Possible mechanisms of cochlear two-tone suppression represented by vector subtraction within a model

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Abstract: This paper investigates possible mechanisms of cochlear two-tone suppression (2TS) in models of the hair cell transducer and the cochlea. The hair cell transducer model can be represented by a saturation function. To simulate cochlear mechanics, a nonlinear transmission line cochlear model is used. The mechano-electric transducer curve of the outer hair cell (OHC) is regarded as the source of nonlinearity in cochlear mechanics. The saturation function approximated by a power series can explain 2TS in the OHC transducer model. However, this mathematical formulation cannot account for cochlear 2TS because the cochlear mechanics is more complicated than the saturation in the OHC transducer. To clarify two-tone interference graphically, it is expressed as a residual vector, the entries of which are the frequencies of the probe and suppressor. In this construct, the stronger of two tones introduced to the system nonlinearly reduces the output by vector subtraction. The model accomplished 2TS and displayed similar horizontal and vertical residual vectors. These analytical results suggest that 2TS is obtained from simple interference between the probe and the suppressor in the cochlear mechanics with nonlinear variation of the OHC transducer current.

Keywords: Suppression, Cochlea, Hair cell, Model, Saturation

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1. INTRODUCTION

A distinctive feature of cochlear nonlinearity is two-tone suppression (2TS), in which one pure tone reduces the cochlear response to a second tone. The dominant and suppressed tones are called the suppressor and probe, respectively. This 2TS phenomenon, first observed in the auditory nerve (AN) half a century ago [1], has been detected in the basilar membrane (BM) [2] as well as the inner hair cells (IHCs) [3] in the past few decades. Reference [2] concluded that 2TS originates from mechanical phenomena at the BM and is generated by an active process.

Some form of saturation is involved, as evidenced by such features of cochlear nonlinearity as the products of compression [4] and distortion [5]. According to experimental measurements, mechano-electric transduction by outer hair cells (OHCs) can be fitted by using the saturation function [6]. This function purportedly explains nonlinearities in cochlear mechanics [7]. To explain 2TS, the saturation function approximated by a power series shows that the output magnitude of one signal is suppressed when the input magnitude of the other signal is increased [8,9]. This mathematical formulation of 2TS is independent of the frequencies of the two signals with a constant output magnitude of the suppressed signal.

Experimental measurement showed a frequency dependence of 2TS [10–12]. In these experiments, a low-frequency suppressor generates the amplitude-modulated responses of the BM for a probe. For this phasic suppression, Geisler and Nuttall proposed a 2TS mechanism based on the saturation function imposed by a low-frequency suppressor on the BM [10]. The low-frequency suppressor operates a rest point on the input–output (IO) property of the saturation function. In contrast, the near-characteristic-frequency suppressor also produces 2TS on the BM response of the probe [2,10–13]. Under this condition, the envelopes of temporal responses are constant [10,11]. Therefore, this tonic suppression cannot be explained by the rest-point operation on the saturation function as described in phasic suppression. These theo-
retical and experimental studies indicate that the saturation function derived from the OHC transducer cannot fully explain both tonic and phasic suppression.

The structure and dynamics of the cochlea are complicated. Vibration of the BM is generated by both fluid dynamics and mechanical motion in the cochlea. The classical cochlear transmission line model reveals the importance of both fluid dynamics and mechanical motion in reproducing BM motion for a tone [14,15]. From this standpoint, the cochlear 2TS phenomenon can be considered a consequence of both fluid dynamics and mechanical motion generated by two tones. Neely and Kim suggested that sharp tuning can be achieved by applying pressure to an active element on the BM within the transmission line model [16]. Other scholars have simulated 2TS using active elements that include simple saturation functions such as the hyperbolic tangent and the Boltzmann function [17–22]. These modeling studies demonstrate that 2TS is caused by a complicated interaction between the probe and the suppressor. However, as described previously, theoretical studies of simpler models such as the saturation function can account for 2TS without frequency dependence [8–10].

