

# THE ROLE OF COMPRESSION AND TRAVELING WAVE PRESSURES IN THE TRANSMISSION OF SOUND OUT OF THE GERBIL COCHLEA

WEI DONG<sup>†</sup>

*Department of Otolaryngology / Head and Neck Surgery, Columbia university,  
New York, NY, 10032, USA*

ELIZABETH S. OLSON

*Department of Otolaryngology / Head and Neck Surgery, Columbia university,  
New York, NY, 10032, USA*

Cochlear emissions provide a noninvasive probe of cochlear mechanics, but their utility is hindered by incomplete understanding of their relationship to intracochlear activity. In particular, recent work has uncovered a question about the mode by which emissions travel out of the cochlea -- whether they emerge via a “fast” compression pressure or a “slow” traveling-wave pressure. We further probed this question with simultaneous measurements of intracochlear distortion products (DPs) at two well-separated locations and DP oto-acoustic emissions (DPOAEs). In the broad frequency range of the local best frequency (BF), the DP responses demonstrate the now well-known forward-traveling-wave character. However, at frequencies substantially lower than the BF, comparisons of both DPOAEs to DPs and of DPs at two locations support a reverse-traveling-wave. Finally, a compression pressure DP was observed when stimulating at high levels (90 dB) with frequencies that were well above the BF. Therefore, the compression / reverse-traveling-wave question appears to be a quantitative question of the relative size of these different pressure modes. In previous and present results we find that the reverse-traveling-wave mode can be dominant both within the cochlea and in the production of DPOAEs.

## 1 Introduction

In forward transmission, two modes -- compression and traveling-wave -- in the cochlea’s response to stapes vibration were predicted theoretically over fifty years ago. The “fast” compression mode is supported by fluid inertia and compressibility (a sound wave); the “slow” traveling-wave mode is based on fluid inertia and partition stiffness [1]. Both modes are evident in intracochlear pressure responses to tone stimulation and can be decoupled by their particular characteristics as illustrated in Fig. 1 [2, 3]. The compression pressure, caused by the stapes vibration, almost instantaneously fills the cochlea and it is nearly spatially invariant. It grows linearly with sound pressure level, is in phase with stapes motion and dominates the pressure at frequencies above the local cutoff frequency (gray region in Fig. 1). The traveling-wave, caused by the pressure difference between the scala vestibuli (SV) and scala tympani (ST), travels much more slowly along the cochlear partition, is modified by the cochlear amplifier and peaks at a specific place (known as the BF place). The traveling-wave can lag the stapes motion by up to several cycles. It shows significant spatial variation around the BF (white region in

---

<sup>†</sup> Work supported by grant NIH R03DC009080

Fig. 1); spatial pressure variations indicate fluid motion, and are substantial at locations close to the basilar membrane (BM) when BM motion is large. Therefore, the traveling-wave is especially pronounced at frequencies around the BF and close to the BM. Interference between the traveling-wave and compression pressure is apparent in the magnitude notches and corresponding phase steps (arrowheads in Fig. 1). At frequencies well below the BF, the small spatial variations in pressure are expected because the BM motion is small and the wavelength is long [4].

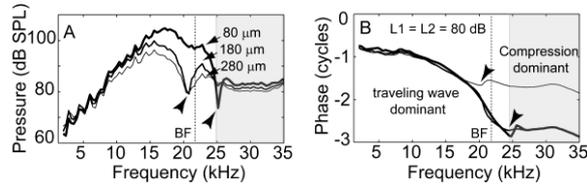


Figure 1 Spatial variation of primary  $f_2$ . (A) Magnitude of pressure. (B) Phase referenced to EC  $f_1$  &  $f_2$  (measured at 3 distances from the BM in turn-one with 22 kHz BF, wg131)

In contrast to this fairly coherent description of the basic intracochlear response to stapes stimulation, the manner in which sound travels out of cochlea is under active experimental and theoretical exploration. With regard to intracochlear DPs and their corresponding emissions, one group measured DPs at two longitudinal locations on the BM and observed a forward-traveling-wave, but no reverse-wave. Their interpretation of these findings was that the DPs, once generated, excited the stapes ~ instantaneously as a compression pressure [5, 6]. On the other side of the debate, detailed intracochlear DP pressure measurements gave evidence for a reverse-traveling-wave and set an upper limit to the contribution of the compression pressure to the emissions [7]. In the present study, the traveling-wave and compression pressure modes of DPs are investigated further: We find that both the traveling-wave and compression pressure are evident in intracochlear DP responses to two tone stimuli. The traveling-wave pressure dominates at frequencies around the BF, while the compression pressure emerges from the noise at frequencies well above the cutoff frequency with high intensity stimulation. However, the results support our previous conclusion that the major contributor to the emission is via a reverse-traveling-wave.

