Searching for Two Tone Suppression Using a Minimal Model for Auditory Transduction

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Contents

List of Figures

1 Introduction

The processing of auditory information is a vital part of our daily lives. The auditory system allows a person to perform various tasks, such as identifying the location of the origin of a sound. It also helps a person make sense of speech, or enjoy music. It is very easy to say that the human brain is capable of performing all these tasks by itself. However, other parts of the auditory system also play a vital part. The acoustic waves go through multiple stages of processing before they even reach the brain.

The transduction of acoustic waves to neural signals takes place in the cochlea in the inner ear. The parts that play an important part in this transduction process are the basilar membrane, the inner hair cells and the primary auditory neurons that synapse onto the hair cells1. In this project, an attempt has been made to model these three systems and their response to certain stimuli has been presented.

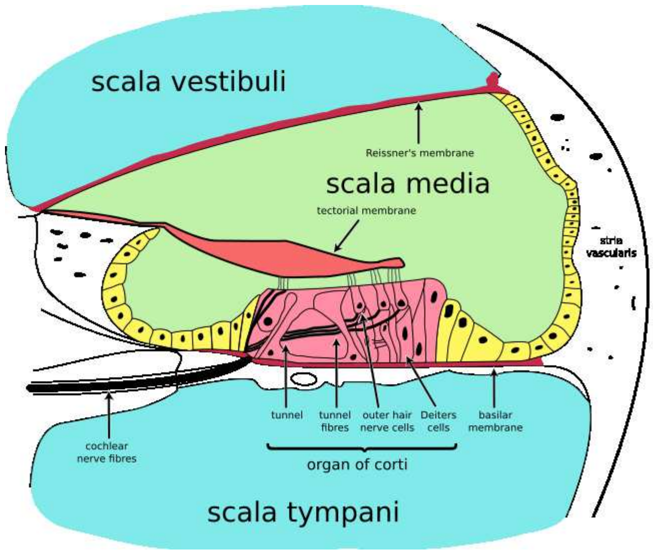


Figure 1: Cross-section of the cochlea

Firstly, the basilar membrane has been modeled as a non-linear oscillator operating at a Hopf bifurcation. Since the inner hair cells offer frequency selectivity to the auditory system, a frequency has been chosen as the natural frequency and all simulations have been performed close to resonance with this frequency, throughout the model.

Next, the inner hair cell is modeled using an RC circuit to which the input current arises from a linear coupling to the basilar membrane displacement. The current into inner hair cell is limited by a maximum and minimum cut-off to account for the maximum and minimum displacements. Finally, the subsequent spike generation in the primary auditory neuron is modeled using an inhomogeneous Poisson process. The probability of firing is taken proportional to the voltage and the time step size. There is a non-zero probability at resting potential (V = 0) to account for the spontaneous firing.

2 The model

2.1 Basilar membrane

The basilar membrane is modeled as a non-linear oscillator with damping. The basilar membrane has different locations corresponding to different characteristic frequencies. The oscillator used to represent the basilar membrane in this model is given by the following equation.

$$\ddot{x} = -(\gamma - \beta e^{-(\frac{x}{x_{th}})^2})\dot{x} - \omega_0^2 x + F_0 sin(\omega t)$$

where, ω_0 gives the characteristic frequency of the particular location in the basilar membrane. γ and β are experimentally determined constants. $F_0 sin(\omega t)$ is the forcing term. The reason for the presence of a non-linear term in the oscillator is due to the large range of frequencies the human ear can detect. x_{th} is the threshold amplitude for non-linearity cut-off. The resonance curve of the oscillator is asymmetric, the response of the oscillator for frequency at the same distance from the characteristic frequency is different.

