

CROSS SPECIES COMPARISON OF OTOACOUSTIC FINE-STRUCTURE

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The spacing of threshold microstructure, spontaneous and evoked otoacoustic emissions, reveal characteristics of human cochlear function. Computer models reveal that all these aspects stem from the filtering of a small amount of random variation in the place frequency map of the cochlea. Is this cochlear fine structure unique to humans or is it characteristic of all mammalian ears? This paper presents evidence for cochlear fine structure in chinchillas having spontaneous otoacoustic emissions (SOAEs) in at least one ear. Chinchilla SOAEs are less stable than SOAEs in most human ears, and occur at higher frequencies. The minimal spacing between independent adjacent SOAEs expressed in the distance on the basilar membrane is smaller than humans. DPOAE in chinchillas and kangaroo rats also show fine structure. The spacing is greater than in humans consistent with estimates of shorter round trip travel time in animals with a shorter basilar membrane. This pattern is consistent with pulsed DPOAE estimates that reveal the response to both components to be shorter than is found in humans. The chinchilla DPOAE measurements are consistent with the predictions of the two source model of DPOAE fine structure. The maxima and minima of the fine structure occurs at the same frequencies for all DPOAEs lower in frequencies than the primaries and is mostly eliminated when the DPOAE frequency is fixed. Group delays of DPOAE obtained with a fixed ratio is modulated by the fine structure in a way consistent with our models and indicate that, in both chinchillas and humans, the component from the dp place can be larger than the component from the generator region.

1 Introduction

Normal hearing human ears exhibit stable patterns of maxima and minima in threshold measurement known as threshold microstructure (*e.g.*[3, 4]). All evoked otoacoustic emissions from humans show similar patterns of fine structure and the spacing of spontaneous otoacoustic emissions shows a similar pattern. Theoretical explorations and computer simulations are consistent with the claim that all types of cochlear fine structure stem from the filtering effect of a tall but relatively broad traveling wave on a very small amount (between

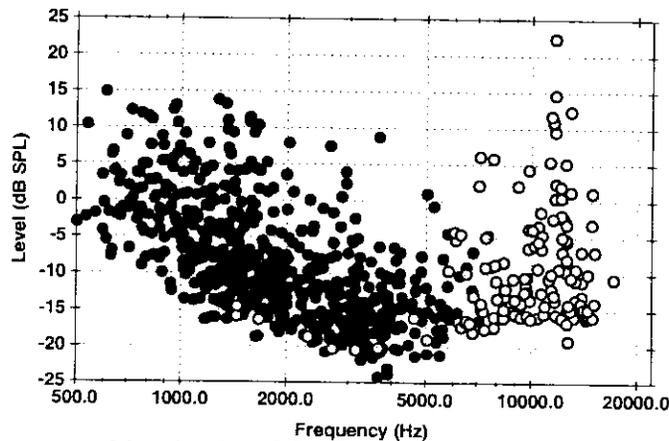


Figure 1: The frequency and levels of all SOAEs detected in the nine chinchillas (open circles). Published data (Talmadge et.al., 1993) on human SOAE obtained with the same analysis is presented for comparison (closed circles).

0.2 and 0.02%) of random variation in the properties of the basilar membrane [16, 13].

DPOAE fine structure in humans can be seen when fine resolution measurements of apical DPOAE (DPOAE lower in frequency than the primaries) are collected with f_2/f_1 ratio fixed, f_2 or f_1 fixed but not when the DPOAE is fixed in frequency (reviewed in [13]). The DPOAE fine structure is due to the interaction of two components coming from different places on the basilar membrane (for review see [14]). One component arises from the generator region (maximum overlap of the two primaries), the other is a reflection from the DPOAEs own, more apical, place. The amount of energy reflected from the DP place is modulated in amplitude and in phase, by the same properties responsible for the spacing of SOAE and threshold microstructure. The modeling framework from our laboratory [13] predicts that the fine structure spacing is approximately equal to the inverse of the round trip travel time of a traveling wave from the base to the distortion product site. Difference in round trip travel time between species would be reflected in the spacing of SOAE and DPOAE fine structure.

