Middle-ear transmission in humans: wide-band, not frequency-tuned?

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Abstract

Postmortem and *in vivo* vibration responses to sound of the stapes and the umbo of human ears are surveyed. The magnitudes of umbo velocity responses recorded *postmortem* decay between 1 and 5 or 10 kHz at rates between 0 and −3 dB/octave. In contrast, the magnitudes of *in vivo* umbo vibration are relatively invariant over a wide frequency range, amply exceeding the bandwidth of the audiogram according to one report. Similarly, most studies of *postmortem* stapes vibration report velocities tuned to about 1 kHz, with magnitudes that decay at a rate of about −6 dB/octave at higher frequencies. In contrast, *in vivo* stapes responses are apparently only mildly tuned. We conjecture that the bandwidth of stapes vibration velocity in humans will eventually be shown to exceed the bandwidth of the audiogram, in line with findings in other amniotic vertebrates.

Introduction

In a recent review, we showed that the magnitudes of stapes (or columella) vibration velocity in the middle ears of several amniotic vertebrates (i.e., mammals, birds, and reptiles) are relatively invariant over a wide frequency range and that their bandwidths generally exceed the bandwidths of behavioral thresholds [1]. In apparent contrast, most studies of stapes vibration velocity in humans report that the middle ear acts as a resonant system tuned to a frequency between 700 and 1200 Hz, with responses' magnitudes decaying at rates of +6 and −6 dB/ octave, respectively, at lower and higher frequencies (Fig. 1). At face value, these results imply that the human middle ear is exceptional among those of amniotic vertebrates in that it severely limits the bandwidth of hearing.

Here we compare the magnitudes of *postmortem* and *in vivo* vibrations of the stapes and the umbo of the tympanic membrane in the ears of humans. This comparison leads us to conjecture that most *postmortem* recordings of ossicular vibrations are flawed and that middle-ear transmission in humans, in fact, does not severely limit the bandwidth of hearing.

Methods

Our survey of ossicular vibration data (Figs. 1 and 2) is extensive but not exhaustive. It includes all available data from the last decade, as well as some older data selected so as to include the work of additional laboratories. The data were extracted from the original figures by digitization with a resolution of 12 points/octave. Displacement units were converted to velocity units, as needed. Expressing the magnitudes of ossicular vibration in terms of velocity (rather than, say, displacement or acceleration) allows for direct comparison with hearing thresholds, since pressure in scala vestibuli near the stapes (essentially the input signal for

sound analysis and transduction in the cochlea) is proportional to stapes velocity over the wide range of frequencies in which cochlear input impedance is resistive [13–17].

Results

In vivo stapes vibration

Huber et al. reported *in vivo* of stapes vibration in humans, recorded from 7 patients undergoing ear surgery [2]. Fig. 1 compares the average magnitudes of stapes vibration velocity from that report (red dashed line), with average curves from 10 *postmortem* studies in temporal bones (continuous lines). At frequencies lower than 1 kHz, the normalized curves follow similar trajectories, regardless of whether they were obtained *in vivo* or *postmortem*. Above 1 kHz, however, most *postmortem* curves follow trajectories with a slope of about −6 dB/octave, whereas the single *in vivo* curve and one *postmortem* curve are relatively flat. Inspection of Fig. 1 indicates that, whereas the magnitudes of *postmortem* velocities, with the indicated single exception [9], are clearly tuned to about 1 kHz, with slopes of +6 dB/octave and −6 dB/octave below and above that frequency respectively, the *in vivo* velocity data are more broadly tuned, with similar velocity magnitudes between 1 and 3.5 kHz. Measured at −10 dB relative to the peak responses, the *in vivo* stapes responses have a bandwidth of 8 kHz or about double the 10 −dB bandwidth of the *postmortem* measurements. The exceptional *postmortem* curve [9] has an even wider bandwidth.

Umbo vibrations in vivo and postmortem

After pioneering investigations measured umbo vibrations in the ears of living humans at frequencies lower than 5 kHz [22,23], three recent studies [18–20] reported *in vivo* measurements over wider frequency ranges. [*] Their results (dashed lines) are plotted in Fig. 2 together with umbo response magnitudes measured *postmortem* in temporal bones (continuous lines). *In vivo* velocity responses of the umbo are nearly flat (± 3 dB) over a wide frequency range extending from 400 Hz to nearly 10 kHz and in one case [20] almost 15 kHz. Measured at −10 dB relative to the peak, the bandwidth of umbo velocity responses is nearly 19 kHz. In contrast, *postmortem* responses vary widely above 2 kHz: some studies [8,20] reported velocity responses that decay with frequency at a rate of about −3 dB/octave and others [3,9] reported responses that remain relatively invariant up to 6 or 10 kHz.