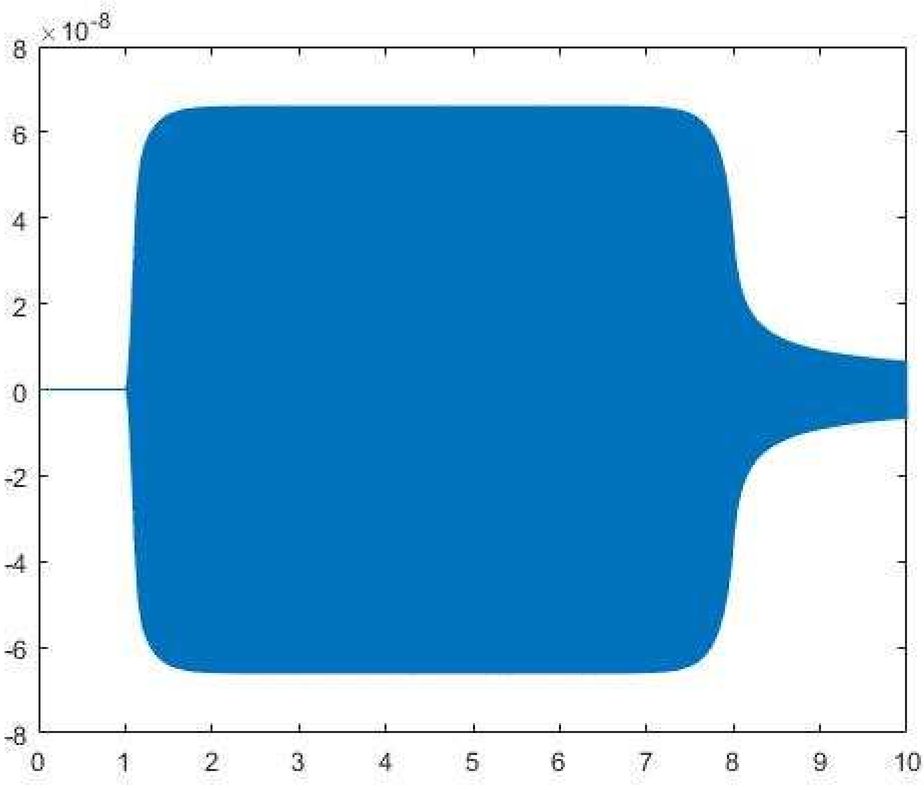


Figure 2: Response of Oscillator

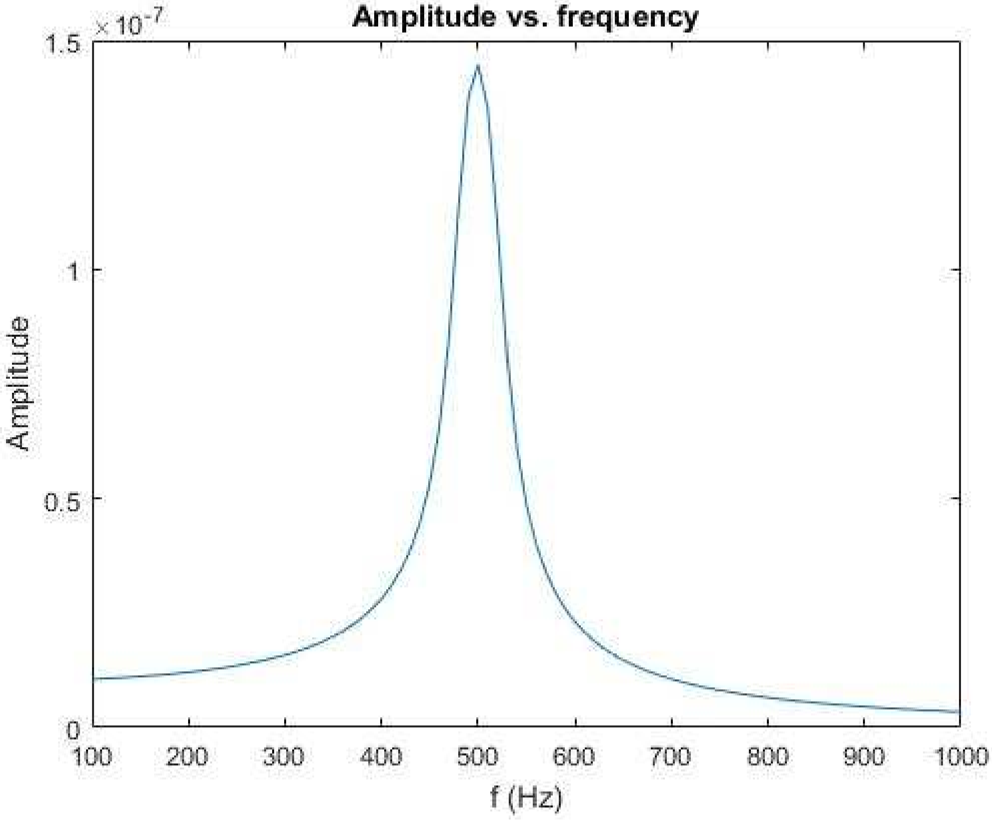


Figure 3: Resonance curve of oscillator

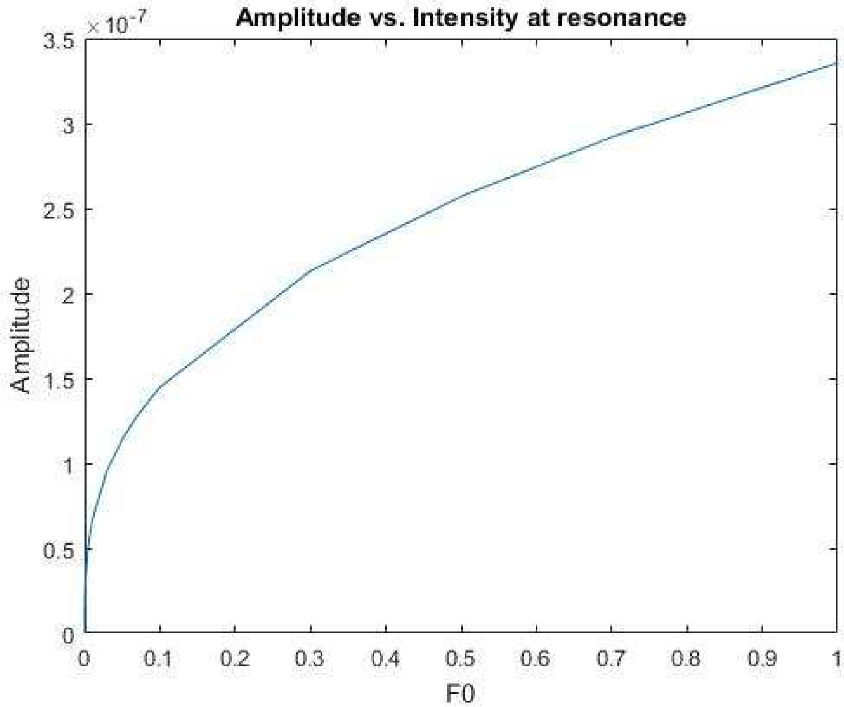


Figure 4: Amplitude vs Intensity of Tone at resonance

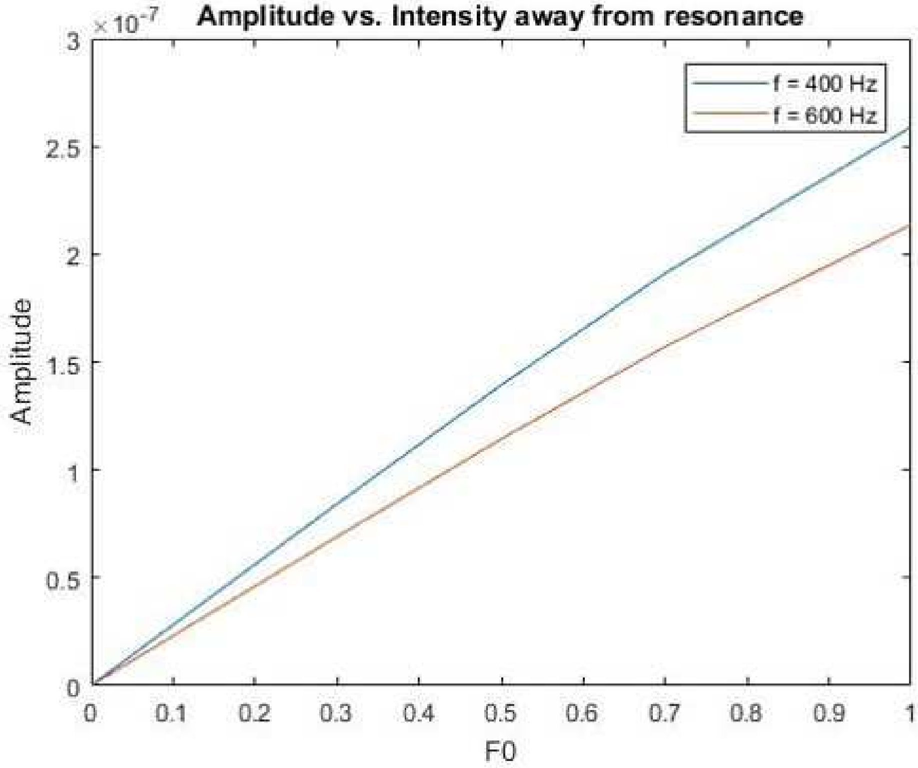


Figure 5: Amplitude vs Intensity away from resonance

2.2 Inner hair cell

The vibrations in the basilar membrane causes ions to move into the hair cells, this ionic current results in the bursting of vesicles that contain neuron-transmitters. The release of these neuron-transmitters results in the firing of neurons. This process of is modeled as an RC circuit. The maximum input current into the inner hair cell is limited due to the maximum displacement possible from basilar membrane vibrations. The current generated in the motion of the hair cell is proportional to it's displacement and the proportionality constant is given by α. The potential is found using the current and the parameters set for R and C in the circuit.