To explore the complicated mechanisms of 2TS in the cochlea, the interaction between the probe and the suppressor for 2TS should be addressed. However, understanding this interaction has remained elusive because 2TS has been separately analyzed for the probe and suppressor. In general, the IO properties for the probe and suppressor are widely used for the representation of 2TS [2,10–13]. This representation can show a suppressed response caused by another tone; however, it cannot explain the influence of a tone on another tone. Instead of the IO property, a representation of the interference between the probe and the suppressor is required to investigate the influence of the saturating property in OHCs on cochlear 2TS.

As mentioned earlier, transmission line models can reproduce 2TS. Consequently, these models can be used to explore 2TS mechanisms to help guide current experimental procedure. In this paper, we develop a cochlear transmission line model including an OHC model and propose a representation of suppression using vector subtraction to explain the relationship between the probe and the suppressor. In Sect. 2, the cochlear mechanics, the models, and the concept of vector subtraction analysis are introduced. In Sect. 3, we show 2TS using the models. A discussion of the results is given in Sect. 4, followed by our conclusions in Sect. 5.

2. MODEL

2.1. Cochlear Mechanics

The cochlea is shaped like a coiled duct and includes two chambers. The chambers are divided by the BM and are filled with fluid. An incoming sound wave affects the cochlear entrance and propagates in the cochlear fluid from the base to the apex. As a consequence of sound wave propagation, a pressure difference is generated between the two chambers. This pressure difference drives the mechanical vibration of the BM. Vibration patterns of the BM depend on the frequencies of the sound wave, as shown in Fig. 1.

The IHCs and OHCs are located on the BM. The IHCs transform mechanical motion into neural information for the AN. In contrast, the OHCs sense mechanical vibration of the BM and exert pressure generated by its motilities [23,24] on the BM. Therefore, cochlear processing consists of feedback via the OHCs on the BM, as shown in Fig. 2. This OHC feedback amplifies the BM motion. However, the OHCs are not considered to be just an amplifier of the BM motion. It has been widely believed that the OHC feedback is the source of cochlear nonlinearities [7].

2.2. Hair Cell Transducer

Hair cells consist of the soma and the hair bundle. BM vibration deflects the hair bundle of the hair cell. Displacement of the hair bundle opens ion channels located at the tip of the hair cell. The opening of the channels causes a voltage difference that drives the OHC motilities [23,24]. Lukashkin and Russell proposed a model for this hair cell mechano-electric transducer located on the tip of the hair cell [9]. The model shows 2TS of the signal processing in the hair cell. In this paper, we introduce the concept that the conductance of the hair cell mechano-electric transducer $G_{\text{tr}}(t)$ can be saturated by applying a second-order Boltzmann function, which relates the probability of
Fig. 3 Conductance of the OHC transducer as a function of hair bundle displacement, fitted to Eq. (1) with parameter values listed in Table 1.

Table 1 List of parameters in the OHC mechanoelectric transducer function (obtained from Ref. [9]).

| Parameter         | Value (unit) | Unit |
|-------------------|--------------|------|
| $G_{tr,max}$      | $7 \times 10^{-9}$ | S    |
| $a_1$             | $65 \times 10^6$ | m$^{-1}$ |
| $a_2$             | $16 \times 10^6$ | m$^{-1}$ |
| $\xi_{c,1}$       | $24 \times 10^{-9}$ | m    |
| $\xi_{c,2}$       | $41 \times 10^{-9}$ | m    |
| $\xi_{c,rest}$    | $2.0 \times 10^{-8}$ | m    |

A transducer channel opening to the displacement of a hair bundle.