## 2 Methods

DPOAEs and intracochlear pressure DPs were simultaneously recorded in the ear canal (EC) and two positions in the basal ST (turn-one and very-basal) in deeply anesthetized young adult gerbil, using techniques and analyses described previously [3, 7]. Two equal - intensity primaries were used with fixed  $f_2/f_1$  ratio, with  $f_1$  &  $f_2$  frequency swept from low to high. One micro-pressure sensor (turn-one) was positioned at a place with the BF ~ 20 kHz through a hand-drilled hole, and the 2<sup>nd</sup> sensor (very-basal) was positioned at a place with BF ~ 40 kHz through the round window opening after removing a portion of the round window membrane.

### 3 Results

In the following we show data found with  $f_2/f_1$  ratio fixed at 1.05. With this low ratio, the results at  $2f_1-f_2$  and  $2f_2-f_1$  were similar on the points discussed below. We use  $2f_2-f_1$  in the figures because the points are illustrated more clearly with this DP.

#### 3.1. *Traveling-wave is dominant at frequencies around the BF*

DP pressure responses showed similar tuning and phase as the primaries [3, 7] when measured close to the BM at frequencies fairly close to the local BF (22 kHz) (thick line in Fig. 2A & B). Similar to its primary responses shown in Fig. 1, at frequencies around the BF, the DP exhibited significant spatial variations as the sensor moved away from the BM (Fig. 2A). The DP phase showed rapid phase accumulation even at location / frequency combinations for which the  $f_2$  pressure was dominated by the compression pressure (gray in Fig. 2B and [3, 7]). Both the DP spatial variation and phase accumulation indicate that the DP pressure was dominated by the traveling-wave. Thus the compression pressure, which would exhibit almost no spatial variation and ~ invariant phase versus frequency response, was never big enough to dominate the DP responses at frequencies around the BF.

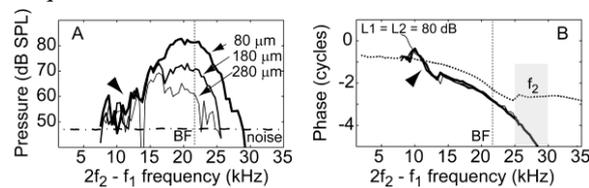


Figure 2 Spatial variation of  $2f_2 - f_1$  DP. (A) Magnitude of pressure. (B) Phase referenced to EC  $f_1$  &  $f_2$ . Dotted line is the  $f_2$  primary phase (measured at 3 distances from the BM in turn-one with 22 kHz BF, wg131)

At frequencies below 14 kHz (arrowheads in Fig. 2), the DP magnitude was less smooth. Its phase varied more rapidly with frequency than the primary phase, indicating a longer delay time. These observations are consistent with previous observations [7] and accompanying interpretation that these DPs were likely generated at more apical positions and were detected on their way out. The lack of pressure spatial variation is as expected for a compression pressure but is also consistent with a traveling-wave mode, which theoretically does not change much at frequencies significantly lower than BF [4, 8].

#### 3.2. *Compression pressure is apparent at frequencies well above the cutoff frequency*

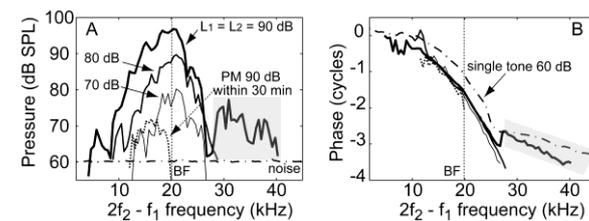


Figure 3 Level-dependence and physiological vulnerability of  $2f_2 - f_1$  DP. (A) Magnitude of pressure. (B) Phase referenced to EC  $f_1$  &  $f_2$ . Dot-dashed line is the single tone phase. Postmortem responses is plotted in dotted lines (sensor positioned at turn-one 10  $\mu$ m from the BM, wg121)

In the turn-one location, the DP was tuned to frequencies around the 20 kHz BF. The tuning became broader and shifted towards lower frequencies as the primary level was increased from 70 to 90 dB SPL (white region of Fig. 3A), similar to the known level-dependent tuning of single tone and primary responses. Its phase lined up with the single tone phase and changed little with the intensity of the primaries (white region of Fig. 3B). As in Fig. 2, both the tuning and phase suggested that the DP was dominated by either forward-traveling or locally generated distortion.