Although all these aspects of cochlear fine-structure have been investigated in humans, SOAEs have infrequently been reported in nonprimate mammals and have mostly been associated with cochlear lesions (reviewed in [1]) and although evidence of DPOAE fine structure can be seen in detailed DPOAE measurements from guinea pigs (*e.g.* [9]) there is little systematic investigation of DPOAE fine structure in nonhuman species. A complete understanding of cochlear fine structure can only be reached when we know how it depends on cochlear properties across species. The discovery that 60% of chinchillas in one colony had SOAEs [6], prompted us to use these animals to test hypotheses as to the source of SOAEs and to determine the characteristics of DPOAE

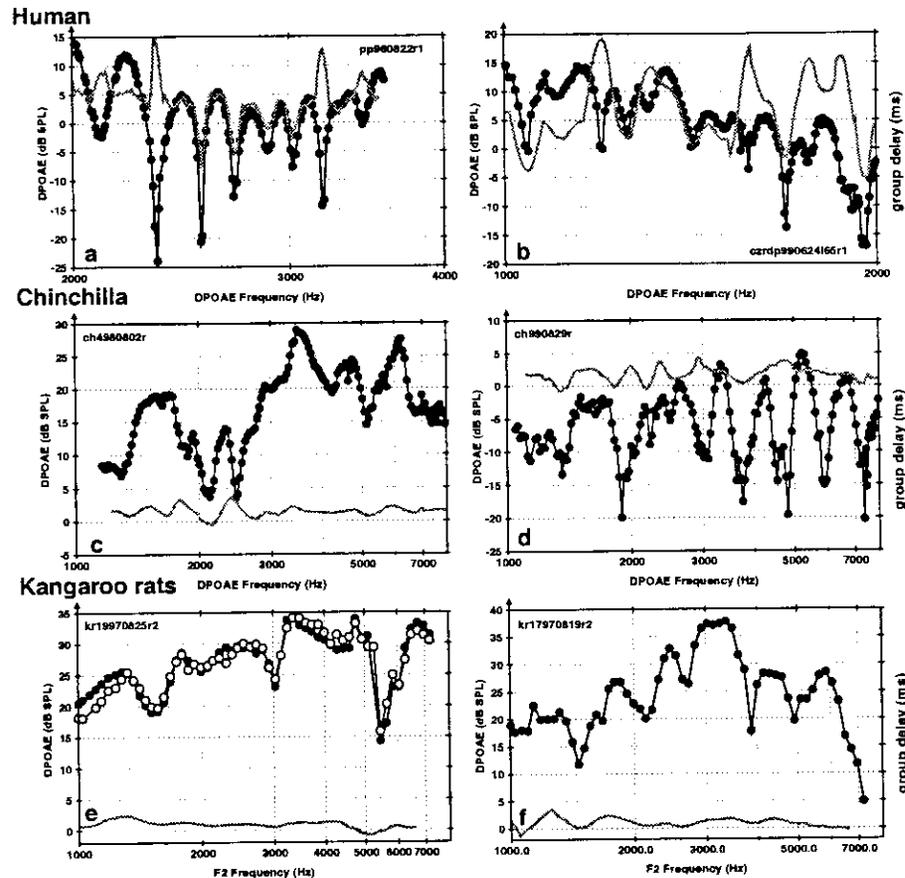


Figure 2: DPOAE level and group delay for $2f_1 - f_2$ dpgrams measured from two representative human subjects (a, b), two chinchillas (c, d) and two kangaroo rats (e *D. ordii*, f *D. spectabilis*). $L_1 = L_2 = 65$, $f_2/f_1 = 1.1$. Note that the human plots cover one octave while the animal data cover 3 octaves

fine structure in this species. The resulting data were compared to data from human subjects and kangaroo rats using similar procedures.