$$G_{tr}(\xi_c(t)) = \frac{G_{tr,max}}{[1 + K_2(1 + K_1)]},$$ (1)

where $t$ denotes time, $G_{tr,max}$ is the maximal transducer conductance, and $K_1$ and $K_2$ are variables given by

$$K_1 = \exp[a_1(\xi_{c,1} - \xi_c(t) + \xi_{c,rest})],$$
$$K_2 = \exp[a_2(\xi_{c,2} - \xi_c(t) + \xi_{c,rest})],$$ (2)

where $a_1$, $a_2$, $\xi_{c,1}$, and $\xi_{c,2}$ are constants and $\xi_{c,rest}$ is the rest point of the hair bundle. Figure 3 shows the IO property of the hair cell transducer $G_{tr}$ in Eq. (1). Table 1 lists the parameter values of the transducer model.

2.3. Cochlear Model

Here, the one-dimensional transmission line model of the cochlea involving feedback from an active process [16] is expanded to include nonlinearity. The transmission line simulates the driving of the BM traveling wave using fluid dynamics. In the one-dimensional transmission line model, the traveling wave propagates in the $x$ direction from the stapes to the helicotrema. $P_d$ denotes the pressure difference between the upper and lower scales of a box divided into compartments by the cochlear BM. $P_d$ drives the BM displacement $\xi_b$. The macromechanical equation of the transmission line model is given by

$$\frac{\partial^2 P_d(x,t)}{\partial t^2} = \frac{2 \rho}{H} \frac{\partial^2 \xi_b(x,t)}{\partial x^2},$$ (3)

where $\rho$ and $H$ represent the fluid density and scale width, respectively. The boundary conditions at the basal and apical ends of the cochlea are given by

$$\frac{\partial P_d(x,t)}{\partial x} \bigg|_{x=0} = 2 \rho \ddot{\xi}(t), \quad P_d(x,t) \bigg|_{x=\text{ap}} = 0,$$ (4)

where $\ddot{\xi}$ represents the inward displacement of the stapes footplate and the double-dot notation denotes its second time derivative.

To produce the sharp tuning observed in the cat’s AN, the BM and tectorial membrane (TM) are represented using the micromechanical model illustrated in Fig. 4. By denoting the pressure by $F(x,t) = (P_d(x,t) - P_s(x,t),0)^T$ and the displacement by $\xi(x,t) = (\xi_b(x,t),\xi_t(x,t))^T$, the equations of motion of the micromechanical model can be written as

$$F = M_p \frac{\partial^2 \xi(x,t)}{\partial t^2} + C_p \frac{\partial \xi(x,t)}{\partial t} + K_p \xi(x,t),$$ (5)

where

$$M_p = \begin{pmatrix} m_1 & 0 \\ 0 & m_2 \end{pmatrix},$$
$$C_p = \begin{pmatrix} c_1 + c_3 & -c_3 \\ -c_3 & c_2 + c_3 \end{pmatrix},$$
$$K_p = \begin{pmatrix} k_1 + k_3 & -k_3 \\ -k_3 & k_2 + k_3 \end{pmatrix}. $$ (6)
The initial conditions are given by
\[ \xi(x, t)|_{t=0} = 0, \quad \frac{\partial \xi(x, t)}{\partial t} \bigg|_{t=0} = 0, \quad P_a(x, t)|_{t=0} = 0. \quad (7) \]

The mechanical excitation of hair cells is assumed to result from the relative shearing displacement between the TM and the reticular lamina (RL). An active element senses the gap between the BM and the TM and provides feedback to the BM, thus amplifying its motion. We define the gap as the hair bundle displacement \( \xi_b \), which depends on the location and time.

\[ \xi_b(x, t) = g(x)\xi_t(x, t) - \xi_i(x, t) \quad (8) \]

Here \( g(x) \) is the lever gain between the BM displacement \( \xi_b \) and the radial displacement of the RL.

