Power-Laws and Loss of Power-Laws in the Tuned Cochlea

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Abstract—The mammalian cochlea is a sophisticated hearing sensor that uses active amplification to enhance weak sounds. The nonlinearity necessary for this task allows a remarkable dynamic range, yet at the same time it removes the superposition principle, resulting in complex interactions of the incoming frequencies and the generation of new frequencies (combination tones). Using a biophysically realistic mesoscopic model of the cochlea, we show that the processing of sound mixtures produces activity profiles consistent with power-laws. Importantly, if the cochlea is parameter-tuned in a way that was earlier shown to effectively model the process of active listening, the power-law distribution is broken.

1. Introduction

Originally borrowed from the study of phase transitions in physics, the notion of criticality has become increasingly popular in the biological and neural sciences. The idea is that a critical state, usually characterized in terms of power-law behavior of some relevant associated observables, would allow the system to be most flexible to perform a multitude of tasks (see e.g. [1]). While evidence for the criticality of certain brain structures has been provided in terms of power-law distributed observables (e.g. [2]), it is by no means clear that these observables are directly relevant to the performance of an active task. Using the well-tested and (on a mesoscopic level) biophysically optimal model of the mammalian inner ear (the so-called 'Hopf cochlea' [3, 4]), we show that power-law relationships in the relevant observables naturally arise, but during active listening are broken.

2. Cochlea activation and generation of power-laws

In the cochlea, an incoming sound of frequency f (a 'pure tone') propagates towards a resonant place on the basilar membrane, where it is amplified and shortly after dissipated. The active amplification was shown to be well-modeled by a stimulated Hopf process

$$\dot{z} = (\mu + i)\omega_{ch}z - \omega_{ch}|z|^2 z - \omega_{ch}F(t), \; z \in \mathbb{C}, \quad (1)$$

where $z(t)$ denotes the complex response amplitude, $F(t)$ is the complex forcing signal, ω_{ch} is the characteristic frequency of the Hopf amplifier and μ is the bifurcation parameter [3, 5, 6, 7]. For $\mu < 0$, the system itself is stable and, upon forcing, acts as a small-signal amplifier, while for $\mu > 0$, stable limit-cycle solutions appear. For the dissipation process (a passive property of the cochlea), a tailored low-pass filter has been shown to model well the effects of the major dissipation processes at work (essentially the viscous losses in the cochlear fluid) [3, 8, 9]. A feed-forward chain of cochlea sections where each section comprises a Hopf amplifier and a low-pass filtering part then forms the Hopf cochlea, a hardware and software device that reproduces all the salient biological measurements of cochlear mechanics [4, 10, 11]. In the Hopf cochlea, the characteristic frequencies of the Hopf amplifiers form a geometric sequence, so that each octave in the frequency range is covered by the same number of Hopf cochlea sections. This yields a logarithmic 'tonotopic map' that is comparable to mammalian cochleae (the flexibility in the choice of frequency range and the number of sections allows a detailed comparison to any mammalian model cochlea, e.g. cat, guinea pig or human). For all experiments described below, we used a software cochlea of 29 sections covering 7 octaves (characteristic frequencies f_{ch} between 14.08 and 0.11 kHz).
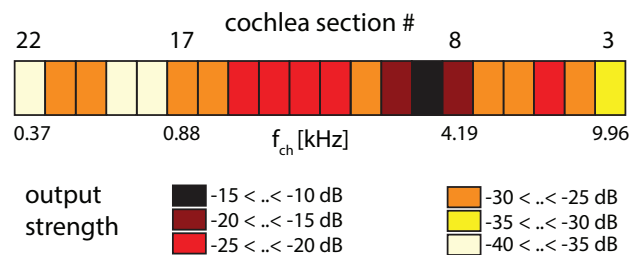

Figure 1: Complex cochlear excitation (relevant sections 3-22 are shown) for stimulation with two harmonic sounds ($f_0^{(1,2)}$ = 3.5, 9 kHz and two overtones each) at -60 dB rms-level/sound.