2.3 Spike generation

The release of neuron-transmitters does not guarantee the firing of the neuron. The probability of the neuron firing is given by the poison process. A uniform random number is used to generate a real number in the interval (0,1) and is compared with probability predicted by the poison process. The neuron is fired if the random real number generated is lesser. Once a neuron is fired it goes into a refractory period for time t_{ref}, during which the neuron doesn't fire. The model studies a single neuron of 500Hz characteristic frequency. The spiking of the neuron at time t is maintained in vector and the total spiking for the given frequency and intensity is maintained in a matrix.

3 Results

The model described in the previous chapter was simulated in MATLAB. The results are described in this chapter.

3.1 Response due to one tone

First, the model was stimulated by an oscillating force containing a single frequency component. The displacement of the oscillator with time for a forcing term amplitude of 0.01 and frequency of 500 Hz is shown in figure 2.

The motion of the basilar membrane leads to a varying current entering the hair cells due to stereocilia motion, which changes the cell's potential. The potential varies in a fashion similar to the displacement of the oscillator. Finally, the release of neurotransmitter at the synapse leads to probabilistic firing of neurons (spike generation), modeled as an inhomogeneous Poisson process. The probability of firing is proportional to the cell voltage. The spikes are shown in the following figure.

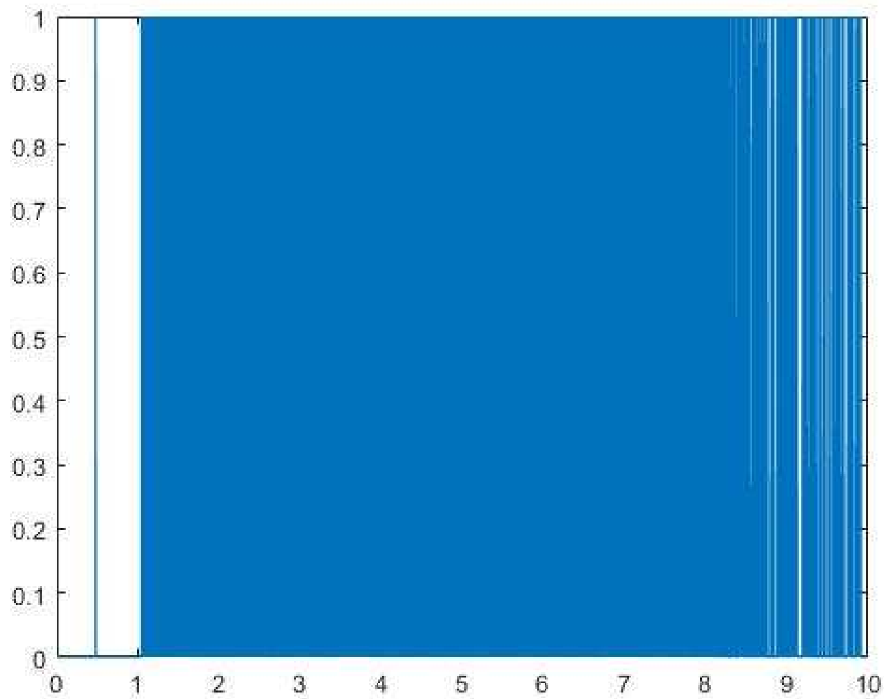


Figure 6: Simulated spike generation in neurons

It is seen that the spike time-series (figure 6) is densely populated when the amplitude is larger (figure 2), and sparse when the amplitude is smaller, indicating the proportionality between amplitude of oscillation of the membrane and the rate of spike generation.