The magnitude of the feedback \( P_a \) is given by
\[ P_a(x, t) = \gamma(c_4\xi_c(x, t) + r_4\xi_c^m(x, t)), \quad (9) \]
where \( c_4 \) and \( r_4 \) are the damping and stiffness coefficients, respectively, and \( \xi_c^m \) is calculated from the mechano-electric transducer \( G_t \) in Eq. (10). For the mechano-electric transducer \( G_t \), both the scale and offset of \( G_t(\xi_c(t)) \) vary according to the following saturation function.

\[ \xi_c^m(t) = \alpha_t[G_t(\xi_c(t)) + \xi_c,rest] - G_t(\xi_c,rest)]. \quad (10) \]

where \( \xi_c,rest \) is the rest point of the hair bundle and \( \alpha_t \) is chosen such that \( \xi_c^m(t) = \xi_c(t) \) when the amplitudes of \( \xi_c(t) \) are <1 nm. For small displacements (<1 nm), our model reduces to Neely and Kim’s model because \( \xi_c^m = \xi_c \) in Eq. (10).

The middle ear transmits ear drum vibrations driven by sound pressure \( P_e \) to the cochlea. The middle ear is modeled as a mass–spring–damper system with one degree of freedom and the following equation of motion:
\[ P_e(t) = m_e\ddot{\xi}_s(t) + c_e\dot{\xi}_s(t) + k_e\xi_s(t), \quad (11) \]
where \( m_e, c_e, \) and \( k_e \) denote the mass, damping, and stiffness of the middle ear, respectively. The initial conditions are given by
\[ \xi_s(0) = 0, \quad \dot{\xi}_s(0) = 0. \quad (12) \]

### 2.4. Vector Representation of Suppression

We propose a graphical representation of suppression using vector subtraction. Suppression is conventionally calculated by subtracting the self-suppressing output shown in Fig. 5(a) (response to sinusoids with no temporal overlap) from the mutual suppressive output in Fig. 5(b) (response to simultaneous sinusoidal inputs). Self-suppression and 2TS are formulated as separate vectors. We also define the vector space set, in which the input frequencies of the probe and suppressor are represented as independent axes (Fig. 5(c)). Each element of the self-suppression vector is set by the responses of the saturation function to pure tones; the 2TS vector expresses the pair of tones entered into the saturation function. Vector subtraction then gives the difference between the self-suppression and 2TS.

Engebretson and Eldredge mathematically formulated self-suppression, 2TS, and their difference [8]. The non-linear saturation function \( G(\xi) \) is expanded into a power series:
\[ G(\xi) = \tanh(\xi) \simeq \xi - \frac{\xi^3}{3}. \quad (13) \]

By denoting the two sinusoidal inputs as \( \xi_1 = A_1 \sin \theta_1 \) and \( \xi_2 = A_2 \sin \theta_2 \), their outputs are calculated as
The distortions of these outputs contain the components $3\theta_1$ and $3\theta_2$, respectively. In their respective one-dimensional spaces $\theta_1$ and $\theta_2$, these outputs equal $\xi_1$ and $\xi_2$ when $A_1$ and $A_2$ are $<<1$ and they saturate when $A_1$ and $A_2$ are $\sim>1$. When two sinusoids are simultaneously input as a 2TS, the output is

$$G(\xi_1 + \xi_2) = G(\frac{A_1^3}{4} - \frac{3A_1A_2^2}{2}) \sin \theta_1$$

$$+ \left( A_2 - \frac{A_2^3}{4} - \frac{3A_2^2}{2} \right) \sin \theta_2 + \text{distortions}$$

Equation (16) indicates that the difference between the two TS and self-suppression is expressed as

$$G(\xi_1 + \xi_2) \sim (G(\xi_1) + G(\xi_2))$$

Equation (16) indicates that the difference between the two outputs is reduced by the higher-amplitude sinusoid. Details of the calculation of both fundamentals and distortions are described in the Appendix.

