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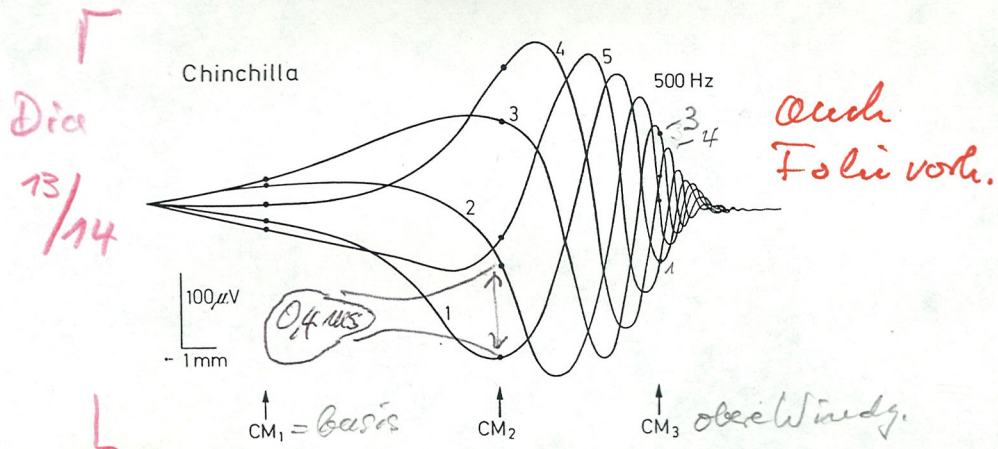


Fig. 7. Spatial gradients of CM recorded from a chinchilla cochlea in response to a 500-Hz tone. The parameter is time at intervals of 0.4 msec. (From unpublished records of BENITEZ, ELDRIDGE, and TEMPLER)

$$T_{500} = 2 \mu s, \frac{2 \mu s}{5} = 0.4 \mu s$$

C. CM Responses as Functions of Input Level and Frequency

As shown in Figs. 6 and 7, the CM responses at any one place are continuously graded in time and resemble low-pass transformations of the acoustic waveforms. The peak-to-peak voltages for the CM responses to tones are summarized as func-

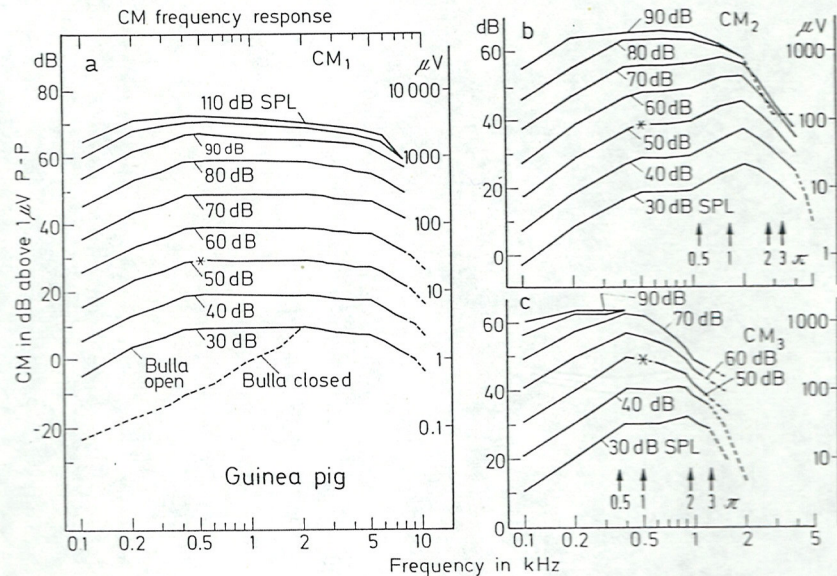


Fig. 8 a-c CM responses to tones as a function of frequency in guinea pig. Parameter is signal level. (a) First turn near round window. (b) Second turn. (c) Third turn. The frequencies at which the responses in the second and third turns lag those in the first turn by 0.5π , 1π , 2π , and 3π radians are indicated in Panels B and C

tions of tonal frequency with input sound pressure level at the tympanic membrane as a parameter in Fig. 8. The three panels show average normal responses measured with differential electrodes across the first, second, and third cochlear turns of guinea pig (after ENGBRETSON, 1970)¹. For sound pressures up to about 70 dB SPL, the responses corresponding to the input frequencies were measured using continuous tones and a wave analyzer with a tracking generator. At higher levels, responses to short, gated tones were measured directly on the face of an oscilloscope. All measures were made with the auditory bulla opened. The stiffness added by the compliance of the small volume of air enclosed behind the tympanic membrane (ZWISLOCKI, 1963) would have changed the slopes for all functions by the difference between the solid line and the broken line for the 30-dB parameter in Panel A of Fig. 8. In addition to sensitivity as a function of frequency, it is possible to derive, from the contours of Fig. 8, information concerning the dynamic ranges for CM output as a function of SPL; combinations of place, frequency and level for which CM responses are linear in the sense of being directly proportional to sound pressure; combinations of place, frequency and level for which CM responses do not grow linearly; and CM amplitude relations among turns at given frequencies and levels.