2 Methods

2.1 Subjects

Nine chinchillas (*Chinchilla lanigera*) identified as having SOAEs at NIOSH [6] were transported to Purdue to be used in this research. Awake animals were placed in a restraint device [11] in a double walled IAC booth. Kangaroo rats (*Dipodomys merriami*, *Dipodomys spectabilis* and *Dipodomys ordii*) were obtained with permission from the deserts in the southwest U.S.A. and constrained in smaller versions of the restraint device). Human subjects were seated in a reclining chair in the same booth. OAEs were obtained using the procedures and microphones previously used with human subjects [12, 14].

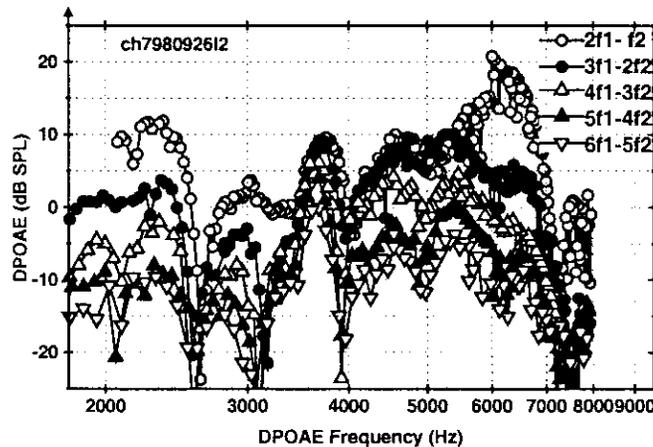


Figure 3: DPOAE level as a function of DP frequency (circles) for several orders of DPOAE obtained when f_2 was fixed at 8000 Hz and f_1 varied ($L_1 = L_2 = 65$ dB SPL). The group delay for the same data is shown by the solid line without symbols. Repeated measured on different days are shown in (e) to indicate the stability of the data.

3 Results

The frequencies of the SOAE in the chinchilla differ from those seen in human subjects in that the detectable emissions were higher in frequency (see Figure 1). Although there were a few emissions near the noise floor above 1500 Hz, there were none more than 2 dB above the noise floor between 1500 Hz and 5 kHz. The modal frequency was approximately 10 kHz. This is consistent with other isolated reports of SOAE in the chinchilla, but is very different than reports of SOAE in guinea pigs, which are mostly near 1 kHz. The bandwidth of the chinchilla emissions are much greater than in human subjects and the emissions are much less stable and can change rapidly with frequency. This is similar to the pattern seen in guinea pigs [7]. When the separation between adjacent stable independent SOAEs is evaluated as a function of the separation on the basilar membrane, based on Greenwood's map [2], the emissions are separated by multiples of 0.2504 mm. This is in contrast to the approximately 0.4 mm we have found for SOAEs from

Despite these differences, there are many similarities in SOAEs and humans. An analysis of the emission reveals that they are oscillations and not filtered noise [15]. The bandwidth of the emission is negatively correlated with the level of the emission ($r = -0.54$, $p < 0.001$) [12], and the frequency of the emission is frequency modulated by the heartbeat [5].

Detailed DPOAE measurements reveal stable DPOAE fine structure in these chinchillas (and in the kangaroo rats). The data presented here were obtained with $f_2/f_1 = 1.1$ in order to permit the examination of several orders of DPOAE. The distance between adjacent DPOAE maxima is greater than in humans (see Figure 2) as predicted from the shorter cochlea in these species.