To graphically verify the interference between the two tones derived from the mathematical expression in Eq. (16), we propose a 2TS analysis method based on vector subtraction. Figure 6 highlights the differences between the vectors of the saturation function $G$ in Eq. (13) for two arbitrary frequencies $f_1$ and $f_2$ under the conditions of self-suppression shown in Fig. 5(a) and 2TS shown in Fig. 5(b). The vectors point vertically or horizontally when the input amplitude of one signal is greater than that of the other signal, which can be calculated by the saturation function given by Eq. (16).
nonlinear case [27]. To reduce the high gain and resolve this instability problem, the damping coefficient in the cochlear model was computed as follows:

\[ 2.8e^{-10}c_i \rightarrow c_i, \quad i = 1, 2, 3, 4. \] (17)

Note that the increased damping does not affect the resonant frequency or the BM traveling wave distribution [27,28].

The frequency \( f_p \) of the probe tone was 14 kHz, and the frequencies \( f_s \) of the suppressor tone were varied from 0.9 to 20 kHz in 0.5 kHz steps (excluding 14 kHz). The intensities \( L_p \) and \( L_s \) were increased from 20 to 80 dB in 10 dB steps. As usual, the probe frequency \( f_p \) was set to the characteristic frequency (CF) of the cochlear region \((x = 5.6\, \text{mm})\), defined as the frequency of maximum excitation at a 0 dB input. Each of the two primary tones was simultaneously presented for 55 ms with rise/fall times of 5 ms. The model outputs were recorded for 10 ms, starting 40 ms after the tone presentation, to allow the system to reach a steady state. In the time domain, the model outputs were the BM velocity \( \xi_b(x, t) \) and BM displacement \( \xi_b(x, t) \), which were separated into probe tone and suppressor tone components, respectively. In the frequency domain, the outputs were BM velocities \( \xi_b(x, f_p) \) and \( \xi_b(x, f_s) \) and BM displacements \( \xi_b(x, f_p) \) and \( \xi_b(x, f_s) \). These components were obtained by fast Fourier transforms (FFTs) of their counterparts in the time domain.

3. RESULTS

3.1. Responses to a Single Tone

Figure 7 (top) illustrates the amplitude of BM displacement obtained from the transmission line model at the CF as a function of the frequency and level of a single imposed tone with and without OHC involvement. In these plots, the CF was 14 kHz, located at \( x = 5.6\, \text{mm} \) from the base. Note that the frequency response curves are sharper at lower input levels. The peak sharpness is characterized by the quality factor \( Q_{10} \) (CF/bandwidth measured at 10 dB below the peak). \( Q_{10} \) was equal to 4.4 at 0 dB, which is comparable to existing experimental data on animals [26]. The frequency responses broadened and the gain was reduced as the input intensity increased. At frequencies of less than half an octave below the CF, the OHC process had little effect on the BM displacement. However, close to the CF, the OHCs amplified the BM displacement by over 50 dB relative to the case of no OHC involvement.

To characterize the degree of compression in the frequency response curve, the rate of growth (ROG) has been defined as the ratio of the varying input level to the changed output level and was calculated at the various stimulus levels in the top panel of Fig. 7. The results with the OHC are presented in the bottom panel of Fig. 7. At frequencies of less than half an octave below the CF, the ROGs closely approximated 1 dB/dB. The ROG values close to the CF were much smaller than 1 dB/dB (approximately 0.10 dB/dB), indicating compressive non-linearity close to the CF.

3.2. Two-tone Suppression in IO Functions

Two-tone suppression has been observed at moderate sound pressure levels in dB [2,10–13]. To determine the input level of the OHC transducer model, we focused on the BM displacement obtained from the transmission line model shown in Fig. 7. In this case, the BM displacement varied from 10 to 1,000 nm at a moderate sound pressure level ranging from 20 to 80 dB. Therefore, the input of the OHC transducer model was determined from 10 to 1,000 nm to simulate 2TS with the OHC transducer model.

