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Comparison of group delays of $2f_1-f_2$ distortion product otoacoustic emissions and cochlear travel times

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Abstract

To help elucidate how distortion-product otoacoustic emissions propagate from their cochlear sites of origin to the middle ear, their group delays were compared with basilar-membrane and organ of Corti travel times measured in guinea pig, gerbil, and chinchilla.

1. Introduction

Twenty-five years after their discovery,¹ it is still not known how distortion-product otoacoustic emissions (DPOAEs) propagate in the cochlea toward the middle ear.^{2–4} $2f_1-f_2$ distortion products (DPs) first arise in the region of the cochlear partition with characteristic frequency (CF) between f_1 and f_2 (the “source region”) and travel on the basilar membrane (BM) toward the region with $CF \approx 2f_1-f_2$.⁵ Although DPOAEs may arise from both regions, I focus here on the DPOAE component that propagates directly from the source region, which appears to be dominant for all but closely spaced primary tones.³ In that region, DPs probably originate at the stereocilia of outer hair cells,⁵ as they do in frog sacculus hair cells.⁶

2. Definitions

The phases of DPOAEs evoked by a fixed tone and a swept-frequency tone vary approximately as a linear function of the swept frequency. Therefore, DPOAE group delays^{7,8} (τ_{DPOAE} 's) may be defined as the negative slopes of the phase-versus-frequency functions.^{9–12} τ_{DPOAE} 's vary inversely with fixed-tone frequency, suggesting a systematic, but still unspecified, relationship to cochlear travel times.^{2–4}

Other definitions:

$\tau_{\text{swept-}f_1} = \tau_{\text{DPOAE}}$ measured with fixed f_2 and swept f_1 .

$\tau_{\text{swept-}f_2} = \tau_{\text{DPOAE}}$ measured with fixed f_1 and swept f_2 .

Signal-front delay ($\tau_{\text{signal-front}}$): the difference in onset times of BM and stapes responses to intense clicks^{8,13} $\approx$ the low-frequency slope of phase versus frequency functions of BM-re-stapes responses to tones.¹⁴ $\tau_{\text{signal-front}}$ is independent of stimulus level.

Weighted-average group delay (τ_{WAGD}): the negative slope of the phase-versus-frequency curve weighted according to the BM response gains^{7,8} = the center of gravity of the impulse response. τ_{WAGD} depends on stimulus level and the health of the cochlea. For well-tuned responses, $\tau_{\text{WAGD}} \approx$ near-CF group delay.

Filter delay: $\tau_{\text{filter}} = \tau_{\text{WAGD}} - \tau_{\text{signal-front}}$.⁸ τ_{filter} depends on stimulus level and the health of the cochlea.

3. Hypotheses on the propagation of DPOAEs

The most common view of the propagation of DPOAEs in the cochlea is that they reach the stapes via retrograde BM traveling waves.^{2,9-11,15} If BM travel time = $\tau_{\text{signal-front}}$ ⁸, this view leads to hypothesis IA: $\tau_{\text{DPOAE}} = \tau_{\text{filter}} + 2\tau_{\text{signal-front}}$. A related, more specific, hypothesis (IB) is that $\tau_{\text{filter}} \approx \tau_{\text{swept-f2}} - \tau_{\text{swept-f1}}$ ⁹. If BM travel time = τ_{WAGD} ¹⁶, another hypothesis (II) states that $\tau_{\text{DPOAE}} = 2\tau_{\text{WAGD}}$. Lastly, hypothesis III states that OAEs propagate via acoustic compression waves in the cochlear fluids.¹⁷ Robles *et al.* alluded to hypothesis III in 1997, when they noted¹⁸ that frog ears broadcast DPOAEs¹⁹ even though their hearing organs do not rest on BMs.²⁰ Other references to hypothesis III have appeared since then.²¹⁻²⁵

