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Two-tone distortion in the basilar membrane of the cochlea

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Abstract

When humans listen to pairs of tones they hear additional tones, or distortion products, that are not present in the stimulus¹. Two-tone distortion products are also known as combination tones, because their pitches match combinations of the primary frequencies (f_1 and f_2 , $f_2 > f_1$), such as $f_2 - f_1$, $(n + 1)f_1 - nf_2$ and $(n + 1)f_2 - nf_1$ ($n = 1, 2, 3 \dots$) (refs 2–4). Physiological correlates of the perceived distortion products exist in responses of auditory-nerve fibres^{5–8} and inner hair cells⁹ and in otoacoustic emissions (sounds generated by the cochlea, recordable at the ear canal)^{7,10–12}. Because the middle ear responds linearly to sound^{13,14} and neural responses to distortion products can be abolished by damage to hair cells at cochlear sites preferentially tuned to the frequencies of the primary tones⁸, it was hypothesized that distortion products are generated at these sites and propagate mechanically along the basilar membrane to the location tuned to the distortion-product frequency^{7,8}. But until now, efforts to confirm this hypothesis have failed^{15,16}. Here we report the use of a new laser-velocimetry technique¹⁷ to demonstrate two-tone distortion in basilar-membrane motion at low and moderate stimulus intensities.

The response of the basilar membrane to two equal-intensity tones was measured at the basal turn of the cochlea in anaesthetized chinchillas. Distortion-product data presented here from a single chinchilla (L17) are representative of similar observations in cochleae from six animals. Figure 1 displays frequency spectra of basilar-membrane responses to primary tones presented at intensities ranging from 60 to 90 dB SPL (decibels ‘sound pressure level’; that is, referenced to 20 μ Pa). In addition to peaks at the primary frequencies (7.08 and 7.79 kHz), the spectra include several peaks at distortion-product frequencies both lower and higher than the primary frequencies, such as $2f_1 - f_2$ and $2f_2 - f_1$. The number and amplitude of spectral peaks in the responses vary in a complex manner with the intensity of the two-tone stimuli. The absolute amplitude of some of the peaks actually decreases as the intensity of the primary tones increases from 70 to 90 dB SPL.

Figure 2a illustrates magnitudes of the $2f_1 - f_2$ and $2f_2 - f_1$ distortion products as a function of stimulus intensity. The magnitudes of the distortion products increased with the level of the primary tones up to 80 dB SPL, whereupon they reached a plateau or decreased with further increases in stimulus level. Figure 2a also shows the dependence on intensity of responses to a single tone at the distortion-product frequency (equal to the characteristic frequency, 8.5 kHz). This curve was used to compute the distortion-product ‘effective level’: the intensity of a single tone at the distortion-product frequency required to evoke a response of the same magnitude as the distortion product produced by a two-tone stimulus. Distortion-product effective levels (Fig. 2b) were highest at the lowest stimulus intensities, ranging between 17 and 24 dB below the level of the primary tones. In other cochleae effective levels of the distortion products were as much as 11 dB less than primary

intensities. In most recordings obtained in six cochleae, effective levels of the $2f_1 - f_2$ and $2f_2 - f_1$ distortion products decreased monotonically as stimulus intensity increased. A similar dependence of distortion-product level on stimulus intensity has been described in auditory-nerve responses to $2f_1 - f_2$ distortion products⁵. At or above 80 dB SPL the distortion-product levels were so low that they could be attributed to distortion generated in the stimulus or measuring systems (short-dash lines in Fig. 2).

The magnitudes of the distortion products that we have measured in the chinchilla basilar membrane are comparable to those found in electrophysiological recordings from auditory nerve⁵⁻⁸ of chinchillas and other mammals, and in psychoacoustical studies in humans²⁻⁴. These prominent basilar-membrane distortion products undoubtedly originated in the cochlea, because artefactual distortion products generated in the acoustical and measuring systems were at least 50 dB less than the level of the primary tones (see Fig. 2) and could not have arisen in the middle ear, as its response is linear even at stimulus intensities much higher than used in the present measurements^{13,14}. The previous failure to demonstrate two-tone distortion products in basilar-membrane responses^{15,16} is probably due to inadequate measuring methodology. In particular, the Mössbauer technique, which has provided almost all the evidence on basilar-membrane mechanical nonlinearities, is not well suited to the measurement of responses to complex stimuli, owing to its own nonlinear characteristics. So it is principally as a result of having used an essentially linear technique (laser velocimetry) that one of the oldest issues in auditory research has been finally settled. Our results, together with other recent basilar-membrane data¹⁷⁻²⁴, suggest that all strongly frequency-dependent nonlinear cochlear phenomena have counterparts in basilar-membrane vibration. Because basilar-membrane responses in damaged cochlea or dead animals are linear^{19,24}, the site of generation of distortion products must be in the living cells of the organ of Corti, probably in the outer hair cells, which almost certainly feed back mechanically to the basilar membrane in normal cochlea^{11,12,23}.

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FIG. 1.

Frequency spectra of basilar-membrane responses to two-tone stimuli measured using laser velocimetry at the basal turn of the chinchilla cochlea. The spectra were obtained by Fourier transformation of responses to tone pairs presented at 60–90 dB SPL. The primary frequencies were chosen such that $2f_2 - f_1$ coincided with the characteristic frequency (CF), the most sensitive frequency for the cochlear location being studied, in this case 8.5 kHz). The spectra have several peaks corresponding to two-tone distortion products, as well as peaks at the primary frequencies. The spectral peaks corresponding to two prominent distortion products in psychophysical studies ($2f_1 - f_2$ and $2f_2 - f_1$) are indicated by arrows. **METHODS.** Basilar-membrane velocity was determined from the Doppler frequency shift of laser light reflected from glass microbeads (10–30- μ m diameter) placed on the membrane through a small hole made in the bony shell of the cochlea¹⁷. Mechanical responses were averaged over 1,024 stimulus repetitions and Fourier-transformed to obtain frequency spectra. For two-tone stimulation, tones were delivered independently using two acoustically coupled earphones. This arrangement minimized the generation of intermodulation distortion products. A silver-wire electrode placed on the round window allowed the recording of the whole-nerve action potential to monitor the physiological condition of the cochlea during surgery and data collection.

FIG. 2.

Magnitudes of the $2f_2 - f_1$ and $2f_1 - f_2$ distortion products as a function of primary-tone intensity (solid lines). The primary-tone frequencies were chosen so that either $2f_2 - f_1$ or $2f_1 - f_2$ coincided with the characteristic frequency (8.5 kHz). *a*, Squares and long-dash line represent the input-output velocity curve for a single tone at the distortion-product frequency. The short-dash line indicates the maximal expected magnitude of artefactual distortion products introduced by the acoustic-stimulus and measuring systems. The $2f_2 - f_1$ data for primary-tone ratio of 1.1 are from the spectra of Fig. 1. *b*, Distortion-product data are plotted as effective level: as intensity of a single tone at the distortion-product frequency required to produce a response of the same magnitude as the distortion product produced by the two-tone stimulus. Effective levels are expressed as decibels relative to primary-tone intensity. The short-dash line indicates that artefactual distortion products were at least 50 dB less than the intensity of the primary tones.