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INSTABILITIES IN A STATE SPACE MODEL OF THE HUMAN COCHLEA

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Abstract

The sharply tuned sense of hearing in humans is believed to be due to active mechanical amplification in the cochlea. One apparently natural consequence of this 'cochlear amplifier' is the existence of spontaneous otoacoustic emissions (SOAEs), narrow-band tones that are detected in the ear canals of approximately half of all normal-hearing individuals. Authors have argued that SOAEs are created by multiple reflections between the middle ear boundary and a dense array of inhomogeneities scattered throughout the cochlea. This theory is contrary to previous ideas which assume independently unstable oscillators in the cochlea.

This work uses a state space formulation of the cochlea to test the predictions of the multiple-reflection theory of SOAE generation in humans. In this model, the local mechanics of discretized segments of the cochlea are represented by lumped elements. Each section includes a frequency-dependent active feedback loop which enhances the motion of the basilar membrane (BM), a thin sheet that divides the cochlea into two fluid-filled chambers. The activity of adjacent segments of the model is coupled together by the cochlear fluid. The linear stability of the cochlear model is evaluated by calculating the eigenvalues of the system matrix.

Instabilities arise across a wide bandwidth of frequencies when the smooth spatial variation of BM impedance is disturbed. The salient features of the multiple-reflection theory are observed in this active model given perturbations in the distribution of feedback gain along the cochlea. Spatially random gain variations are used to approximate what may exist in human cochleae. The average spacings of adjacent unstable frequencies agree with the most commonly observed value in human SOAE data. Nonlinear time domain simulations of unstable models illustrate how instabilities in the cochlea develop into limit cycles similar to SOAEs.

1. INTRODUCTION

The cochlea is the fluid-filled auditory organ located in the inner ear; it is responsible for converting mechanical motion induced by acoustic waves, impinging on the eardrum and passing through the middle ear to the cochlea's oval window, into electrical impulses which are interpreted by the brain. A partition known as the basilar membrane (BM) divides the cochlea into two fluid-filled chambers, or scalae. The BM is most stiff near the base of the cochlea (by the oval window) and less so toward the apex. This results in a passive mechanical tuning where higher frequencies resonate near the base, and lower frequencies at the apex. This tuning in frequency and position along the cochlea is further sharpened by an active process known as the cochlear amplifier (CA). The CA also enables humans to detect extremely quiet sounds on the order of 0 dB SPL in the ear canal.

The strongest direct evidence in support of the existence of a CA has long been the discovery of spontaneously emitted narrow-band tones, first detected in the ear canal of humans by Kemp in 1979[1]. These tones are denoted spontaneous otoacoustic emissions (SOAEs). It is now widely accepted that the outer hair cells situated in the organ of Corti are the driving force of the CA, and actively enhance the motion of the basilar membrane (BM) [2]. However, the precise mechanism underlying the generation of SOAEs is still in debate. A further mystery is that there is a commonly observed value in the average log-normalised spacing between SOAE frequency neighbours, termed the preferred minimum distance (PMD).

Zweig and Shera [3] propose that SOAE production is due to multiple reflections of the travelling wave between a dense array of inhomogeneities in the cochlea and the middle ear boundary. In this theory, the PMD between SOAE frequencies arises naturally due to the characteristics of the travelling wave in the cochlea. The authors of [3] demonstrate this theory with a phenomenological model of the cochlea; in contrast, the present paper uses a state space formulation of a mathematical model of cochlear mechanics to evaluate the validity of these ideas.

2. METHODS

2.1 Model Description

The state space model of the human cochlea is based on the formulation of [4], with a number of revisions to the original parameters given in [5]. The complete list of revisions can be found in [6]. This section gives a brief outline of the model and its formulation, while more curious readers are directed to the aforementioned references.

The cochlea is modelled as a box which is divided into 500 sections. Each section of the BM is represented by a lumped element model, shown in Figure 1.a. The values of the springs and dampers vary as a function of position along the cochlea and are given in [6]; the masses are assumed to be constant. The active feedback force is a pressure acting on the BM that is dependent on the relative displacement and velocity between the two masses—M_1 which represents the BM, and M_2 which represents the tectorial membrane, a gelatinous membrane positioned over the BM. The 'micromechanical' models act independently of each other, and are coupled via the cochlear fluid, as shown in the macromechanical model in Figure 1.b.