Figure 8 plots the IO function of the OHC transducer model (Eq. (1)). The left and right columns show the OHC transducer conductance by the probe and suppressor, respectively. Both the probe and suppressor displacements were increased from 10 nm (thin lines) to 1,000 nm (thick lines). The frequencies of the probe and suppressor were set to 14 and 13 kHz, respectively. However, the IO property was not affected by the frequency as shown in
Eq. (16). The conductance for the probe decreased with increasing suppressor displacement. In the suppressor plots, the conductance decreased with increasing probe displacement.

BM vibration is distributed spatially for two tones [29]. To avoid this problem, Murakami and Ishimitsu evaluated the energy of the BM vibration in terms of the overall response of the BM [29]. The energy of the BM vibration $E_b(\omega)$ is given by

$$E_b(\omega) = \frac{1}{2} K(\omega) \int_0^L (\xi_n(\omega))^2 \, dx$$

(18)

where $K(\omega) = m_1 W \omega^2$ ($\omega = 2\pi f$), $f$ is the frequency of the sound, $W$ is the width of the BM, and $m_1$ is the BM mass per unit area.

Figure 9 plots the IO function of the BM energy at the CF produced by two-tone excitation as functions of the suppressor and probe levels. The numbers to the right represent frequency ratios. The left and right columns show the BM energy for the probe and suppressor, respectively. Both the probe and suppressor levels were increased from 20 dB (thin lines) to 80 dB (thick lines) at the four frequency ratios that were investigated ($f_s/f_p = 0.11, 0.93, 1.07, \text{ and } 1.43$). For the low-frequency suppressor ($f_s/f_p = 0.11$), the BM energy for the probe was reduced at suppressor levels of 50 dB and above. However, for the suppressor, the shapes of the IO functions did not change with the probe level. For similar frequencies ($f_s/f_p = 0.93 \text{ and } 1.07$), the BM energy for the probe was constant at suppressor levels below 40 dB. However, at suppressor levels of 40 dB and above, the BM energy for the probe decreased with increasing suppressor level. In the suppressor plots, the BM energy for the probe decreased with increasing probe level. For the high-frequency suppressor ($f_s/f_p = 1.43$), the BM energy for the probe was reduced slightly. The BM energy for the suppressor decreased at probe levels of 70 dB and above.

3.3. Vector Representation of 2TS

Figure 10 shows the differences in the vectors of the OHC transducer model in Eq. (1) under the conditions in Fig. 8. The difference vectors were calculated from the
vectors of self-suppression and 2TS as shown in Fig. 5. For low-amplitude displacement, the difference vector does not exist. However, with increasing input amplitude, the vectors point vertically or horizontally when the input amplitude of one displacement is greater than of the other displacement.

Figure 11 plots the vector differences of the given cochlear model under the conditions of self-suppression and 2TS for two suppressor frequencies. At \( f_s/f_p = 0.11 \) (top of Fig. 11), the energy of the probe is clearly suppressed by the higher energy of the suppressor, whereas the energy of the suppressor is minimally reduced (note the slight shift toward the left). In the cases of \( f_s/f_p = 0.93 \) and 1.07, the energy is greatly suppressed by the companion tone. Finally, at \( f_s/f_p = 1.43 \), the energy of the probe is suppressed by the suppressor except at very high probe energies, where the energy of the suppressor is reduced.

Let us compare the two vectors \( \mathbf{v}_{ohc} \) and \( \mathbf{v}_{bm} \) plotted in Figs. 10 and 11. We define the similarity between the two vectors using the dot product:

\[
\text{similarity} = \cos \theta = \frac{\mathbf{v}_{ohc} \cdot \mathbf{v}_{bm}}{||\mathbf{v}_{ohc}|| \cdot ||\mathbf{v}_{bm}||}. \quad (19)
\]