The differences between postmortem and in vivo ossicular vibrations

Fig. 3 summarizes the data of Figs. 1 and 2 and compares the human audiogram [25] with the velocity-vs.-frequency curves of ossicular responses. Fig. 3 shows that ossicular velocity responses, both *in vivo* and *postmortem*, and audiometric thresholds vary in direct proportion to one another at frequencies lower than 1 kHz (the frequency at which the curves were normalized). Between 1 and 8 kHz, both the audiogram and the ossicular-velocity response curves measured *in vivo* are relatively flat as a function of frequency. In one case (red dashed line), the 10−dB bandwidth of *in vivo* umbo vibration velocity extends to 20 kHz, amply exceeding the bandwidth of the audiogram [20].

Two groups of experimenters have published both *in vivo* and *postmortem* vibration data for human ears obtained and analyzed with similar techniques. Their data can therefore be used to advantage in a quantitative evaluation of the differences between *postmortem* and *in vivo* responses. Fig. 4 plots the ratios (expressed in decibels) between the magnitudes of *postmortem* and *in vivo* velocity responses of the umbo and the stapes reported by the Goode

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[*]The 1993 measurements of Goode et al. [21] are not shown here because they were superseded by a much more extensive dataset from the same laboratory [20]. The 1993 data [21] were incorrectly reproduced in Fig. 9–16 of [24], giving the impression that the magnitude of umbo velocity *in vivo* decays above 500 Hz at a rate of −6 dB/octave.

[20] and Huber [2,8] groups, respectively. This figure suggests that the *postmortem* effects on both stapes and umbo vibrations resemble low-pass filtering with corner frequencies between 1 and 2 kHz and high- frequency slopes of roughly −6 dB/octave.

Conclusions and speculations

The literature contains several statements to the effect that ossicular vibrations in cadaveric temporal bones are representative of ossicular vibrations in living humans. For example: in a report on umbo vibrations, Nishihara and Goode commented that "the human temporal bones showed very similar results to the normal … ears" (26, p. 91). Similarly, in their investigation of stapes vibration, Huber et al., found "no major differences in the results from the live human subjects and temporal bone preparations" (2, p. 31) and concluded that "the temporal bone is a very good model for studying middle ear mechanics" (27, p. 13). The present review disputes that belief, presenting evidence that, in fact, there are substantial differences between *in vivo* and most *postmortem* measurements.

We conjecture that the finding of wide-band umbo vibration velocities (red dashed lines in Figs. 2 and 3) will be replicated. We also conjecture that when stapes velocities are measured *in vivo* at sufficiently high frequencies, their bandwidth will also be found to be comparable to that of the audiogram. In other words, the human middle ear is not exceptional among those of amniotic vertebrates and resembles them in acting as a wide-band pressure transformer which only minimally limits the performance of cochlear frequency analysis. Finally, we note that the present results support the hypothesis that high-frequency hearing in humans is determined by the high-frequency slopes of the auditory-nerve fibers with the highest characteristic frequencies [28,29], as is it appears to be the case in other amniotic vertebrates [1].