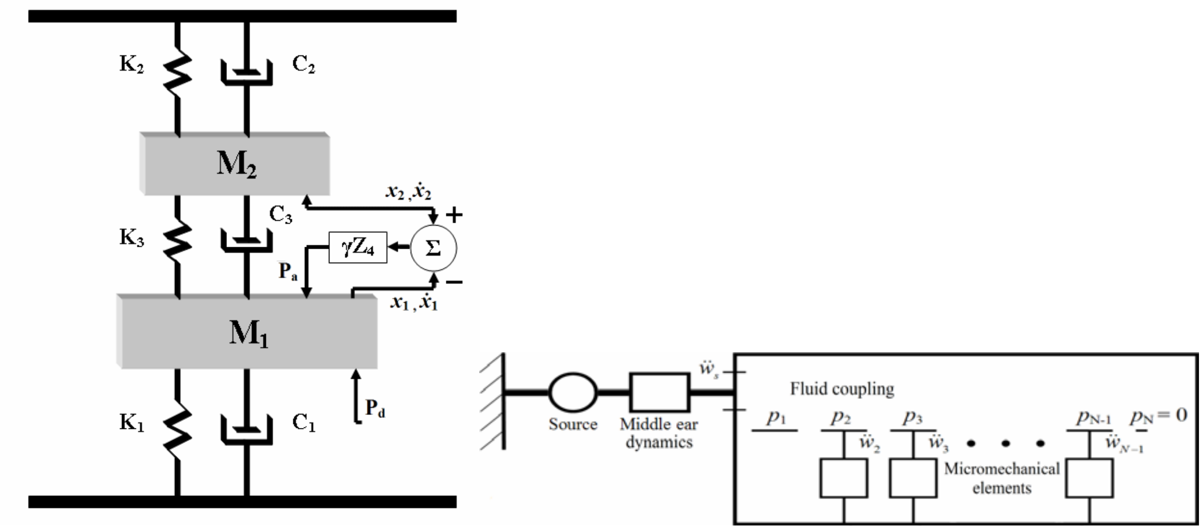

Figure 1.a-b Micromechanical model (a. left) and macromechanical model (b. right).

A wave equation describes the motion of the travelling wave in the cochlea, and the model has boundaries at the base (middle ear impedance) and apex (helicotrema—a hole at the end of the partition that equalizes the pressure between the two fluid channels in the cochlea). A finite difference approximation is used to discretize the spatial derivatives in the wave equation and boundary conditions of the cochlea. The local activity of the cochlear partition segments is related to the fluid mechanics by:

$$\mathbf{F}\mathbf{p}(t) - \ddot{\mathbf{w}}(t) = \mathbf{q}(t), \quad (1)$$

where $\mathbf{p}(t)$ and $\ddot{\mathbf{w}}(t)$ are the vectors of pressure differences and cochlear partition accelerations, $\mathbf{F}$ is the finite-difference matrix that approximates the wave equation and $\mathbf{q}(t)$ is the vector of source terms. The cochlear micromechanics of isolated partition segments are described by individual matrices. When Equation (1) is substituted into an equation combining all the uncoupled elemental matrices, the coupled model of the cochlea can be described by the state space equations

$$\dot{\mathbf{x}}(t) = \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{u}(t), \quad (2)$$

and

$$\mathbf{y}(t) = \mathbf{C}\mathbf{x}(t) + \mathbf{D}\mathbf{u}(t), \quad (3)$$

where **A** is the system matrix, $\mathbf{x}(t)$ is the vector of state variables, **B** is the input matrix, $\mathbf{u}(t)$ is a vector of inputs proportional to $\mathbf{q}(t)$, $\mathbf{y}(t)$ is the output variable (selected by **C**), **C** is the output matrix, and **D** is an empty feed-through matrix. A complete description of these matrices can be found in [4].

The stability of the model can be determined by calculating the eigenvalues of the **A** matrix, which are the system poles. Figure 2 shows the stability for the nominal cochlea with the micromechanical feedback gain, γ, set equal to 1 at all locations along the cochlea. Note that these poles have been re-oriented such that frequency runs along the x-axis in kHz and σ along the y-axis. σ corresponds to the system response's rate of growth or decay at a given frequency; any poles with a positive value of σ will result in system instability at that frequency.