The predictions of the four hypotheses are

$$\text{IA: } \tau_{\text{DPOAE}} = \tau_{\text{filter}} + 2\tau_{\text{signal-front}} = (\tau_{\text{WAGD}} - \tau_{\text{signal-front}}) + 2\tau_{\text{signal-front}} = \tau_{\text{WAGD}} + \tau_{\text{signal-front}}$$

$$\text{IB: } \tau_{\text{filter}} \approx \tau_{\text{swept-f2}} - \tau_{\text{swept-f1}}, \text{ implying that } \tau_{\text{swept-f1}} \approx 2\tau_{\text{signal-front}}$$

$$\text{II: } \tau_{\text{DPOAE}} = 2\tau_{\text{WAGD}}$$

$$\text{III: } \tau_{\text{DPOAE}} = \tau_{\text{filter}} + \tau_{\text{signal-front}} = \tau_{\text{WAGD}}$$

Figure 1 indicates the τ_{DPOAE} 's predicted by the hypotheses as well as $\tau_{\text{signal-front}}$, $2\tau_{\text{signal-front}}$, τ_{WAGD} , and $2\tau_{\text{WAGD}}$ for several BM sites of "active" gerbil and guinea pig cochleae (i.e., exhibiting nonlinear level dependence of both response magnitudes and phases⁵). Note that at the base, $\tau_{\text{signal-front}} < \tau_{\text{filter}}$ and $\tau_{\text{WAGD}} \approx \tau_{\text{filter}}$, whereas near the apex, $\tau_{\text{signal-front}} \approx \tau_{\text{filter}}$ and $\tau_{\text{WAGD}} \approx 2\tau_{\text{signal-front}}$.

4. DPOAE delays in human ears

Hypothesis IB was formulated to explain DPOAE data from human ears, in which $\tau_{\text{swept-f1}}$ was thought to equal twice the cochlear travel time inferred from gross neural data.¹² However, such equality is uncertain.¹¹ Most importantly, the inferred travel times may be unreliable, since they have not been calibrated against BM vibrations or recordings from auditory-nerve fibers.

5. Comparison of DPOAE group delays and BM travel time measured in different groups of animals

Comparisons of DPOAE and BM delays can be carried out more reliably and accurately in experimental animals than in humans (Fig. 1). Figures 1(a) and 1(b), respectively, show $\tau_{\text{swept-f1}}$ for gerbils and $\tau_{\text{swept-f1}}$, and $\tau_{\text{swept-f2}}$ for guinea pigs, measured with moderate level stimuli. Figure 1 also shows travel times for "active" BM responses evoked by comparable-level stimuli and the corresponding τ_{DPOAE} 's predicted by hypotheses IA, IB, II, and III. At most frequencies, the comparisons of Fig. 1 contradict hypotheses IB and II and are consistent with hypotheses IA and III but do not distinguish clearly between the latter.

6. Comparison of DPOAE group delays and BM travel times in the same ears of experimental animals

Ideally, comparisons of DPOAE delays and BM travel times should be carried out using recordings of both in individual animals. Three such comparisons are available in the literature.²³⁻²⁵ The earliest is described in a 1998 abstract²³ by Narayan *et al.*, who measured DPs simultaneously as OAEs in the external ear canal and as BM vibrations, in chinchillas. The abstract states that, using the swept- f_1 paradigm and recording BM vibrations at the f_2 place,

“the BM and OAE DP phases...had similar group delays (0.5–0.8 ms)... (and)... were similar to those measured at the BM for responses to tones at near-CF frequencies. This similarity indicates that DPOAE group delays measured with f_1 sweeps largely reflect the ‘filter’ delays at the BM. [‘Signal-front’ ... delays at the 10-kHz BM site (measured from responses to clicks) amount to only 25 μ s].” In other words, Narayan *et al.* interpreted their results as inconsistent with hypothesis IB. Those results also contradict hypothesis II and are consistent with (but do not distinguish between) hypotheses IA and III.