3.2 Response due to two tones

When an oscillator is stimulated by two tones of different frequencies (f_0 and f_1), the spectrum of the response contains corresponding Fourier amplitudes (X_{f0} and X_{f1}). It is experimentally observed that both amplitudes are smaller than they would be in absence of the other tone. This phenomenon is known as two-tone suppression. In this section, we present the results of simulations with two tones of varying intensities and frequencies.

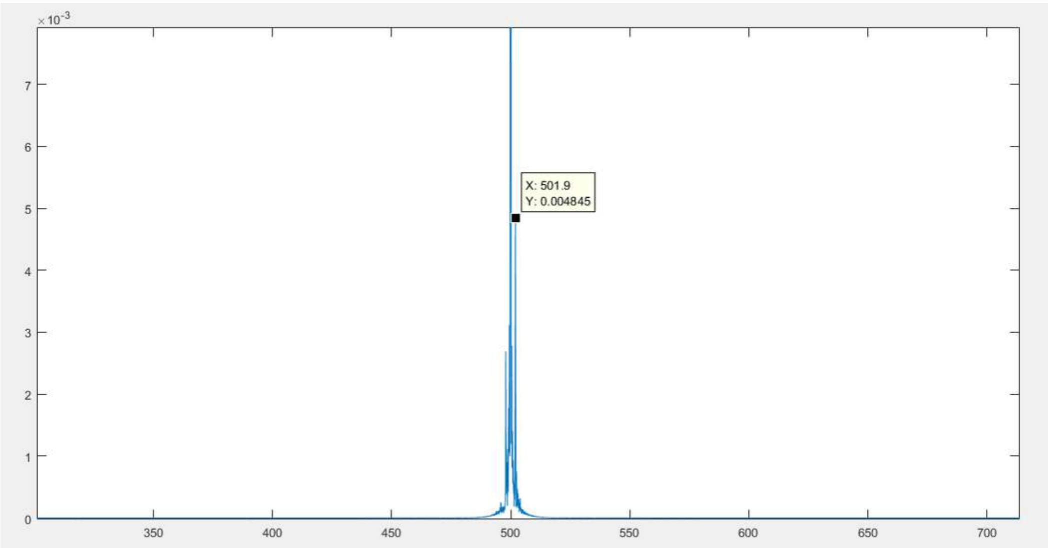


Figure 7: Fourier spectrum of response of the oscillator

The model was stimulated by an oscillating force containing two components. The analysis was performed, first by varying the ratio between intensities of the two tones while keeping their frequencies constant, and then by varying the frequency of the second (suppressor) tone while keeping the first (probe) tone at characteristic frequency and both tones at constant intensities. The Fourier amplitudes due to the two frequencies were extracted from the spectrum of the response.

Suppression at membrane level

Fourier amplitudes of the response were plotted for probe tone frequency of 500 Hz (equal to characteristic frequency) and suppressor tone frequency of 502 Hz. First, the ratio of intensities of the two tones is varied from 0 to 5 in steps of 0.1.