1. Sensitivity as a Function of Frequency

Except for the influence of the impedance of the middle ear at low frequencies, the CM response in the first turn is nearly independent of frequency out to about 5 kHz. The gradual decrease in CM response between 5 kHz and 10 kHz, which is not always present, is attributed in part to the middle ear and in part to one of the limitations in the method of differential recording of CM. With this electrode configuration, the voltage attenuation with distance along the cochlear partition is about 6 dB/mm (TASAKI *et al.*, 1952). Thus, the voltage recorded by a pair of differential electrodes has been integrated from sources over a distance of about 1 mm either side of the electrode placement. TONNDORF (1958) and WHITFIELD and ROSS (1965) note that these electrodes underestimate the source voltages when the traveling waves become short because opposing phases appear within a critical distance. KOHLLOFFEL (1971, 1972b) reported high sensitivity at this place up to at least 10 kHz with both electrical and laser methods. Thus, it is reasonable to attribute some of the gradual decline in sensitivity up to 10 kHz to these limitations on the method.

The CM responses from the second turn are shown in Fig. 8B. At low levels, they are greatest for frequencies around 2 kHz. For these frequencies, the phase of CM_2 lags the phase of CM_1 by 1–2 π radians. Again, the responses at lower frequencies primarily reflect the transmission characteristic of the middle ear. At

¹ Electrode placements are considered "good" if, as in Fig. 6a, the waveforms show good common-mode rejection of voltages from other turns and if the traveling-wave delays yield usual phase differences between turns. For all turns there is a tendency, similar to that reported by WEISS *et al.* (1971a), for voltages at the electrode in scala vestibuli to dominate at the relatively lower frequencies and for voltages at the electrode in scala tympani to dominate at the higher frequencies. The relative efficiency with which each electrode records local voltages appears to vary independently. For this reason, individual functions recorded from "good" placements vary as much as 8 dB around the trends shown in Fig. 8.

CM requires a synthesis of all of the information of these figures and of both the strengths and the weaknesses of the methods employed to record these responses. Many of the positive features of the method of differential recording are apparent in the figures and have been discussed elsewhere by *TASAKI et al.* (1952), *TONNDORF* (1958), *TEAS et al.* (1962), and *DALLOS* (1969a). Specific limitations will be discussed later in the contexts of specific measurements.