The resulting similarity ranges from \(-1\), indicating that they are exactly opposite, to \(1\), meaning that they are identical, with 0 indicating no correlation and values in between indicating an intermediate similarity or dissimilarity. Figure 12 presents a histogram of the similarities of the vectors \( \mathbf{v}_{ohc} \) and \( \mathbf{v}_{bm} \) for the four suppressor frequencies \( (f_s/f_p = 0.11, 0.93, 1.07, \text{and} 1.43) \) used in the previous figures. The similarities are concentrated around 1. This indicates that the vectors \( \mathbf{v}_{ohc} \) and \( \mathbf{v}_{bm} \) were highly correlated. In particular, for \( f_s/f_p = 0.93 \) and 1.07, the probabilities were approximately 100%. However, for
4. DISCUSSION

4.1. Analysis of 2TS

In this paper, we have sought to reproduce 2TS within the models of the OHC transducer and the cochlea shown in Figs. 8 and 9, respectively. These phenomena were analyzed by using the concept of vector subtraction. Under these conditions, Fig. 12 showed that the residual vectors of the OHC transducer and the cochlea shown in Figs. 10 and 11 match. These analytical results indicate a basic feature of 2TS, i.e., a stronger tone suppresses the response of a weaker tone. The probe and suppressor are the weaker tone and stronger tone, respectively. Despite the complicated cochlear mechanisms, these phenomena were obtained from models of the OHC transducer and the cochlea. In this section, we discuss the link between the OHC transducer and the cochlea.

The experimental measurement showed constant and temporally varying envelopes in the suppressed responses [2,10–13]. The theoretical consideration provided mechanisms for both types of suppression, with the saturation function representing the OHC transducer [8–10]. The saturation function can account for tonic suppression induced by the near-CF suppressor [8,9]. In contrast, for phasic suppression induced by the low-CF suppressor, the rest-point operation on the saturation function was proposed [10]. However, the link between the OHC transducer and the cochlea has been unclear. It has been proposed that an active OHC process amplifies the cochlear response, as shown in Fig. 4.16 of Ref. [30].

The active OHC process has been widely accounted for by many investigators (for a review, see Ref. [31]). In the present cochlear model, BM responses to a pure tone are amplified and depend on the input level, as shown in Fig. 7. This result is realistic because it implies that compression is solely caused by attenuated cochlear amplification, itself imposed by the saturation properties of the OHCs. According to the IO property of the OHC transducer model, the output of the OHCs was linear at low displacement levels and saturated at higher levels, which is consistent with compression [4].

Figures 8 and 9 showed 2TS of the IO functions of the OHC transducer current and BM motion, respectively. Their natures match the theoretical data of the OHC transducer current [9] and the experimental measurement of BM motion [12]. For the near-CF suppressor, the shapes of the IO properties obtained from both models were similar. However, for lower- and higher-CF suppressors, the shapes of the IO functions showed different trends.

To investigate the interference between the probe and the suppressor for 2TS, Figs. 10 and 11 showed 2TS of the vector representations of the modeling results. In these figures, horizontal and vertical vectors indicate that the stronger tones suppress the responses for the weaker tones, and angled vectors indicate that the responses for each tone are equally suppressed when the two-tone levels are closed. These trends shown in both the OHC transducer model and the cochlear model are consistent with the mathematical explanation of 2TS in Refs. [8,9] (see the Appendix). In particular, as mentioned previously, the shapes of the IO functions in the two models differed for lower- and higher-CF suppressors, as shown in Figs. 8 and 9. However, for these conditions, the present analysis method reveals the basic nature of 2TS shown in Fig. 11.

Figure 12 showed a quantitative comparison of the residual vectors in Figs. 10 and 11. For the near-CF suppressor, the vectors in the models are identical. This result implies that the interference of the two tones as a function of the OHC transducer current directly affects 2TS on the BM motion. However, for the lower- and higher-CF suppressors, half of the residual vectors were not correlated. This trend can be accounted for by the fact that the BM responses for the lower-frequency tones are not suppressed by the higher-frequency tones as shown in Fig. 11.