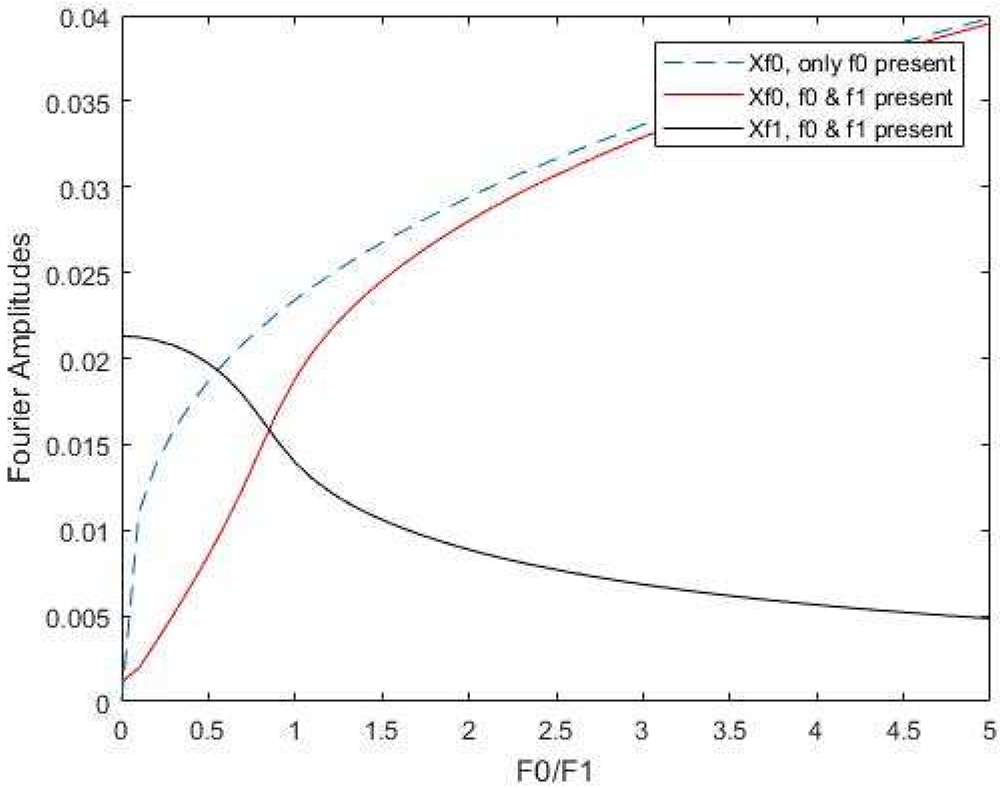


Figure 8: Fourier amplitudes of membrane displacement

In the above plot, the blue dashed curve represents the response of the membrane when stimulated with the probe tone alone (in the absence of the suppressor tone). The solid red curve represents the response due to the probe tone in presence of the suppressor. As expected, the response due to the probe tone in the latter case is reduced compared to the former. We also note that the amount of suppression decreases as the ratio F_0/F_1 increases (when either the intensity of the probe tone increases for a fixed suppressor intensity, or the intensity of the suppressor decreases for a fixed probe intensity). The solid black curve represents the response due to the suppressor tone when both the tones are present.

In order to study the suppression as a function of frequencies of the two tones, Fourier amplitudes due the two frequencies were plotted against the difference between them, as shown in the following plot.

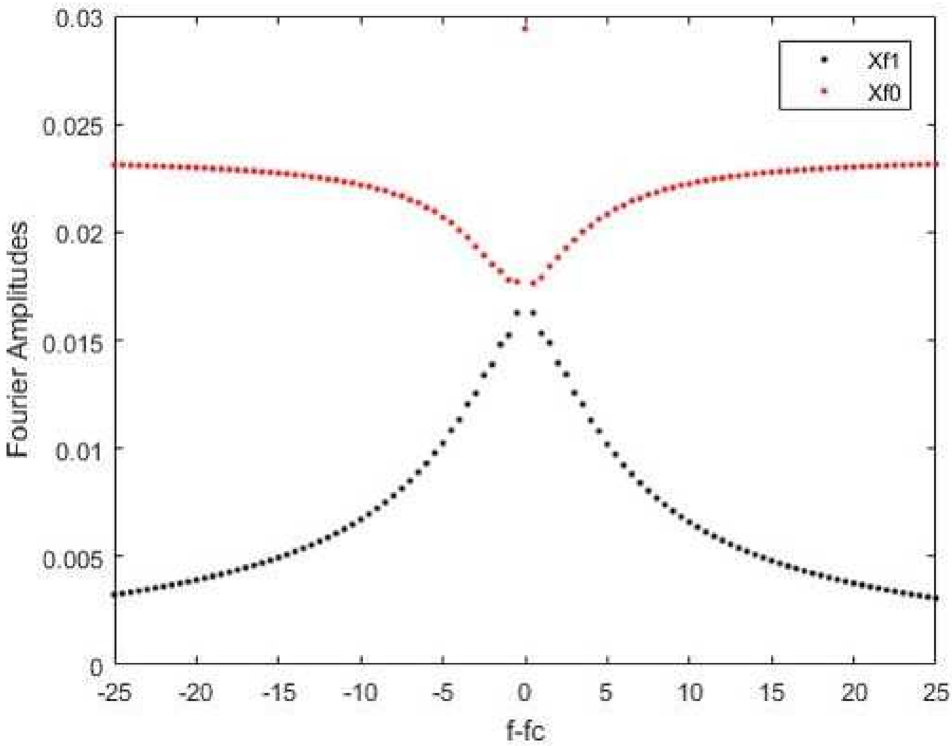
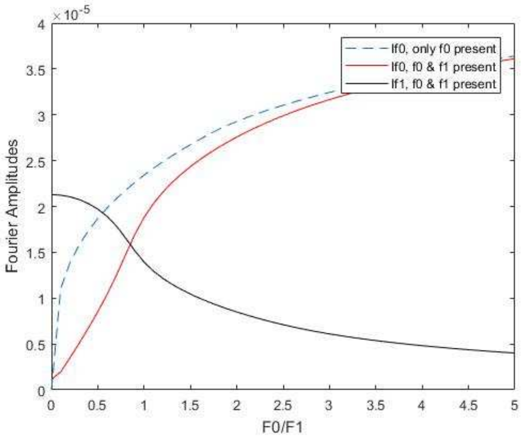


