. The predictions are more reliable for the species with a body mass and papillar length in the range of three orders of magnitude covered by the sample illustrated in Fig. 2 (e.g., *Archaeopteryx*) and will only provide rough estimates for species where data have to be extrapolated beyond this (e.g., *Allosaurus* and *Brachiosaurus*).

Body temperature is an additional factor affecting the response frequency in archosaurs [22], including birds [20]. A 10°C temperature change can lead to a frequency shift of as much as one octave. Although the issue of homeothermism and body temperature in dinosaurs is not fully resolved, some evidence suggests that simply due to their enormous body mass, large dinosaurs had a relatively constant body temperature that was well above ambient temperature [21], reaching values close to the body temperature of recent birds. With these caveats in mind, the present analysis suggests that, like many modern birds, *Archaeopteryx* had best hearing around 3 kHz and an upper limit of hearing below 7 kHz. Hearing in the large dinosaurs was limited to a much lower frequency range with an upper frequency limit below 3 kHz.

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Note added in press:

For the vestibular system of *Brachiosaurus brancai*, Clarke has used a similar morphometric analysis and attempts to predict the performance of this extinct species based on data from extant species. [Clarke AH (2005) On the vestibular labyrinth of *Brachiosaurus brancai*. J Vestib Res 15:65–71]

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