4.2. Advantages and Disadvantages of Vector Subtraction Representation for 2TS

In this paper, we have proposed a vector subtraction representation for cochlear 2TS and have successfully analyzed cochlear 2TS as considered in Sect. 4.1. In this section, we discuss the advantages and disadvantages of the proposed analysis method.

To explain cochlear 2TS, IO functions have been widely used [9–12]. In this paper, Figs. 8 and 9 showed the IO functions representing cochlear 2TS. The IO functions can be easily calculated from each frequency component. For this reason, this method can be easily applied to both experimental and theoretical data when the frequency components are separated. As shown in Fig. 5, the proposed vector subtraction representation is calculated from each frequency component. This calculation method is similar to the calculation of the IO function. Therefore, as with the previous method, the proposed method can also be easily applied to both experimental and theoretical data.

For modeling studies, cochlear models can be classified into transmission line models [17–22], phenomenological models of the cochlea [32,33], and simple models of cochlear partition [34,35]. The purposes of these models depend on the subject of the study. Despite these different starting points, these models incorporate a simple saturation property representing the OHC system and can account for cochlear 2TS. The similarity of this model construction to that of the proposed cochlear model suggests that the
vector subtraction method can be used to analyze 2TS on the BM motion in cochlear models.

The proposed analysis method is based on the separation of each frequency component. In this paper, we employed the FFT to separate the frequency components. This method can effectively separate frequency components of steady-state responses. However, the time-varying response affects the accuracy of the calculation result. In fact, experimental measurements show 2TS on the time-varying BM response [10,12]. Therefore, when applying the proposed method to a time-varying response, it is necessary to consider the calculation inaccuracy.

5. CONCLUSION

To investigate possible mechanisms for 2TS within a cochlear model including an OHC model, we developed an analysis method based on vector subtraction with a distinctive residual response to a two-tone input. Both models showed a similar 2TS nature of the IO functions and similar vectors representing suppression. As a consequence of the vector analysis, the following possible mechanisms of 2TS were suggested. First, the frequency dependence of cochlear 2TS cannot be explained solely by the OHC transducer model. Second, 2TS is obtained from simple interference between the probe and the suppressor in the cochlear mechanics with a nonlinear variation of the OHC transducer current.

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APPENDIX: FUNDAMENTALS AND DISTORTIONS IN THE CUBIC SYSTEM

The fundamentals and distortions in the cubic system $\xi^3$ are obtained from sinusoidal inputs. First, we consider the input of a sinusoid, $A \sin \theta$, to the cubic system $\xi^3$. The output of the system for the sinusoid is

$$(A \sin \theta)^3 = \frac{A^3}{4} (\sin \theta - \sin 3\theta). \tag{A-1}$$

In this case, the output contains the fundamental $\theta$ and the cubic distortion $3\theta$.

Next, we calculate the output of the cubic system for two sinusoids, $A_1 \sin \theta_1 + A_2 \sin \theta_2$, as follows:

$$(A_1 \sin \theta_1 + A_2 \sin \theta_2)^3 = \left( \frac{A_1^3}{4} + \frac{3A_1^2A_2}{2} \right) \sin \theta_1 + \left( \frac{A_2^3}{4} + \frac{3A_1^2A_2}{2} \right) \sin \theta_2$$

$$- \frac{3A_1^2A_2}{4} (\sin(\theta_2 + 2\theta_1) + \sin(\theta_2 - 2\theta_1))$$

$$- \frac{3A_1^2A_2}{4} (\sin(\theta_1 + 2\theta_2) + \sin(\theta_1 - 2\theta_2)). \tag{A-2}$$

In this case, the output contains the two fundamentals $\theta_1$ and $\theta_2$ and the four distortions $\theta_2 + 2\theta_1, \theta_2 - 2\theta_1, \theta_1 + 2\theta_2$, and $\theta_1 - 2\theta_2.$

Y. MURAKAMI and S. ISHIMITSU: VECTOR REPRESENTATION OF TWO-TONE SUPPRESSION