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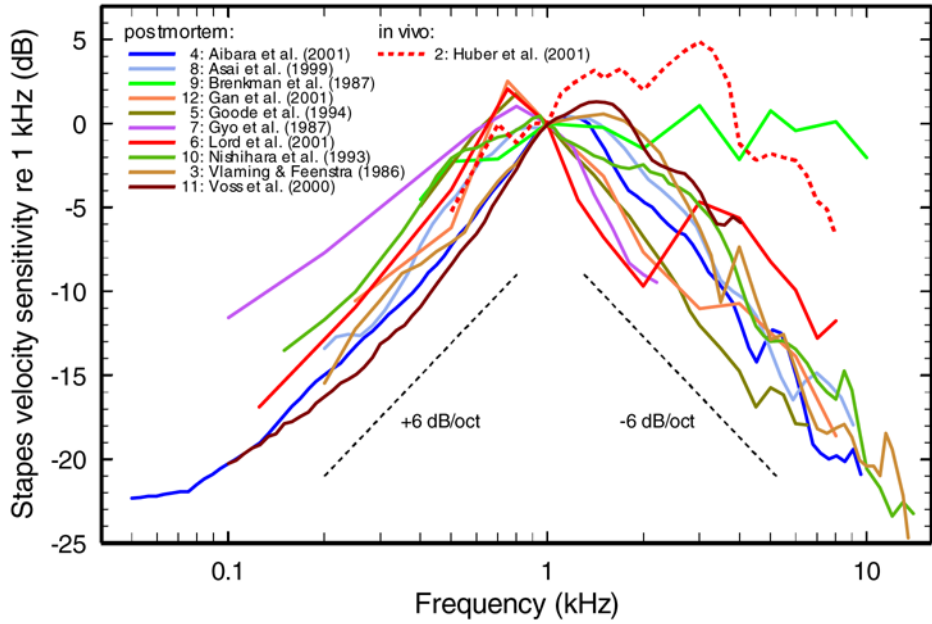
Fig. 1.
The frequency dependence of stapes vibration velocity in human ears, *in vivo* and *postmortem*. The magnitudes of stapes velocity were normalized to 1 kHz and plotted as a function of frequency using a decibel scale. The *in vivo* data (red dashed line) were taken from [2], Fig. 5. The curve from Vlaming and Feenstra is a median computed from 4 individual curves presented in their Fig. 5 [3]. Other *postmortem* data (solid lines) were taken from [4], Fig. 3; [5], Fig. 1; [6], Fig. 2; [7], Fig. 4; [8], Fig. 5; [9], Fig. 7; [10], Fig. 2; [11], Fig. 4; [12], Fig. 5. (Those reading a black-and-white version of the paper should refer to the color version of this figure in the online archival version.)
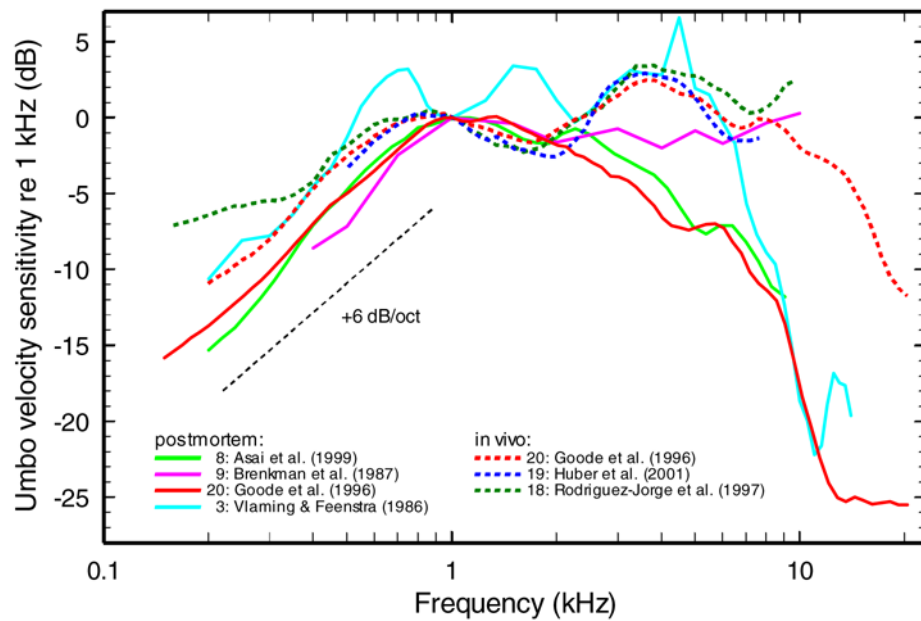
Fig. 2.
The frequency dependence of umbo vibration velocity in humans, *in vivo* and *postmortem*. The magnitudes of umbo velocity were normalized to 1 kHz and plotted as a function of frequency using a decibel scale. The *in vivo* data (dashed lines) from [18] were computed from their Fig. 6, according to the equation, $[(\chi + SD) - (\chi - SD)]/2$, where χ = mean, SD = standard deviation of the mean. Other *in vivo* data were taken from [19], Fig. 5, and [20], Fig. 4c. The *postmortem* curve from Fig. 4c of [20] represents data from 3 other studies by the same group: [5,10,21]. The *postmortem* curve from [3] represents medians computed from 4 individual measurements given in their Fig. 2. Other *postmortem* data (solid lines) were taken from: [8], Fig. 5 and [9], Fig. 7. (Those reading a black-and-white version of the paper should refer to the color version of this figure in the online archival version.)
