Reply to Ren and Porsov: Reverse Propagation of Sounds in the Intact Cochlea

Sebastiaan W. F. Meenderink and Marcel van der Heijden
Department of Neuroscience, Erasmus MC, P.O Box 2040, 3000 CA Rotterdam, The Netherlands

REPLY: In a Letter to the Editor, Drs. T. Ren and E. Porsov raised some methodological and interpretational issues concerning our recent study (Meenderink and van der Heijden 2010) in which we derived cochlear travel delays from recordings of cochlear microphonic (CM) potentials and ear canal sound pressure in response to multitone stimuli. Here, we address these issues.

Contamination by neurophonic potentials. Using tone sweeps, we extensively checked for the presence of neurophonic potentials, which were easily spotted by their large (>2 ms) group delays. They did occur, but only for frequencies <1 kHz and at levels <50 dB SPL. The neurophonic potentials must be phase-locked to the stimulus and their group delay must exceed an 800-μs synaptic delay (Palmer and Russell 1986). The frequencies of our f2 component and distortion products (DPs) (>6 kHz), combined with the observed f1 group delays (<200 μs) place all frequency components safely outside the danger zone. Thus contamination by neurophonics is out of the question.

Phase unwrapping. The group delays (Fig. 3) on which we base our conclusions were all computed from phase–frequency plots. In contrast to the suggestion by Ren and Porsov, the f2 period is irrelevant: the reported delays are envelope delays (that’s the beauty of using tone complexes). The nearly 100-Hz frequency spacing between DP frequencies leaves a 10-ms delay periodicity, so the cochlear delays were estimated without ambiguity (assuming they did not exceed 10 ms).

Large middle-ear delays. As explained in the article (Meenderink and van der Heijden 2010, p. 1452), the discrepancy in middle-ear delays is largely apparent, in that the cited studies report wideband delays. Extracting wideband delays from our data produced values similar to those of the cited papers. Moreover, the assumption that we overestimated middle-ear delays would only strengthen the argument for slow reverse propagation. Both arguments are discussed in the article.

Location of CM-DP generators. In our study, we used simultaneous acoustic and CM recordings of stimulus components and DPs to dissect round-trip delays into forward and reverse contributions. As with all collective responses, such an analysis is based on indirect evidence. The delays illustrated in Figs. 3 and 4, however, argue strongly against generation of CM-DPs near the round window. In fact, they agree much better with CM-DP transduction near the DP-generation region. Importantly, our use of multitone DPs allows a much larger frequency spacing of primaries than would be possible with customary two-tone DPs. This different stimulus configuration may well account for differences with Brown and Kemp (1985), as addressed in our report.

Slow reverse propagation or not? That is the real question. As we and others have discussed, some of the findings reported by Ren (2004) allow interpretations other than a complete absence of reverse traveling waves; the recordings may have been obtained from a region contributing to DP generation, where forward DP propagation dominates. DPs may well be generated more basal to “the f2 region.” A more basal generation site also coincides with the faster end of the traveling wave, which only slows down when nearing its peak region. Any DPs returning from such basal generation sites will travel fast. In fact, in the basal, stiffness-dominated region of the wave, the distinction between transverse waves and pressure waves becomes increasingly marginal, rendering questions on their difference somewhat academic.

Our own data, however, also allow interpretations other than the existence of slow reverse propagation. In the article, we mention the possibility that part of the nearly 500-μs delay between DP generation and recording in the ear canal originates from additional forward travel (Meenderink and van der Heijden 2010, p. 1453). In this scenario, DPs, after being generated, continue their forward trip before turning around and reaching the ear canal. Ironically, the assumption of a more basal generation site can now be invoked to support fast backward propagation: even a “slow” reverse traveling wave that originates from the basal generation site is too fast to account for the observed delays, necessitating an extra stretch of slow forward propagation.

The study reported by Ren (2004) is reminiscent of that by Allen and Fahey (1992) in several aspects. Both studies provide empirical support for a lopsided dominance of inward propagation, perhaps supporting feedforward models of the cochlea (Geisler 1993). They argue against established views and have sparked a lively debate on cochlear mechanics. In spite of the title of our article, we do not think that the debate on the existence of reverse traveling waves has yet been resolved.

GRANTS
This work was supported by The Netherlands Organization for Scientific Research VENI Grant 863.08.003 to S.W.F. Meenderink.

REFERENCES