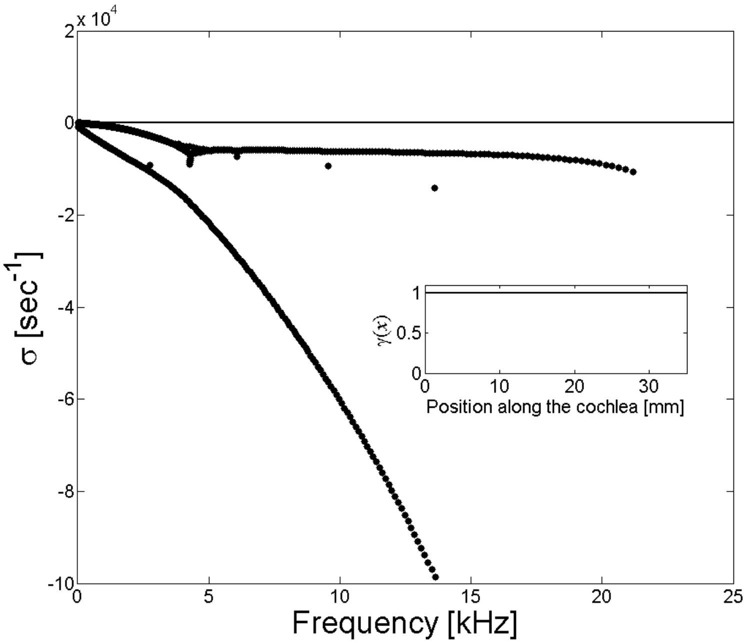

Figure 2. Stability plot of the nominal cochlea; micromechanical feedback gain vs position inset.

2.2 Predictions of Zweig and Shera [3]

According to [3], only frequencies with responses that undergo an integer number of cycles of phase change while propagating back and forth between the middle ear boundary and a cochlear reflection site will interfere constructively across multiple reflections, thus becoming unstable. Furthermore, the response must peak in the region of the cochlear inhomogeneity such that enough energy is reflected to overcome the damping between the reflection sites. It is believed that the average distance between resonant positions of SOAEs along the cochlea is related to the characteristics of the travelling wave in its peak in the following manner:

$$\overline{\Delta x}_{SOAE} \approx \frac{1}{2}\lambda_{peak}, \tag{4}$$

where λ_{peak} is the wavelength of the travelling wave in its peak region. Consequently, the predicted normalised spacing between SOAE frequencies is

$$f/\Delta f \approx 2l/\lambda_{peak}, \tag{5}$$

where l is the cochlear length scale, the distance over the cochlea by which the resonant frequency changes by a factor of e. The length scale of the cochlear model is roughly 7mm, and the wavelength of the state space model's travelling wave at its peak is approximately 0.9 mm for much of the cochlea. Thus, the predicted spacing between SOAE frequencies is approximately 15.

The measured normalised spacing between two adjacent SOAE frequencies, f_a and f_b, is defined as the ratio of their geometric mean of divided by their difference,

$$f/\Delta f = \frac{\sqrt{f_a f_b}}{|f_a - f_b|}. \tag{6}$$

The measured PMD in humans is approximately 15 when expressed in terms of $f/\Delta f$ [3].

3. RESULTS

3.1 Step Change in Gain

The authors of [3] assume a dense array of inhomogeneities within the cochlea, each of which acts as a reflection site. In this section, a step-change discontinuity in the micromechanical feedback gain as a function of position is introduced as an isolated inhomogeneity. The stability of a cochlear model with a step-decrease from $\gamma = 1$ to $\gamma = 0.88$ at $x = 16.3$ mm is shown in Figure 3.a. Three frequencies are unstable, at 1.85 kHz, 1.98 kHz and 2.11 kHz. The $f/\Delta f$ spacing between the two higher frequencies is approximately 15, whereas the spacing between the two lower frequencies is approximately 13.5. This is consistent with expectations, as a decreased gain (as is present here in positions apical of 16.3 mm) results in a less sharply tuned response (longer travelling wave wavelength) which in turn decreases the predicted $f/\Delta f$.

A nonlinear time domain simulation was performed in order to evaluate the unstable system response to a click. In order to approximate the nonlinear nature of the CA, a hyperbolic tangent function was imposed upon each micromechanical feedback loop to limit the active pressures. The MATLAB ordinary differential equation solver *ode45* was employed, and the output time-vector set to a sampling rate of 100 kHz. The results of the time domain simulation are displayed in Figure 3.b-d.