Figure 9: Suppression as a function of frequency

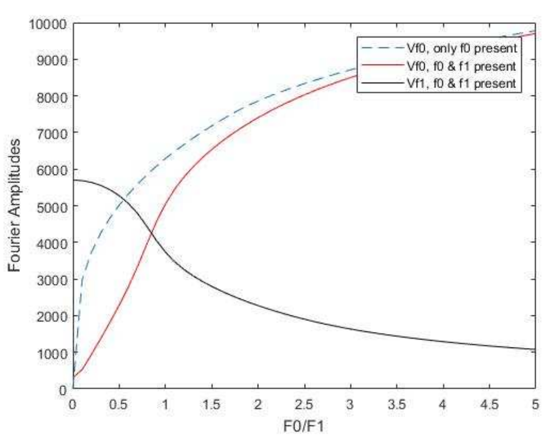
Here, the red curve depicts the Fourier amplitude due to the probe tone and the black curve depicts the amplitude due to the suppressor tone. The probe tone is kept constant at 500 Hz, while the frequency of the suppressor tone is varied from 475 Hz to 525 Hz. It is observed that as the suppressor frequency approaches the probe frequency, the probe tone is more and more suppressed, until both the frequencies are equal. At this point (f - fc = 0), the two forcing terms add constructively, and the oscillator behaves as if it is being stimulated by a tone of singe frequency (whose intensity is simply the sum of the two intensities). This causes a discontinuity in the curve (the red dot at the top of the plot). Beyond this point, as the frequency difference increases, the suppression decreases.

Suppression at current/voltage level

Since the current flowing inside the hair cell and the potential of the hair cell are also proportional to the membrane displacement, these too are suppressed. The Fourier components of current and voltage due to the presence of the second tone are shown in the following plots.



(a)



(b)

Figure 10: Fourier amplitudes of: (a) current flowing in the cell, (b) potential of the cell

Suppression at neuron spiking level

A similar analysis was performed at the level of neuronal spikes, by taking Fourier amplitudes of spike time-series (figure 6). The suppression from the previous stages is carried over to this stage, as shown in the following plot.