While the cochlear excitation pattern is simple for pure tones, the picture becomes much more complex in the case of incoming sound mixtures of different frequencies $f_1, f_2, ...$ Here, the nonlinearity of the active process leads to the generation of new frequencies, so-called combination tones, the presence of which was already known to 18th century musicians Georg Sorge and Giuseppe Tartini.

For a two-tone input of frequencies f_1, f_2, the (predominantly cubic) nonlinearity in the cochlea generates combination tones $2f_1 - f_2, 3f_1 - 2f_2,...$ which then propagate towards their respective place of amplification. These cubic combination-tones are well-audible also for non-trained listeners, and have been shown to have a key effect on pitch perception [12, 13]. For a more complex, but still entirely natural input such as a mixture of different harmonic complexes $f_0^{(1)}, 2f_0^{(1)}, 3f_0^{(1)}, ...; f_0^{(2)}, 2f_0^{(2)}, 3f_0^{(2)}, ...; ..$, a plethora of combination tones of various strengths emerges. The generation and subsequent amplification of these combination tones then lead to a complex cochlear excitation profile, cf. Fig. 1, where the cochlear excitation is sketched in terms of the output strength measured at each section. Here, we used an input mixture of two harmonic sounds, where a harmonic sound is assumed to be of the form $\propto \sum_k^n 1/k \, e^{2\pi i k f_0 * t}$, i.e. with fundamental f_0 and $(n-1)$ overtones of relative amplitude $1/k$.
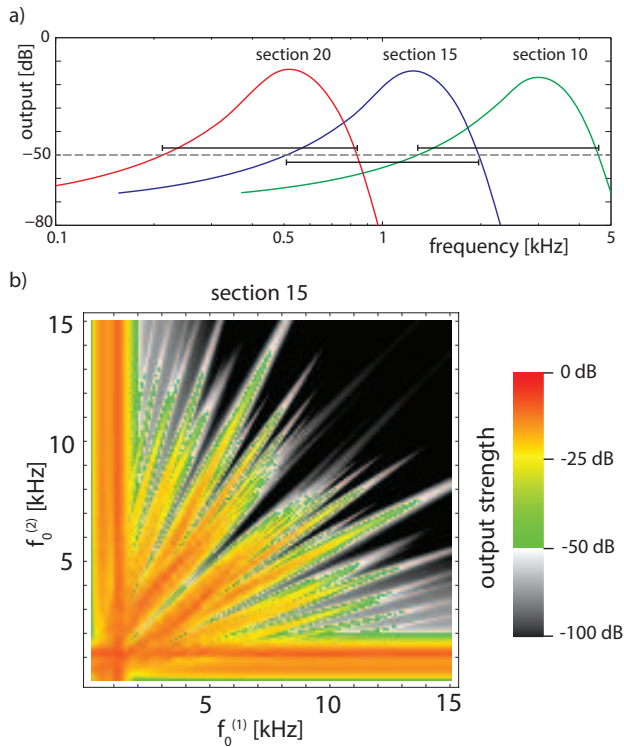

a)

b)

Figure 2: Cochlea section responses ($\mu = -0.2$). Output profiles for a) single pure-tone stimulation (-70 dB) and b), stimulation with two complex tones of fundamental frequencies $f_0^{(1,2)}$ (-60 dB rms per complex tone).

Given the complex nonlinear nature of cochlear excitation, one may now ask in what statistical activity distribution along the cochlea these interactions result. To address this question, we stimulated the Hopf cochlea with two-sound mixtures of random fundamental frequencies and fixed input levels. Motivated by comparisons to psychoacoustic experiments, we define a hearing threshold of
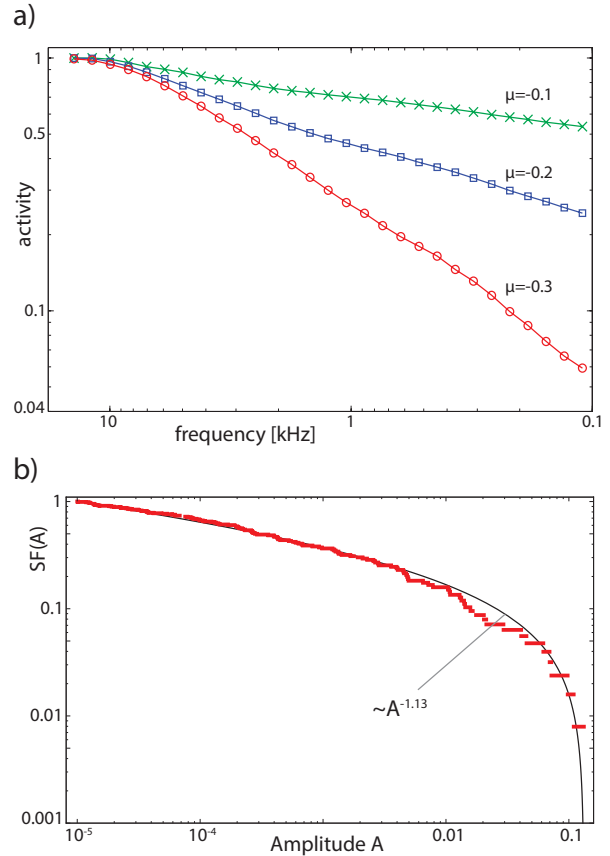