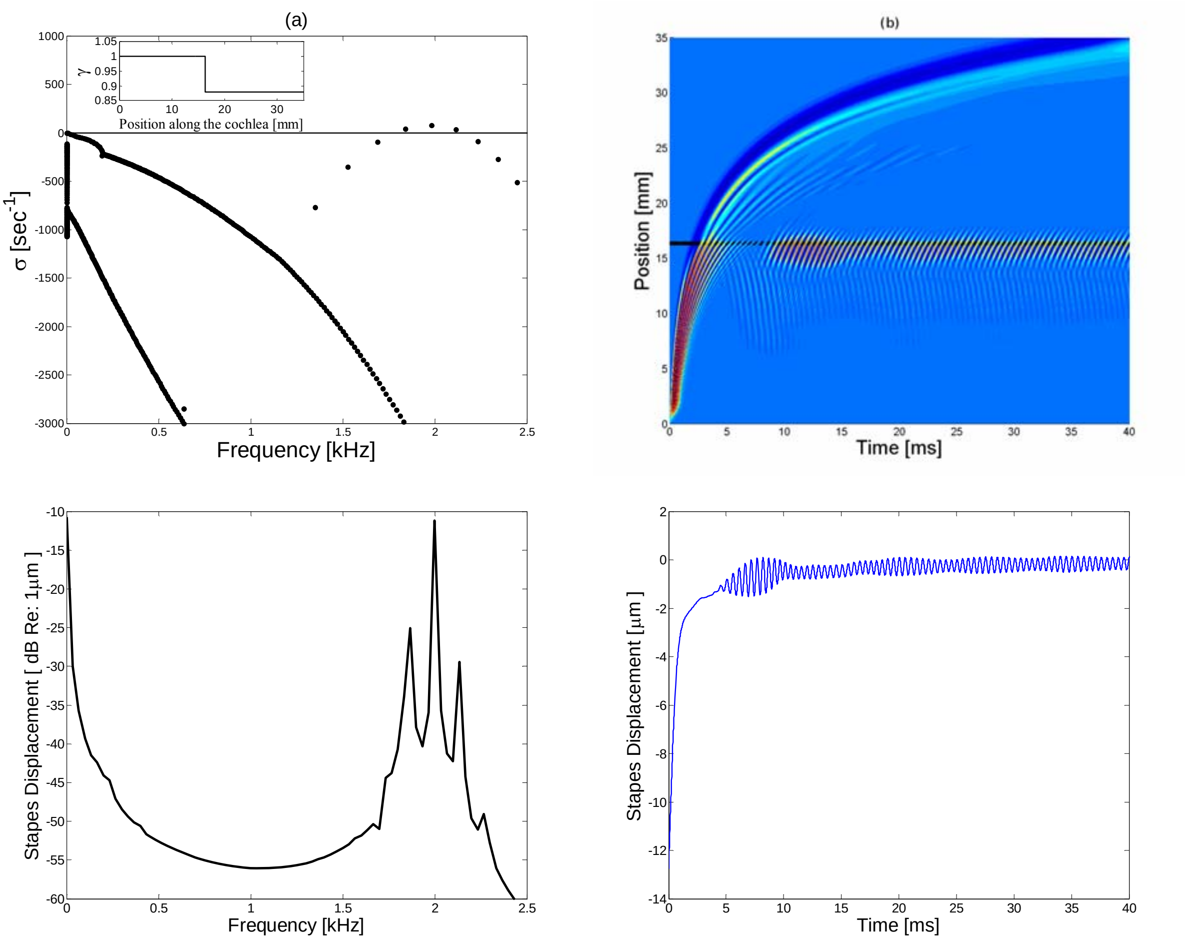

Figure 3.a-d. Stability plot of a cochlear model (a) with a 12% step-decrease in gain, γ, at x = 16.3mm, and resultant time domain simulation results (b-d). (b) represents a mesh of BM velocity against position and time; a black line at 16.3 mm shows the location of the step-discontinuity. (c) Power spectrum of stapes (middle ear boundary) displacement with initial transient discarded. (d) stapes displacement as a function of time.