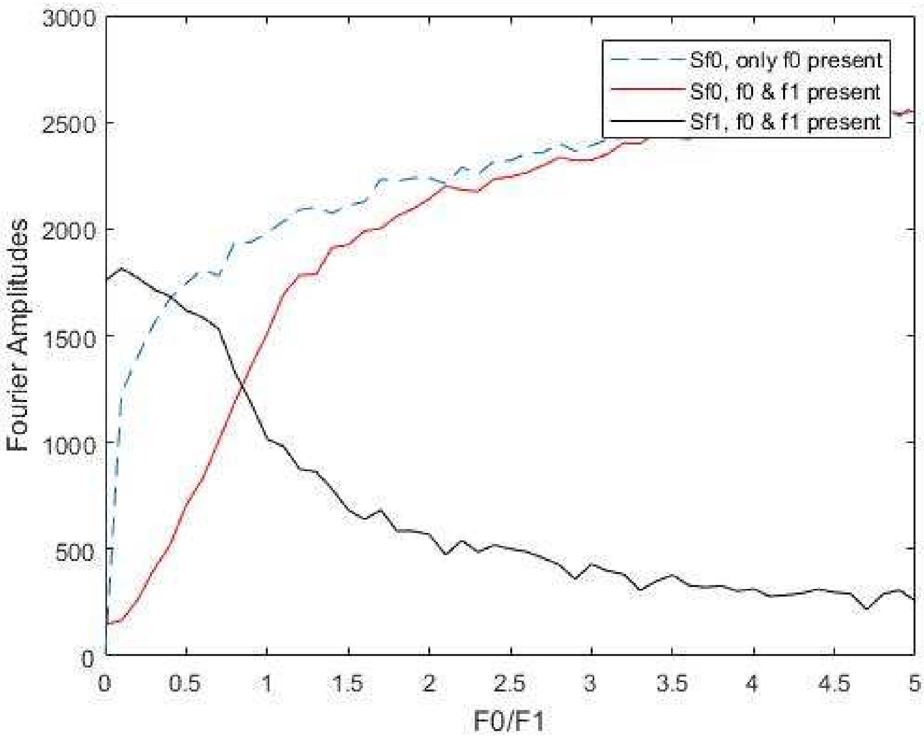


Figure 11: Suppression in spike timeseries

Suppression in average spike count

The average spike count is the number of times the neuron fires during the period of simulation. The quantity was plotted as a function of ratio of the two intensities, as shown in the following figure.

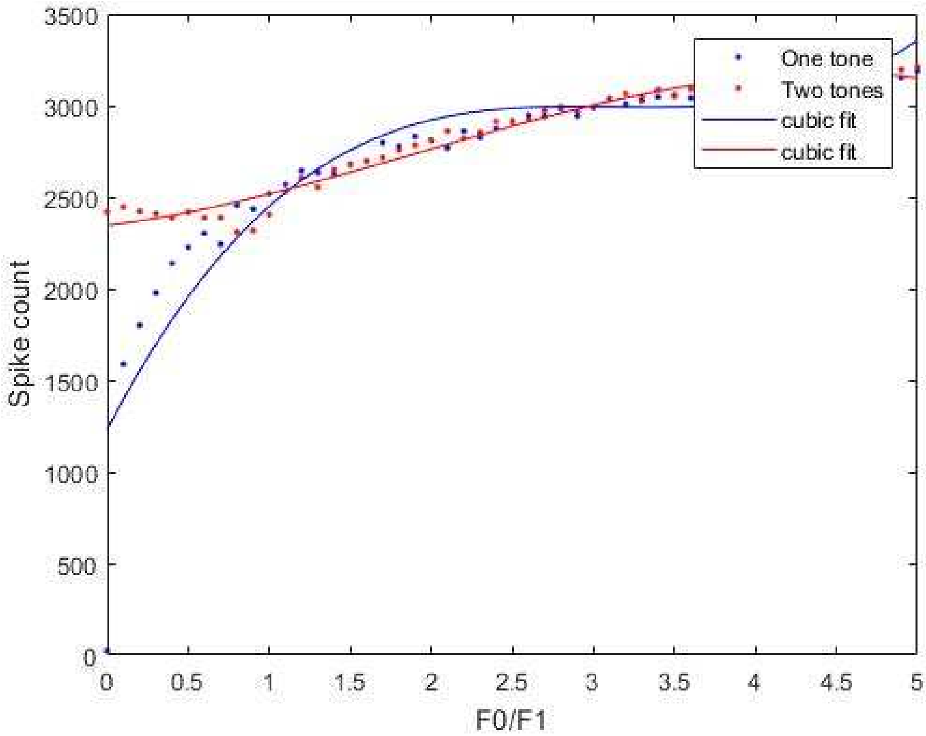


Figure 12: Suppression in average spike count

The red dots represent the average spike count in the presence of the probe tone alone, while the blue dots represent the average spike count when both the probe (500 Hz) and suppressor (502 Hz) tones are present. The solid lines are cubic fits of the data. It is observed that below a certain ratio of intensities, i.e., when the probe tone intensity is too low compared to suppressor, the average spike count is larger than the case when only probe tone was present. This is because the suppressor frequency still lies within the resonance curve (though not at the center), and is intense enough to elicit more response than the low intensity probe tone.

4 Conclusion

In this project we have looked into the phenomenon of two tone suppression inside the inner ear. From our analysis, we conclude that the suppression occurs at the membrane level (the oscillator in our model), and is carried over to the neuronal spike level.

Acknowledgments

We want to express my sincerest gratitude to Dr. Toby Joseph, Department of Physics, BITS Pilani - K K Birla Goa Campus, for giving us the opportunity to work on this project and for his immense counsel throughout its course. Without his continual guidance and encouragement, we would not have been able to succeed in this endeavor.

References

[1] Julicher et. al., Physical basis of two tone interference in hearing, PNAS, 2001.

[2] Ruggero et. al., Two-Tone Suppression in the Basilar Membrane of the Cochlea: Mechanical Basis of Auditory-Nerve Rate Suppression, Journal of Neurophysiology, 1992.