Temporal interactions in basilar-membrane and otoacoustic-emission responses to pairs of clicks

Karolina K. Charaziak[1], Wei Dong[2], Alessandro Altoè[3] & Christopher A. Shera[1,4]

[1]Keck School of Medicine, Caruso Department of Otolaryngology, University of Southern California; [2]VA Loma Linda Health Care System and Otolaryngology, Loma Linda University; [3]Department of Signal Processing and Acoustics, Aalto University; [4]Department of Physics and Astronomy, University of Southern California.

Correspondence: karolina.charaziak@usc.edu

INTRODUCTION

Click-evoked otoacoustic emissions (CEOAEs) can change when another click stimulus (suppressor) precedes or follows the evoking test click (Fig. 1). One might naively expect that the strongest interactions occur when the delay between two clicks, Δt, is set to zero (Fig. 2B). However, measurements in humans reveal an unexpected pattern where the temporal suppression of CEOAE is strongest when the suppressor click precedes the test click by a few milliseconds (Fig. 2A).



Fig. 1. Cartoon illustrating the concept of temporal suppression of CEOAE response.

It has been hypothesized that temporal suppression of CEOAE response arises through nonlinear interactions between the mechanical vibrations produced by the two clicks on the basilar membrane (BM). The shift of the maximal suppression from zero Δt should then also be observable in the BM vibrations. We test this idea in gerbils, where CEOAE suppression also peaks at nonzero Δt (Fig. 2C) but, unlike in humans, direct measurments of the BM motion in response to pairs of clicks are possible.

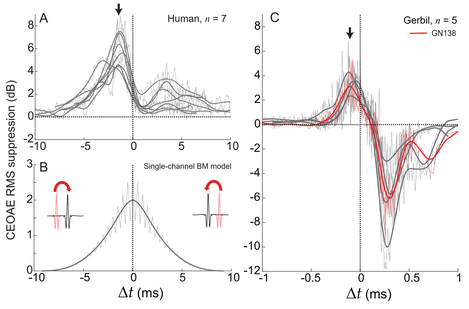


Fig. 2. The suppression of the CEOAE root-mean-square amplitude caused by the suppressor click following ($\Delta t > 0$) or preceding ($\Delta t < 0$) the evoking click measured in humans (A) and gerbils (C) (Charaziak & Shera, 2016). Negative "suppression" corresponds to enhancement. Predicted suppression in the BM responses from a single-channel model with instantaneous nonlinearity is shown in panel B (Kapadia and Lutman, 2000). Thick lines correspond to smooth curves.

METHODS

All experiments were carried out in deeply anesthetized Mongolian gerbils (n = 5). The OAE-probe system (ER10X, Etymotic Research) was sealed to the bony rim of the ear canal after resecting the pinna and cartilaginous part. The bulla was widely open to visualize the round-window membrane, which was then removed. Reflective micro-beads were spread over the BM and the opening then covered with a glass cover slip. The laser-Doppler vibrometer (LDV) was focused on one of the beads to measure its velocity. The animals were sacrificed upon termination of data collection. Animal care protocols were approved by the VA Loma Linda Healthcare System.

Stimuli were generated digitally (System III, Tucker-Davis Technologies; 200 kHz sampling rate) and delivered through one of the sound sources of the OAE probe system. Clicks of ~100-µs duration (Fig. 3) were shaped in the frequency domain using a recursive exponential window to generate a flat spectrum (3-dB bandwidth 11–28 kHz) at the OAE probe microphone. The "double-click" paradigm was utilized for stimulus presentation, where single clicks and pairs of clicks (separated by Δt) were presented in an interleaved manner: $[p_1]$, $[p,p_1]$ and $[p,p_\downarrow]$ with arrows indicating the polarity of the click (Kemp & Chum, 1980). The Δt was varied randomly with 10 µs steps over 0–0.5 ms range, with step size increasing gradually up to 164 µs for longer Δt. If not stated otherwise the click level was set at 75 dB peSPL. All time waveforms are plotted *re* centroid of the test click. BM vibration data from one sensitive preparation are shown (ID 138) but similar patterns were observed in the other animals (e.g., Fig. 2C).

RESULTS

I. Basilar-membrane responses to click stimuli at varying intensities

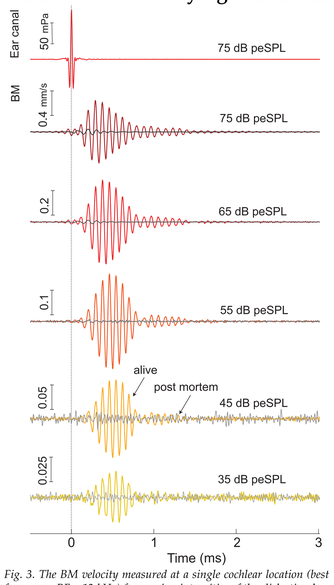


Fig. 3. The BM velocity measured at a single cochlear location (best frequency, BF = 12 kHz) for varying intensities of the click stimulus. Post mortem responses are shown in gray.

