HARMONIC COMPONENTS IN HAIR CELL RESPONSES

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INTRODUCTION

The harmonic structure of gross cochlear potentials has been studied in considerable detail (Newman et al., 1937; Wever and Bray, 1938; Wever and Lawrence, 1954; Dallos, 1973). In contrast, harmonic distortion in intracellular responses has received only minimal attention. Thus the presence of harmonic distortion may only be surmised from published response waveforms in a variety of hair cell types, both reptilian and mammalian (Russell and Sellick, 1978; Crawford and Fettiplace, 1981; Holton and Weiss, 1983). A quantitative description of the harmonic content of tone-evoked responses from hair cells has not been provided. This is unfortunate since knowledge of distortion generation is essential for the description of a nonlinear transducer, such as the hair cell. Moreover, certain nonlinear transfer characteristics may be fully identified from the harmonic structure of their output. Consequently, a determination of the harmonic content of hair cell receptor potentials is a desirable objective. This is particularly true for mammalian hair cells where a comparison between harmonic production by inner and outer hair cells may reveal essential information about their, conceivably different, transducer properties. Preliminary data on harmonic generation by mammalian hair cells have been reported (Dallos and Oesterle, 1985).

METHODS

Detailed description of the preparation, experimental techniques and stimulus conditions has been published before (Dallos, 1985). All data reported herein were obtained from intracellular recordings in guinea pig cochleas. Measurements were made from hair cells located in the fourth and third turns of the cochlea. The approximate best frequencies of these recording locations are between 200-270 and 800-1000 Hz. Glass micropipette electrodes were introduced into the organ of Corti through the stria vascularis/scala media route (Dallos et al., 1982). The electrode track is roughly parallel to the reticular lamina, passing first through Hensen's cells, then outer tunnel, outer hair cells (OHC), pillar and phalangeal cells, inner hair cells (IHC), border cells and finally, if advanced far enough, into the inner sulcus.

The dc resistance of the recording electrodes ranged between 80-200 MΩ. Their bandwidth, after capacitance compensation, usually extended to
Stimuli were tone-bursts having 5 msec rise-fall envelopes. Data reduction consisted of fourier analysis of windowed averaged waveforms, providing dc and harmonic magnitudes and phases. The analysis bandwidth was limited to 2 or 3 kHz by a sharp-cutoff anti-aliasing filter.

Harmonic distortion in the sound field was measured the same way as that of the hair cell responses, i.e., as fourier components computed from averaged tone burst sound responses. At 90 dB (re 20 μPa) the second harmonic was 52.7 dB below the fundamental at 200 Hz and more than 60 dB below for all frequencies above 300 Hz. Higher harmonics were always smaller than the second.

RESULTS

In this paper the emphasis is on deciphering what differences, if any, exist between the nonlinear properties of inner and outer hair cells. The approach is to compare the harmonic structure of receptor potential responses. The basic character of harmonic response components is established with the aid of Figures 1 and 2. In Figure 1 recordings are shown from one IHC and one OHC, both from the fourth turn of the cochlea. Harmonic magnitudes are presented as peak voltages. The magnitudes of the fundamental and the second to fifth harmonics are shown as a function of stimulus level. The input frequency, 200 Hz, is near the best frequency (BF) of the fourth turn recording location. The highest harmonic frequency, 1 kHz, is within the passband of both the recording electrode and the OHC membrane low-pass filter (Dallos, 1984; 1985). This frequency may be about an octave beyond the cutoff of the IHC membrane's low-pass filter (Dallos, 1984).

The fundamental component of the response for both cells exhibits a familiar saturating pattern (Russell and Sellick, 1978; Goodman et al., 1982; Patuzzi and Sellick, 1983; Dallos, 1985). In the stimulus range shown, the fundamental input-output function continues to grow, even though there are many examples, some shown later, where these functions actually decrease at the highest levels. Two cells were chosen for demonstration that produced approximately equal responses at the highest level, about

Fig. 1. Magnitudes of the first five fourier components (indicated by the appropriate numbers) as functions of sound level (reference 20 μPa) in response to 200 Hz tone bursts from one inner (left panel) and one outer hair cell (right panel). Both cells are located in the fourth turn of the guinea pig cochlea. Ordinate represents peak voltages of the intracellular receptor potential.