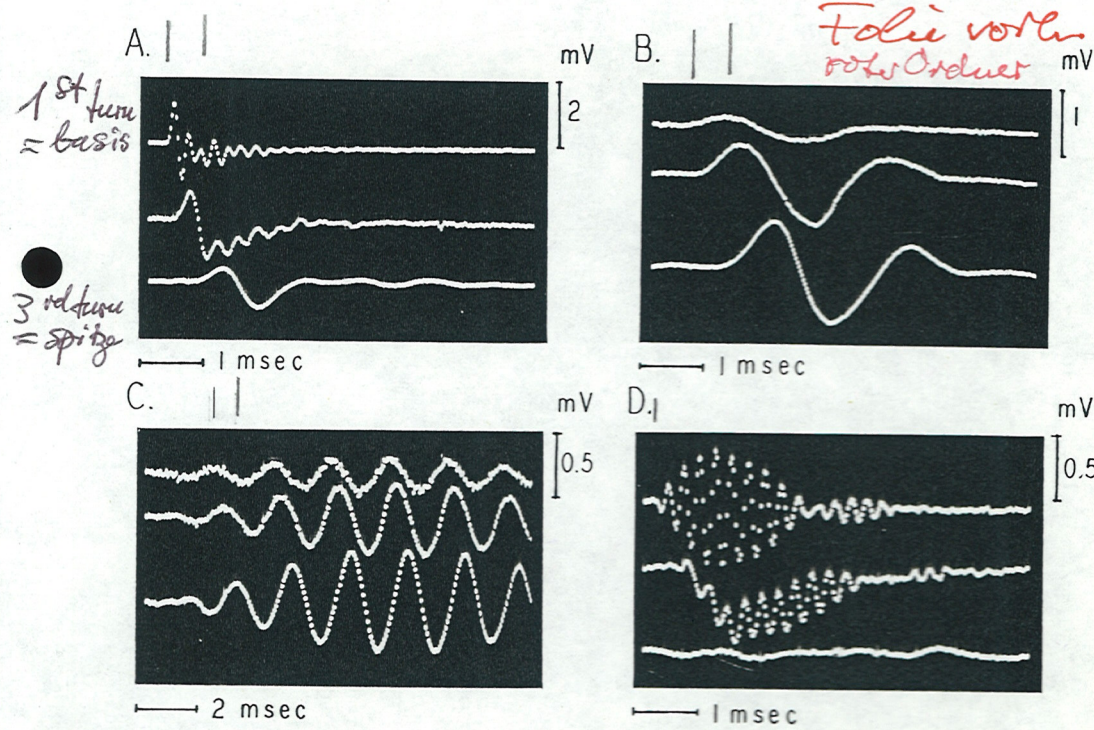


Fig. 6A—D. CM voltage waveforms as a function of time recorded from the first (top), second (middle), and third (bottom) turns of the guinea pig cochlea in response to four different acoustic signals. A. Wide-band click. B. 650-Hz low-pass click. C. 500-Hz tone-pip. D. 4000-Hz tone-burst

Cochlear Microphonics

Examples of the CM electrical waveforms recorded from three cochlear turns of the guinea pig are shown in Fig. 6. The responses to a click containing acoustic energy through a wide band of frequencies and to a thump with energy confined below 650 Hz are shown in Panels A and B, respectively, and are typical for acoustic transients. Comparable responses to bursts of tone at a low frequency, 500 Hz, and at a high frequency, 4000 Hz, in Panels C and D are typical for acoustic tones.

BÉKÉSY (1951a) used a microelectrode that touched the basilar membrane and that vibrated with a trapezoidal pattern in time to demonstrate that CM voltages were a function of displacement rather than velocity of the basilar membrane. The CM waveforms in the panels of Fig. 6 are, thus, to a first approxi-

mation, proportional to the displacements in each turn for each of the four signals used to elicit the responses. These waveforms a) are graded in time, b) show delays between turns, and c) demonstrate a selective sorting of spectral energy among places as for a series of low-pass filters.

The instantaneous waveforms are continuously graded in time. Those for the responses to the two tone-bursts and to the low-pass click correspond closely to the acoustic waveforms. Such patterns differ clearly from the all-or-none responses of single neurons and from the more stereotyped negative and positive waveforms of various neural evoked responses. For each acoustic signal, the onset and later features of the waveforms in the second and in the third turns show progressive delays with respect to the waveforms in the first turn. Such delays are consistent with the traveling waves described by BÉKÉSY and with the changes in phase as a function of place as shown in Fig. 5.

The responses to the two signals with acoustic energy confined to low frequencies, the 500-Hz tone-burst and the low-pass click, grow larger as the wave response reaches the third turn. But, note that in each case the responses in the first and second turns are substantial. The response to the one signal with energy confined to the high frequencies, the 4000-Hz tone-pip, is maximal in the first turn, is distorted and shows a strong asymmetrical nonlinearity in the second turn, and, except for delayed onset and offset transients, is absent in the third turn. The above relations are all consistent with a pattern for traveling waves that begins near the base and grows slowly out to some place of maximum response before decaying abruptly at more apical places. The low-pass filtering implied by these relations shows most clearly when the signal is a wide band acoustic click as in Panel A. The responses from the third and second turns are low-pass transients with a modest amount of "ringing" at a frequency characteristic for each of the locations. The ringing in the response of the first turn may be in part, attributed to a resonance in the earphone and, in part, to the properties of the CM response at this place.

B. Electrical Traveling Waves

Longitudinal voltage patterns in space at successive times can be reconstructed from waveforms such as those in Fig. 6 when the places at which the measurements were made are known. Figure 7 shows five patterns derived from voltages recorded from the three cochlear turns of chinchilla in response to a 500-Hz tone-burst. The curves are shown at approximately 0.4-msec intervals. The necessary interpolations are provided by values interpolated for peak voltages as a function of place and for the spatial locations of onsets, peaks, and zero-crossings as a function of time on plots similar to those shown by *TEAS et al.* (1962, Figs. 5 and 6). The simple requirement that the voltage transitions through the measured places be smooth in space and time compels the spatial patterns to take the form shown in Fig. 7. These replicate BÉKÉSY's findings well enough to make it certain that traveling waves also occur at physiological sound levels and are not an artifact of the high levels required for visual or Mössbauer observations.