The BM responses to acoustic clicks measured in a sensitive gerbil preparation are consistent with previous reports (Recio et al., 1998; Cooper, 2000). Although the BM response peaked at earlier times at higher stimulus levels, the zero-crossings of the time waveforms remained relatively unaffected. The waxing and wining of the waveform at later times likely results from multiple cochlear reflection of the traveling wave (Shera and Cooper, 2013).

In the frequency domain (Fig. 4), the BM responses demonstrate compressive nonlinearity near the BF for clicks > 50 dB peSPL (abolished *post mortem*).

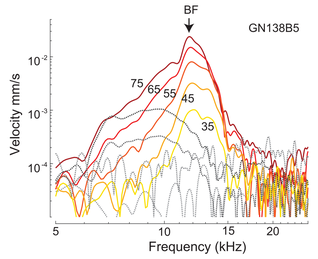


Fig. 4. Spectral representation of the BM responses in Fig. 3.

II. Expected temporal overlap between BM responses to pairs of clicks

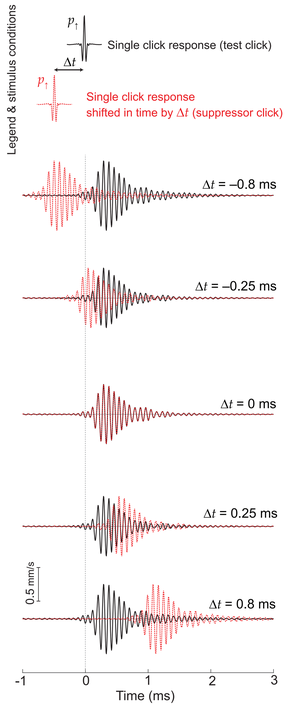


Fig. 5. The BM responses to the test click (black) and suppressor click (dotted red) presented in isolation for varying Δt conditions. (Click @ 75 dB peSPL.)

III. BM responses to pairs of clicks

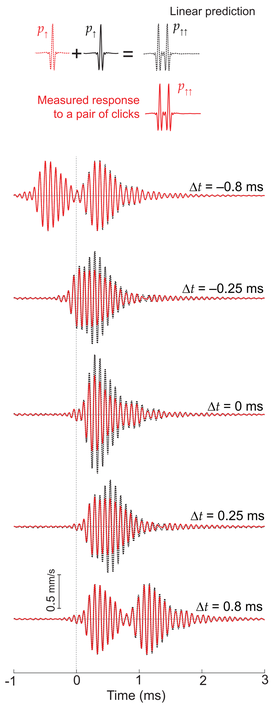


Fig. 6. Predicted (linear superposition of waveforms in Fig. 5; dotted black) and measured (red) BM responses to pairs of clicks separated in time by Δt.

Figure 5 shows expected BM responses to clicks separated in time by Δt as derived from BM responses to clicks presented in isolation. The maximal overlap between the respective click responses occurs for Δt = 0 ms. Figure 6 shows the predicted (black) and measured (red) BM responses to the pairs of click. Due to cochlear compression the measured response was less than predicted by linear superposition of the click responses, especially so for small Δt.

To assess the change in the BM response to the test click in the presence of the suppressor click, the BM response to the suppressor stimulus itself needs to be eliminated. This can be done by reversing the polarity of one click in the pair on alternating trials so that the response to the suppressor click can be canceled out (see legend in Fig. 7; Kemp & Chum, 1980). **The so called "derived-suppressed" response then represents the BM response to the test click in the presence of the suppressor click (cyan, Fig. 7).** The BM response to the test click is reduced in magnitude in presence of the suppressor click (Fig. 8; black) with the maximal reduction occurring for suppressor clicks preceding the test click by ~0.1 ms, unlike predicted by the model (Fig. 2B). When the suppressor click was lower/higher in level than the test click, the suppression decreased/increased and shifted towards more/less negative Δt (Fig 8; cyan & red).

The suppression demonstrated a pattern of local modulation with a period corresponding to half of the period of the BF (Fig. 8, thin lines), as also observed in the model (Fig. 2B, thin lines). Further assessment of the timing characteristics of the suppression patterns is possible through derivation of the suppression residual response (Figs. 9, 10). From these plots it is evident that suppressor click only affects the test click response after its own response reaches maximum at the BM (red arrows).