Figure 3: Power-laws in the cochlea. a) Section activity ($N = 10000$ trials) for different levels of flat tuning and two complex tones of random fundamental frequencies as input, for fixed sound levels (-60 dB). b) Distribution of the maximal strength A of tones present in the cochlea (stimulus and CT) upon two-sound stimulation ($f_0^{(1,2)} = 1331, 2120$ Hz). Plotted is the survival function $SF(A) = 1 - P(A)$, where $P(A)$ is the cumulative probability distribution. Black line: Best power-law fit (exponent from maximum likelihood estimation).

-50 dB to denote the output strength (at a cochlea section) where the perception of a sound is just possible [12, 13]. While such a value gives the best fit to the audibility threshold of combination tones, we checked that a different choice (e.g. -40 or -60 dB) does not essentially change any of the following results. The fundamental frequencies are chosen randomly from a uniform distribution on the interval (0,15) kHz. Fig. 2a) shows the responses of three cochlea sections to simple pure-tone stimulation of different frequencies. The activity of the section, which we defined as the proportion of cases where the response at the section is above the implemented hearing threshold, is roughly constant on a logarithmic frequency scale, i.e. $\propto f_{ch}$, where f_{ch} is the characteristic frequency of the section. The more complex case of two harmonic sounds as input is depicted in Fig. 2b). Here, the interactions in the

cochlea give rise to highly non-trivial 'receptive fields' of the sections, where the contributions of the combination tones are easily identified as the non-vertical/horizontal structures. Contrary to the common perception that combination tones are just a simple by-product that can be safely ignored, they seem to account for the major part of cochlear excitation. Fig. 3a) shows the corresponding activity profiles over all cochlea sections on classic log-log-scale for different levels of μ-settings, for two-sound-mixtures and -60 dB input level (rms) per sound. Here, the activity is not proportional to f anymore, but surprisingly the power-law behavior continues to hold, however now with nontrivial exponents $\propto f^{\beta}$, $0 < \beta < 1$.

To obtain a second measure to characterize the state of the cochlea, we focused on the case of a two-sound input with fixed (but arbitrary) frequencies and examined the generated combination tone responses in detail. Here, the generality of the relation of the two fundamentals (not a simple p:q ratio, where p and q are small integers) yields a multitude of combination tones, and renders the identification of the relationships between these combination tones difficult. To circumvent this difficulty, we consider the distribution of the frequencies occurring in the cochlea (both the stimulus frequencies and the combination tones) in terms of the maximal strength (amplitude) they reach. This is achieved by tracking the tones (frequencies) in the Fourier transform through the cochlea sections and recording each tone's maximal value. Fig. 3b) shows the results for a stimulation with fundamental frequencies $f_0^{(1,2)} = 1331, 2120$ Hz, five harmonics and -70 dB rms-level for each sound. The survival function SF (complementary cumulative distribution) is very well-fit by a power-law of exponent $\beta = 1.13$. For similar experiments with different input sound levels and frequencies, the obtained β-values are all between 1.1 and 1.2.