The single formal report of comparisons of DPOAE and BM delays in individual animals was published recently by Ren.²⁴ One of Ren’s experiments, in gerbils, was a refined version of the one by Narayan *et al.*:²³ using a swept- f_1 paradigm, he measured the group delays at $2f_1-f_2$ of the DPOAEs and BM vibrations at the f_2 site and, additionally, stapes vibrations. This permitted ascertaining that the group delays for BM and DPOAE responses at $2f_1-f_2$ were nearly identical and shorter (by 50–130 μ s) than those of stapes responses. Ren interpreted his results as rejecting hypothesis II and supporting hypothesis III. Ren’s results also contradict hypothesis IB but cannot discriminate between hypotheses IA and III. Ren also measured BM responses to two-tone stimuli as a function of longitudinal cochlear position. Such unique recordings allowed direct observation of the DP traveling wave. The associated phase lags increased systematically as a function of distance from the stapes, indicating that DP waves traveled only in the forward direction, again rejecting hypothesis II.

The findings of Ren and Narayan *et al.* clash with a recent abstract by Cooper and Shera,²⁵ who recorded simultaneously DPOAEs and BM vibrations near the 30-kHz site of the guinea pig cochlea. Cooper and Shera found that $\tau_{\text{DPOAE}}=2\tau_{\text{WAGD}}$, as predicted by hypothesis II. The discrepancies between the results for individual guinea pig versus those for gerbil and chinchilla might reflect different stimulus paradigms: the study on guinea pigs²⁵ measured $2f_2-f_1$ and used swept primaries with narrowly spaced frequencies ($f_2=f_1 + 100$ Hz), whereas the studies on individual gerbils and chinchillas measured $2f_1-f_2$ with fixed f_2 (=BM CF) and swept f_1 .^{23,24} A longer τ_{DPOAE} (re τ_{WAGD}) for $2f_2-f_1$ than for $2f_1-f_2$ may reflect the respective dominances of long- and short-latency components.³ Another difference is that the BM recordings in guinea pigs²⁵ (in contrast with the recordings in chinchillas²³ or gerbils²⁴) were made at the extreme basal end of the cochlea, where the organ of Corti is especially vulnerable to injury (p. 360 of Ref. 26).

7. Summary and conclusions

- a. The presence of DPOAEs in the ears of frogs, whose hearing organs lack BMs, suggests that hypothesis III may also apply to mammals.¹⁸
- b. Comparisons of BM travel times and DPOAE group delays from different groups of gerbils and guinea pigs (Fig. 1) and measurements in individual ears of gerbils²⁴ and chinchillas²³ contradict hypotheses IB and II and are consistent with hypotheses IA and III but cannot discriminate between the latter.
- c. Comparisons of BM and DPOAE group delays in the same ears of guinea pigs²⁵ are exceptional in that they support hypothesis II.
- d. Reliable comparisons of DPOAE and BM group delays, capable of constraining models of DPOAE propagation,^{2–4,27,28} will require more complete sets of correlated BM and DPOAE data for the same species, preferably for individual ears, than are available at present.

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Fig. 1.

Comparisons of DPOAE group delays and cochlear travel times in Mongolian gerbil and guinea pig. DPOAEs were stimulated with pairs of fixed- and swept-frequency tones; their group delays were measured from phase vs. frequency curves for the swept tones. The abscissae indicate the fixed-tone frequency for DPOAE data and CF for BM data. The bracketed red symbols indicate the range of τ_{WAGD} 's for active BM responses as a function of stimulus level (the shortest delays typically corresponding to the highest levels). (A) gerbil. Blue circles: $\tau_{\text{swept-f1}}$ from Fig. 7 of Ref. 29; blue squares: $\tau_{\text{swept-f1}}$ from Fig. 6C of Ref. 30. BM data from Refs. 26, 31, and 32. (B) Guinea pig. $\tau_{\text{swept-f1}}$ and $\tau_{\text{swept-f2}}$ trend lines from Table I of Ref. 33. Since these trend lines cover only the 1.5–11 kHz frequency range, (Ref. 33) they have been

extrapolated to allow comparison with cochlear vibrations at sites with higher (Refs. 34–36) or lower (Ref. 37) CFs.