IV. BM response to the test click in the presence of the suppressor click

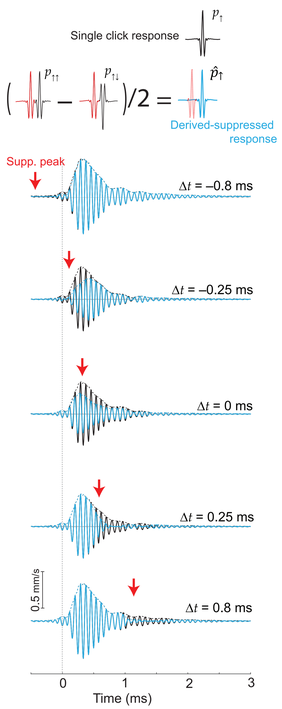


Fig. 7. BM responses to test clicks presented in isolation (black) or in the presence of suppressor clicks (i.e., derived suppressed response; cyan). Because the response synchronizes to the click polarity by adding/subtracting the responses to the pairs of clicks, one can cancel the following/preceding "suppressor" click (and its response) to derive the "suppressed" waveform. The red arrows indicate the time instant of expected maximal BM response to the suppressor click based on Fig. 5.

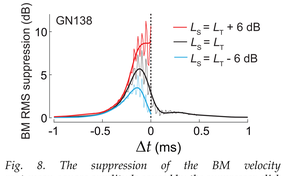


Fig. 8. The suppression of the BM velocity root-mean-square amplitude caused by the suppressor click presented at varying levels (L_s) re. test click level (see legend). For unequal level conditions only suppression for negative Δt could be calculated.

V. Change in the BM response to a click stimulus due to presence of a suppressor click

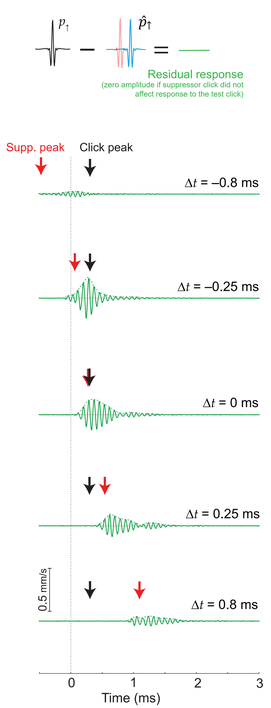


Fig. 9. The BM suppression residual waveforms obtained for varying Δt conditions. The black and red arrows point to time instants of maximal BM response to the test and suppressor clicks, respectively.

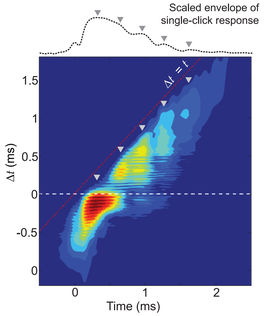


Fig. 10. Contour plot of suppression residual envelopes (e.g., dashed lines in Fig. 9) across all tested Δt conditions (y-axis). A nonlinear scale is used for the amplitudes to enhance the visibility of the low-intensity details with warmer colors corresponding to higher magnitudes. An example of the scaled envelope of the BM response to the test click is shown above the contour plot. The gray triangles point to lobes in the BM envelope that likely arise through multiple cochlear reflections.

SUMMARY

- Temporal suppression of the BM responses to pairs of clicks peaks at nonzero Δt corresponding roughly to 1 period of the BF (Fig. 8). This result could explain similar shifts present in the CEOAE temporal suppression curve (Fig. 2).
- Unlike the gerbil CEOAEs, no enhancement was observed in the BM response at the BF for suppressor clicks following the test click ($\Delta t > 0$ ms).
- BM suppression at the BF demonstrates a pronounced pattern of local minima and maxima (Figs. 8 and 10) that appears to arise from local interactions of the oscillating BM responses.
- The shift in the peak of the BM suppression towards negative Δt may arise as a consequence of cochlear dispersion and the asymmetry of two-tone suppression, (i.e., high-frequency components being more effective suppressors; Fig. 11) rather than indicating an non-instantaneous action of the cochlear amplifier (see also poster #689).

Why does maximal suppression occur for negative Δt ?

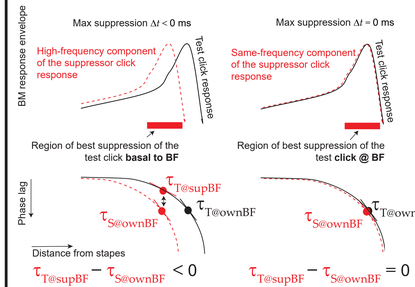


Fig. 11. Cartoon explaining the shift in the peak of maximal suppression towards negative Δt through cochlear dispersion. If the region of best suppressibility of the test click extends basal to its own BF place, than due, to cochlear dispersion, the test click response travels through that region at higher speed ($\tau_{T@supBF}$) than the high-frequency component of the suppressor click response that peaks at that basal region ($\tau_{S@ownBF}$). Thus, the suppressor click must precede the test click so that their frequency components of interest overlap at the region of best suppressibility (i.e., $\tau_{T@supBF} = \tau_{S@ownBF}$). In contrast, if the suppression of the test click occurs at its own BF place then the same-frequency components of the suppressor click will arrive at that location at the same time as the test click.

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