3. Loss of power-laws

In humans and other mammals, neural feedback loops from cortical and sub-cortical brain areas provide input to more peripheral components of the auditory system. As one part of this feedback system, neurons from the brainstem (so-called medial olivocochlear efferents) synapse on the cochlea's outer hair cells (the structures that are responsible for the active amplification in the ear). While the role of these efferent connections is still not fully understood, there is strong evidence that they play an important part in the process of active listening (selective attention) [14, 15, 16, 17]. We have recently investigated to what extent the peripheral hearing system can assist a listener in focusing on an auditory signal [18]. Using pitch as a guiding feature (cf. [19, 20, 21] for pitch, pitch perception models and relevant physiological data), we developed a specific measure of the tuning error that, for a mixture of two competing sounds, estimates how much the cochlear output is biased towards the signal component of interest. Working
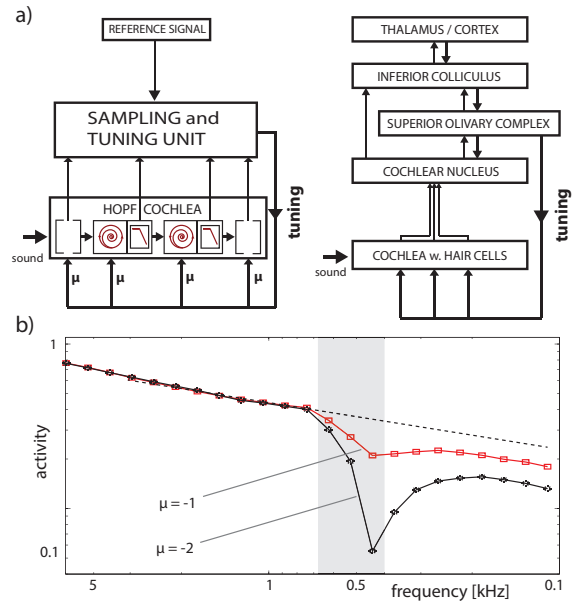

Figure 4: Loss of power-laws. a) Hopf-cochlea tuning scheme (left) and biological tuning scheme (right) [18]. b) Activity profiles when sections 19-21 of the cochlea (CF= $622, 523, 440$ Hz) are tuned away from $\mu = -0.2$ to values $\mu = -0.3, -0.5, -1, -2$.

with real-world sound examples and an evolutionary strategy in the tuning unit, the approach demonstrated not only that the activity of the biological efferent connections can be well-modeled by the tuning of the bifurcation parameters (the μ-parameters) in the Hopf cochlea, but also that these efferent connections provide a very effective way to control the complex interactions in the cochlea and to tune the cochlea towards a signal component of interest. Fig. 4a) provides an overview of the cochlea tuning scheme and a comparison to the biological example (cf. [18] for details).

Figure 4b) shows the influence of a hypothetical listening process on the cochlear activation curves. For this, the μ-parameter of sections 19-21 of the cochlea (characteristic frequencies between 400 and 600 Hz) are shifted from $\mu = -0.2$ to more negative values, which models the suppression of an unwanted sound of a frequency around 500 Hz. In addition to the obvious loss of power-law behavior of the cochlear activation curves, a corresponding effect is also observed in the distribution of combination tone strengths. Generally, tuning leads to an effective suppression of disturbing combination tones [13], and in the optimal case, to a complete collapse of the distribution of CT strengths.

4. Discussion

The processing of sounds in the mammalian inner ear is an impressively complex and still not fully understood

process. In many scientific investigations and technical applications (e.g. hearing aids or cochlear implants), the ubiquity and significance of combination tones is not yet adequately taken into account. Considering the fact that these combination tones propagate along the auditory pathway without apparent loss of quality or strength (cf. [22] for recent measurements in the gerbil inferior colliculus), a proper analysis of interactions in the cochlea is of utmost importance.

Using the Hopf cochlea as our model, we have demonstrated that despite the complexity of combination tone generation in the cochlea, simple power-law relationships hold for the statistical activation of the cochlea sections. Implementing a task of active listening, which is achieved by tuning some cochlea sections away from the bifurcation point, however breaks these power-laws. This suggests that observables relevant for our organism (such as the total statistical activation of a cochlea section) may indeed be power-law distributed, but that this only holds for a state of passive perception.

Acknowledgments

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