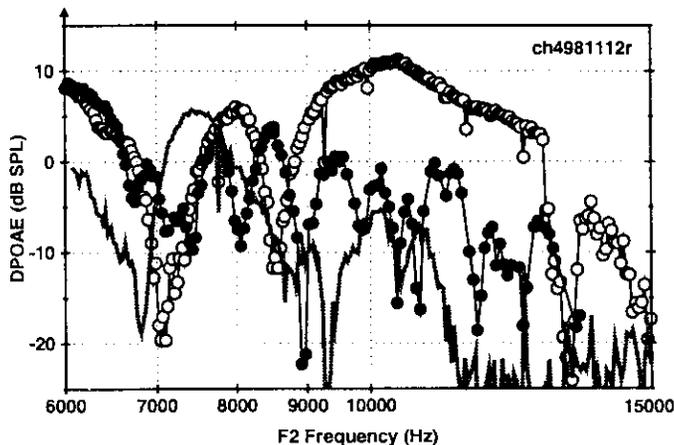


Figure 4: DPOAE level as a function of f_2 frequency for $2f_1 - f_2$ (open circles) and $3f_1 - 2f_2$ (no symbols) of DPOAE obtained when $2f_1 - f_2$ was fixed at was fixed at 6000 Hz while f_1 and f_2 were both varied. DPOAE obtained in the same session when f_2/f_1 was fixed at 1.1 are included for comparison (closed circles). The SOAE pattern detected in the same session is indicated by the gray line without symbols. $L_1 = L_2 = 65$ dB SPL.

An alternative test of the two source model for DPOAE fine structure is to compare several orders of DPOAEs generated with f_2 fixed and f_1 varied (f_1 sweep) when they are all plotted as a function of their own frequency. Because f_2 is fixed and f_1 is at a different frequency for each order, the only properties that are constant are the DPOAE place and the separation between the DPOAE and the generator regions (two source model). The spacing of the points increases with increasing order. Consequently, if the fine structure stems from the primary frequency, one would expect the width of the fine structure to increase for higher order DPOAE. As is seen in human data, the maxima and minima of the different orders of chinchilla fine structure occur at the same frequencies and thus have the same spacing (See Figure 3).

Similarly, when an individual DPOAE is fixed in frequency (and f_2 , f_1 and f_2/f_1 all varied) the fine structure should be reduced. Only one order of DPOAE can be fixed at any time so fine structure should be detected in other orders of DPOAE measured during the same session. Figure 4 shows representative data from the chinchilla. All the data are plotted as a function of f_2 so that one can see the pattern of $2f_1 - f_2$ with changing primaries. There is clear fine structure in both the fixed ratio and $3f_1 - 2f_2$ data, but little fine structure in $2f_1 - f_2$.

4 Discussion

Cochlear fine structure as revealed by SOAEs and DPOAE fine structure appear to be characteristics of these non primate species. The fixed f_2 and fixed dp data are consistent with a two source model of DPOAE generation

developed in research with humans. Basilar membrane measurements indicate that the number of waves to peak is approximately constant across frequency (reviewed in [8]). Since the distortion products are generated at the region of maximum overlap of the two primaries, the phase of generator component is expected to vary very slowly with frequency [13, 14, 10]. The component from the dp place is reflected by the same characteristics responsible for the other evoked otoacoustic emissions, SEOAE and threshold microstructure. These reflections are place fixed and their phase is expected to vary rapidly with frequency. The relative amplitude of these two components will thus determine the pattern of phase change with frequency. If the component from the generator region is largest, the phase variation will fluctuate around the slowly varying phase from the generator region. If the component from the dp place is largest, the local phase change is dominated by this component and the phase can rapidly rotate through more than one cycle [14, 10]. Group delay, the derivative of the phase, can indicate which component is larger. Theoretical and empirical investigations [14] have shown that group delay and amplitude are positively correlated when the source from the generator region is largest, but negatively correlated when the dp source is largest. The pattern of group delay in Figure 2 is consistent with the pattern of interaction of the two components seen when the DPOAE is pulsed on by pulsing the level of one of the primaries [14]. In humans and chinchillas we see both patterns. It is rare to see evidence that the DPOAE region is larger in kangaroo rats.

The latency of the chinchilla and kangaroo rat emissions measured using a pulsed DPOAE paradigm ([14]), is much shorter than in humans, the broader fine structure (and SOAE) spacings has a very natural explanation in terms of the framework of the models from our group [13]. The examination of DPOAE fine structure can provide a tool for the evaluation of interspecies differences.

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