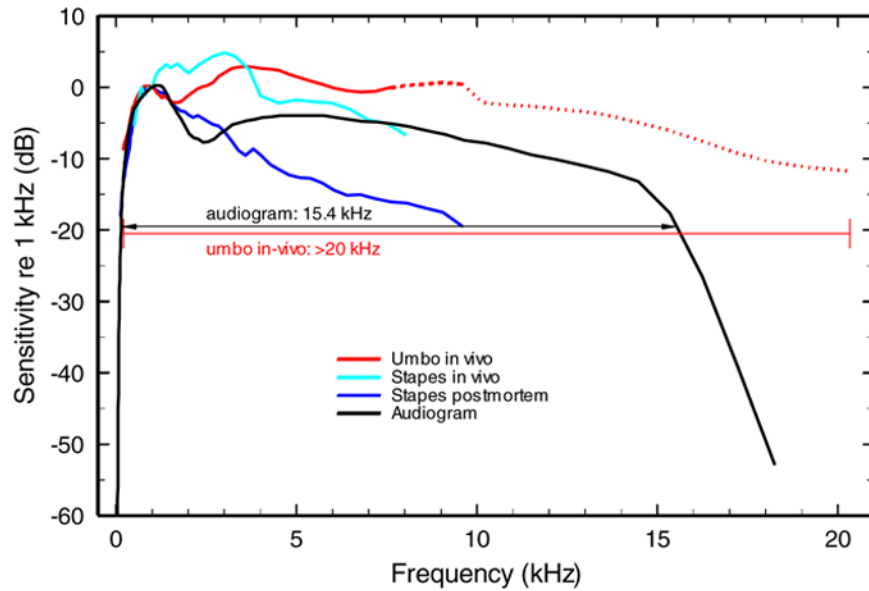
Fig. 3.
A comparison between the human behavioral audiogram and the magnitudes of vibration velocity of the stapes and umbo, *in vivo* and *postmortem*. Black line: human behavioral audiogram from [25]. Red line: *in vivo* umbo data of Fig. 2: the solid segment indicates medians computed from three studies (Fig. 2); the thick-dash line segment represents two studies; the dotted line represents one study. Light blue line: the *in vivo* stapes data of Fig. 1[2]. Dark blue line: group medians for the *postmortem* stapes data of Fig. 1. (Those reading a black-and-white version of the paper should refer to the color version of this figure in the online archival version.)
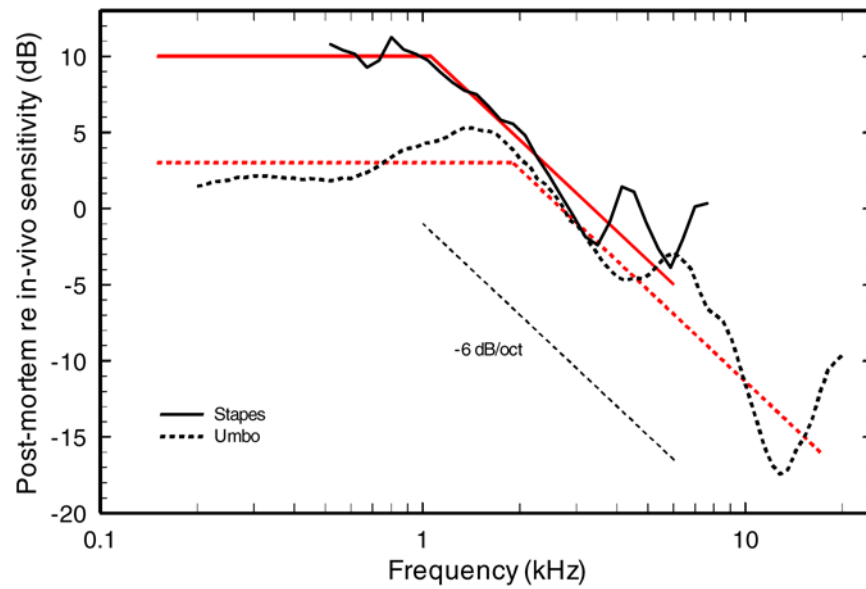
Fig. 4.
Relative magnitudes of *postmortem* and *in vivo* vibrations of the stapes and umbo. The magnitudes of *postmortem* vibration velocity are expressed in decibels relative to *in vivo* velocity. The relative magnitudes of umbo and stapes velocity are indicated by the solid and dashed lines, respectively. The umbo data are from [20]; the stapes data are from [2,8]. The red lines represent low-pass filters with corner frequency between 1 and 2 kHz and high-frequency slopes of −6dB/octave. (Those reading a black-and-white version of the paper should refer to the color version of this figure in the online archival version.)