It is clear from Figure 3.c that the power spectrum of the stapes displacement reflects the linear stability plot in Figure 3.a; the three unstable frequencies are strongly expressed. From the mesh of Figure 3.b, it is possible to discern a significant reflection of the travelling wave at the location of the step-discontinuity at 16.3 mm. The backward-travelling waves are especially visible from 5 ms onward. The frequency content of these reflected waves is tuned to the resonant frequencies of the region of the cochlea surrounding the discontinuity. When the reflected waves bounce off of the middle ear, starting at approximately 6 ms as seen in the stapes displacement of Figure 3.d, they again peak at their resonant locations as is visible from approximately 9 ms onward. The amplitude of the response is limited by the nonlinearity in the feedback loop, as seen in the stapes displacement of Figure 3.d. In order to understand why only three distinct frequencies become unstable, as opposed to the range of frequencies that peak in the vicinity of the discontinuity, it is instructive to examine the frequency responses of these three unstable frequencies in the nominal, stable cochlea.

Figure 4.a-d shows the frequency response of the three unstable frequencies of Figure 3.a in a stable cochlea with a uniform gain of γ = 1 at all positions.

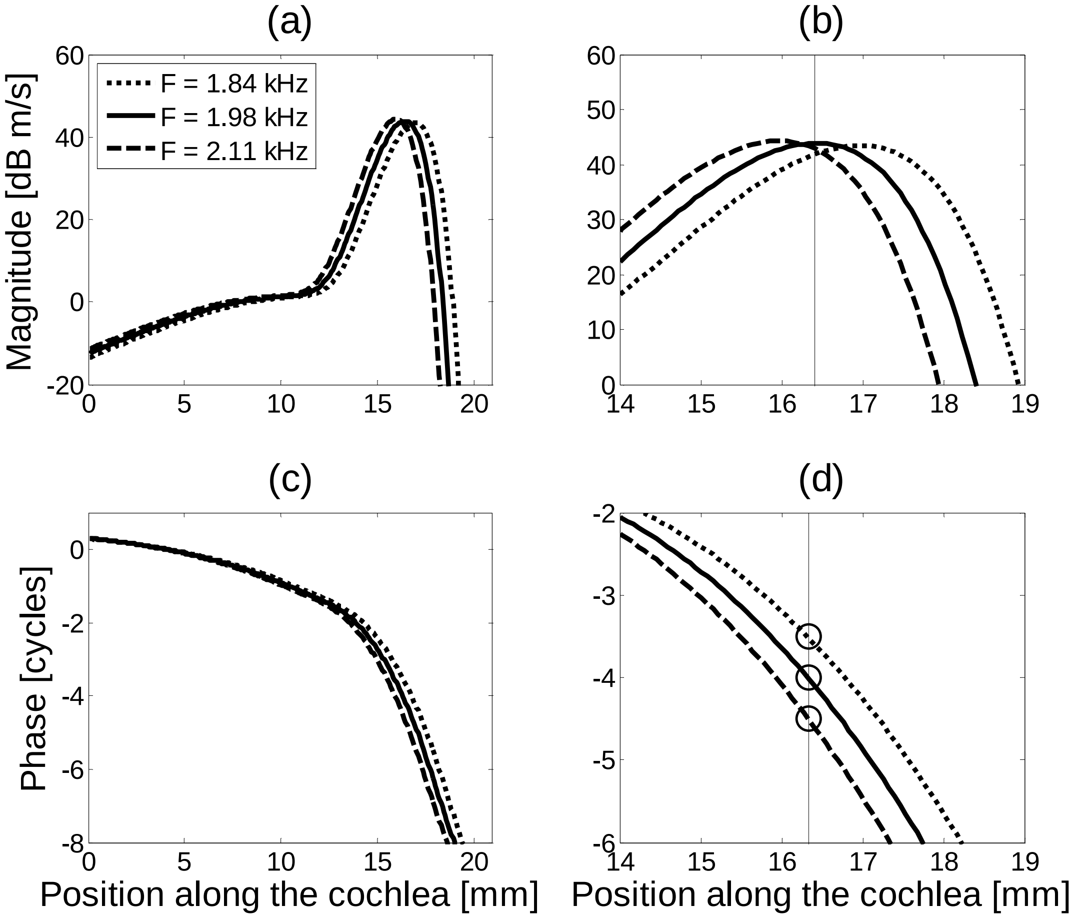

Figure 4.a-d. Frequency response of a stable cochlea at 18.4 kHz, 1.98 kHz and 2.11 kHz. (a) and (b) represent the magnitude of the response, while (c) and (d) show the phase. (b) and (d) show the magnitude and phase in detail with a vertical line at 16.3 mm, marking the location of the discontinuity in the unstable cochlea of Figure 3. Circles in (d) mark -3.5, -4 and -4.5 cycles at 16.3 mm.

