Mechanisms of Mammalian Otoacoustic Emission

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1. Introduction

This chapter is not a survey of the literature. Neither is it particularly comprehensive, nor especially up to date. Rather, the aim is to provide an accessible introduction to a way of thinking about otoacoustic emissions that we have found productive. We show that a few general principles, systematically applied, can account for a remarkable variety of otoacoustic phenomena. Paramount among these principles is the fact—undisputed, underappreciated, and often utterly ignored—that evoked otoacoustic emissions arise from spatially distributed regions within the cochlea, not from discrete, pointlike sources. Interference among the many wavelets originating within these distributed source regions contributes essentially to shaping the sounds emitted by the ear.

2. Sources of Reverse Waves

Mammalian otoacoustic emissions (OAEs) involve the production of reverse-propagating waves within the cochlea. Reverse waves carry energy back toward the stapes, where it influences the motion of the ossicles; some fraction of the wave energy is thereby transmitted through the middle ear and appears in the ear canal as sound. Although reverse transmission through the middle ear has considerable influence on OAE amplitudes (e.g., Keefe 2002; Puria 2003), our focus here is entirely on mechanisms of emission generation within the cochlea.

2.1 Theoretical Source Types

Theoretically, one might hypothesize that reverse waves could originate from at least two different source types: (1) wave scattering off preexisting mechanical perturbations that exist independently of the stimulus wave (“reflection sources”) and (2) wave generation by sources (or perturbations) induced by the stimulus itself via harmonic or intermodulation distortion (“distortion sources”). Reflection and distortion sources are a more mechanistic nomenclature for the
emission sources\cite{Kemp1983} identified as “place-fixed” and “wave-fixed.”

2.1.1 Scattering by Preexisting Mechanical Perturbations

Preexisting mechanical perturbations can create reverse waves by disturbing the otherwise smooth forward flow of stimulus energy, a process equivalent to “scattering” the incoming wave. At the micromechanical level, the properties of the cochlear partition presumably vary somewhat irregularly with position (e.g., due to spatial variations in the number, geometry, or mechanical characteristics of the outer hair cells). In primates, for example, anatomical studies suggest that “general irregularity” and “cellular disorganization” characterize the arrangement of outer hair cells in the apical turns of the cochlea\cite{Engstrom1966, Bredberg1968, Bredberg1984, Lonsbury1988}. These micromechanical perturbations (or “roughness”) arise from the discrete cellular architecture of the organ of Corti and appear superimposed on the more gradual variation of parameters responsible for the position–frequency map. Mechanical perturbations can occur in both the passive and the active mechanics. For example, they may result from spatial variations in the density of radial fibers in the BM, or from cell-to-cell variations in the forces produced by hair cells, perhaps due to differences in the density of prestin molecules or the geometry of the hair bundle.

2.1.2 Wave-Induced Sources or Perturbations

Alternatively, the wave sources (or the mechanical perturbations that scatter the wave) can be induced by the stimulus wave itself. For example, nonlinearities in the mechanics can induce regions of mechanical distortion that act in effect as sources of wave energy. Unlike preexisting perturbations, these perturbations/sources are induced by the stimulus wave, and they therefore move with the wave when the stimulus frequency is varied. Regions of mechanical distortion can both “scatter” the energy in the incident wave and, via harmonic and intermodulation distortion, create sources at frequencies not present in the stimulus. For example, if two different stimulus tones are played simultaneously, intermodulation distortion occurs in the region of wave overlap. The region of induced intermodulation distortion acts as a source of waves (e.g., at combination-tone frequencies) that travel away from the source region in both directions. The mechanical nonlinearities in this example may arise from any number of mechanisms, including the “reverse transduction” via somatic electromotility of distortion in OHC receptor potentials and/or the nonlinear gating of stereociliary transduction channels.

2.2 Distinguishing Source Types Experimentally

How might reverse waves originating from these two theoretical source types be distinguished experimentally? An answer to this question lies in the frequency-dependence of their phase\cite{Kemp1983, Shera1983}.