However, with 90 dB stimulation the DP response could be recorded up to 40 kHz, above the local cutoff frequency (gray region in Fig. 3). Interestingly, the phase in the high frequency region was similar to the single tone phase plateau, thus the high frequency response appears to be dominated by the compression pressure. In our interpretation of the observation, the supra-cutoff-frequency DP was generated in the overlapping region of the traveling-wave  $f_1$  &  $f_2$ , basal to our turn-one observation point, and what we measured was the compression pressure component of this basally generated DP. Thirty minutes post-mortem the DP was substantially reduced, only measurable at frequencies from 12 to 20 kHz with 90 dB stimulation, illustrating that the DP was physiologically vulnerable and not an artifact.

### 3.3. Transmission of DP inside the cochlea

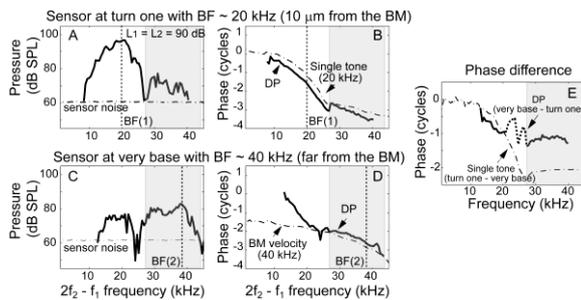


Figure 4 Simultaneous pressure responses measured at turn-one site (upper) and very-basal site (lower). (A & C) Magnitude. (B & D) Phase referenced to EC  $f_1$  &  $f_2$  phases. (E) Phase difference. (wg121)

The DPs shown in Fig. 3 were measured simultaneously, with the 1<sup>st</sup> sensor in the turn-one location (~20 kHz BF) and the 2<sup>nd</sup> sensor positioned at the very-basal (BF ~ 40 kHz) site. This simultaneous two-longitudinal-location measurement allowed us to directly explore the transmission of DPs in the cochlea. The 90 dB responses in Fig. 3 are replotted in Fig. 4A & B together with the simultaneous measurement at the very-basal site. Only 90 dB SPL data are shown because the DPs were above the noise in a wide frequency range. When measured in the extreme base, the DPs were tuned to the local BF (Fig. 4C), similar to their behavior when measured in turn-one (Fig. 4A). In turn-one, the phase was similar to the single tone pressure response phase at frequencies up to 27 kHz (Fig. 3B & 4B). The measurement at the very-basal location was not made very close to the BM and thus the single tone phase did not show a forward-traveling-wave to use for comparison (e.g., see spatial phase variations in Fig. 1 and [2]). However, a reasonable comparison phase can be found in the BM velocity phase measured with a Polytec vibrometer (different animal) and the DP

phase was found to be similar (Fig. 4D). Thus, at frequencies around their BF the DPs at both locations were predominantly locally generated and/or forward-traveling. At the basal location (Fig. 4C) DPs in the region of the BF and DPs at lower frequencies were separated by a sharp notch at  $\sim 24$  kHz, suggesting destructive interference between two modes – possibly locally generated and reverse-wave, or something different.

Comparison of DPs measured at the two longitudinal locations:

(i) DPs  $\sim 30 - 40$  kHz (gray regions of Fig. 4). The DP extended to frequencies well above its cutoff frequency when measured in turn-one (Fig. 4A) and the phase was plateau-like (Fig. 4B), indicating that it was a compression pressure. This is supported by the fact these DPs were almost in phase with their counterparts measured at the basal location; this can be seen in the gray region of Fig. 4E, where the very-basal phase is referenced to the turn-one phase.

(ii) DPs  $\sim 12 - 20$  kHz (within white regions of Fig. 4). As noted just above, at the turn-one location, these DPs appeared to be locally generated/forward-traveling (Fig. 4A). Measured at the basal location, the same DPs were smaller by  $\sim 20$  dB (Fig. 4C) and the DP phase changed rapidly with frequency (Fig. 4D), departing from that of the forward-traveling phase (here indicated by the BM velocity phase). This is consistent with the picture that these DPs were measured on their way out of the cochlea by the very-basal sensor. (The rapid phase-frequency response is consistent with a “reflector” type emission [9]. The phase comparison of the two locations (basal – turn-one) in Fig. 4E was similar to that of the forward-traveling-wave phase in the  $12 - 20$  kHz frequency region, strongly supporting the dominance of the reverse-traveling-wave in transporting the signal from turn-one (near its generation point) to the more basal position.

(iii) DPs between  $20 - 30$  kHz. The phase of the DP at the very basal site is making a transition between steep (reflected) and primary-like (locally generated). The very-basal DP cannot be expected to be related to the turn-one DP in that case, and when they are related (dotted line in Fig. 4E) the result is not meaningful.