It is clear from Figure 4 that the frequency responses of the three unstable frequencies peak in the vicinity of the discontinuity of Figure 3, with the most unstable frequency peaking almost exactly at 16.3 mm. However, the phases of these responses at the location of the discontinuity are the key, passing through -3.5, -4.0 and -4.5 cycles. If reflected back to the stapes, the travelling waves of these frequencies would undergo a total round-trip phase-change of 7, 8 and 9 cycles, thus meeting the requirements for instability as outlined by [3].

3.2 Random Variations in Gain

In a biological cochlea, it is likely that deviations from a perfectly smooth variation of parameters will occur. In these simulations, the micromechanical feedback gain as a function of position is perturbed with band-limited Gaussian white noise. The white noise is passed through a 5^{th} order Butterworth band-pass filter in order to prevent the wavelengths involved from exceeding the length of the cochlea (35mm) or falling below the scale of the cochlear discretization (~0.07 mm). The peak-to-peak amplitude of the perturbation is 10% of nominal. Figure 5.a shows a typical stability plot for a cochlea with randomly perturbed gain distribution, while Figure 5.b displays the histogram of normalized spacings for 200 examples of perturbed cochlear models.

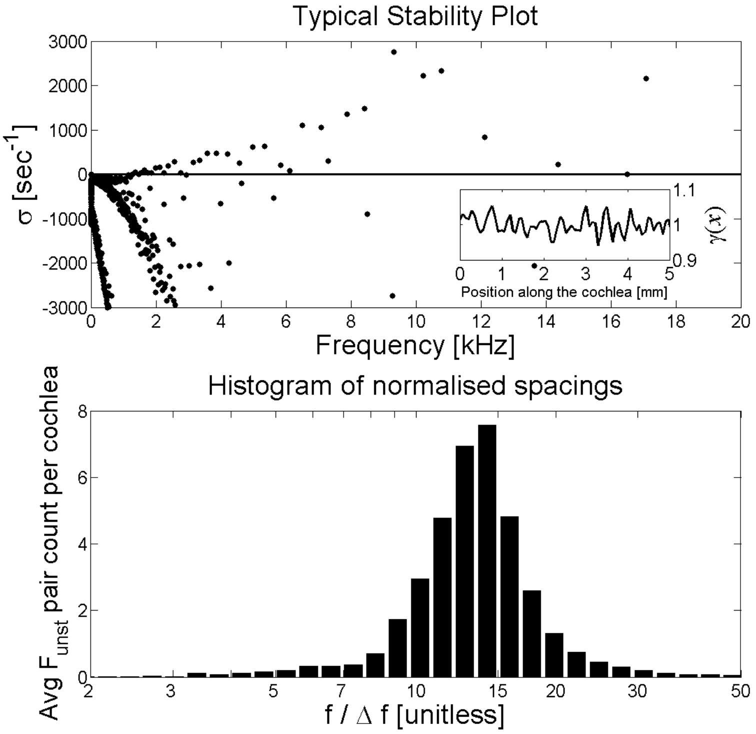

Figure 5.a-b. (a) typical stability plot with sample distribution of gains inset; note that only the first 5 mm of this $\gamma(x)$ are shown for clarity. (b) averaged histogram of the normalised spacings for 200 cochlear models arranged in log-bins.

From Figure 5, it is apparent that a wide range of frequencies can become unstable when the gain is perturbed. The average normalized spacing of unstable frequencies peaks at approximately 15, which is in good agreement with published results of clinically measured SOAE spacings in humans [7].

4. CONCLUSIONS

The state space formulation of the human cochlea is able to determine the stability of a given model. Nonlinear time domain simulations have demonstrated that linearly unstable frequencies evolve into limit-cycles similar to SOAEs when simulated in time. The normalised spacings of unstable frequencies given random distributions of gain in the cochlea agree well with measured results in humans. Furthermore, the phase responses of unstable frequencies in a stable cochlea suggest that an integer round-trip phase-change is necessary for instability. The observations made here support the theory and predictions of [3].

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