#### 4 Discussion

In order to quantify the contribution of reverse-traveling-wave and compression pressure to the emissions, intracochlear pressure at DP frequencies was simultaneously measured at two longitudinal locations in the basal ST of the gerbil cochlea: one was at a turn-one place with BF of  $\sim 20$  kHz, the other at a very-basal site with BF of  $\sim 40$  kHz. The intracochlear DP pressure was shaped by cochlear filtering and tuned to the BF of its own place. In a wide frequency region near the BF, the DP appeared to be locally generated or forward-traveling [7]. With intense primary level, the DP could be measured at frequencies well above the local BF. In this case, the DP had the plateau-like phase expected for a compression pressure. In another data set, these high frequency / high level DPs did not vary with distance from the BM, also consistent with a compression

pressure. As stated above, the DPs measured at high primary level are physiologically vulnerable, and thus are not due to system or middle ear distortion.

The micro-pressure-sensor measures the pressure in the cochlea. As illustrated in Fig. 5, the character of the measured DP is expected to depend on the relative positions of the  $f_1$  &  $f_2$  overlapping region and the sensor location. *At frequencies well below the BF*, the DP was often variable in amplitude with a phase that departed from the forward-traveling-wave phase, consistent with it being generated apical to the measurement location and on its way out of the cochlea when measured. In support of this, the comparison of DPs measured at different cochlear locations (as shown in Fig. 4E), or of DPs to DPOAEs (as in [7]) indicates the existence of a reverse-traveling-wave. *At frequencies around the BF*, the local DP appeared to be locally generated / forward-traveling and it makes sense that, due to its forward-traveling character, this region cannot generally be examined for reverse-traveling-wave [7]. *At frequencies well above the local cutoff frequency*, a compression pressure DP was evident as shown in Figs. 3 and 4 (A & B). The high frequency DP was likely generated at a position basal to the turn-one sensor and the reasonable path by which this DP reached the sensor is through the fluid as a compression pressure. This DP might have arisen because at the high sound pressure level there was substantial nonlinear generation in a broad region where there was not much longitudinal phase change. Then the distortion would be in phase over a long region and be effective in generating a sizeable compression pressure. Thus, our measurements of intracochlear pressure clearly demonstrate the existence of compression pressure DPs.

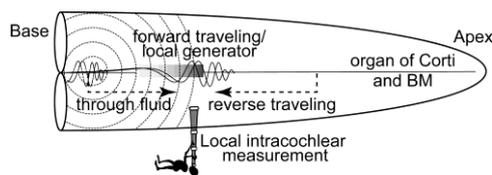


Figure 5 Illustration of DP transmissions in the cochlea

two-site BM velocity measurement, where the two sites were separated by 0.45 mm [6]. With the larger separation, the more basal site was not within the generation region of the  $< 20$  kHz DPs, and this absence of locally generated distortion made it possible to detect the reverse-wave.

## 5 References

1. Peterson, L.C., Bogert, B.P., 1950. A dynamical theory of the cochlea. *J. Acoust. Soc. Am.* 22, 369-381.
2. Olson, E.S., 1998. Observing middle and inner ear mechanics with novel intracochlear pressure sensors. *J. Acoust. Soc. Am.* 103, 3445-63.
3. Dong, W., Olson, E.S., 2005. Two-tone distortion in intracochlear pressure. *J. Acoust. Soc. Am.* 117, 2999-3015.

Nevertheless, the two-site intracochlear pressure measurement indicated that the reverse-traveling-wave was dominant in transporting DPs basalward. This result conflicts with the two-site BM velocity measurements of Ren and colleagues [5, 6]. In our measurements, the separation of the two sites ( $\sim 1.44$  mm [10]) was longer than the

4. Taber, L.A., Steele, C.R., 1981. Cochlear model including three-dimensional fluid and four modes of partition flexibility. *J. Acoust. Soc. Am.* 70, 426-36.
5. Ren, T., 2004. Reverse propagation of sound in the gerbil cochlea. *Nat. Neurosci.* 7, 333-4.
6. He, W., Nuttall, A.L., Ren, T., 2007. Two-tone distortion at different longitudinal locations on the basilar membrane. *Hear. Res.* 228, 112-22.
7. Dong, W., Olson, E.S., 2008. Supporting evidence for reverse cochlear traveling waves. *J. Acoust. Soc. Am.* 123, 222-40.
8. Yoon, Y.J., Puria, S., Steele, C.R., 2007. Intracochlear pressure and derived quantities from a three-dimensional model. *J. Acoust. Soc. Am.* 122, 952-66.
9. Shera, C.A., Guinan, J.J., Jr., 1999. Evoked otoacoustic emissions arise by two fundamentally different mechanisms: a taxonomy for mammalian OAEs. *J. Acoust. Soc. Am.* 105, 782-98.
10. Muller, M., 1996. The cochlear place-frequency map of the adult and developing Mongolian gerbil. *Hear. Res.* 94, 148-56.