Representation of auditory signals by neuronal spike trains

Bachelor project report

Maëlle Colussi

Computational Neuroscience Laboratory (LCN) - EPFL
Professor in charge: Prof. Wulfram Gerstner, Assistant in charge: Moritz Deger

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1. Introduction

The neuronal representation of sound is the result of the encoding of acoustic signals done through the peripheral auditory system. The spike trains resulting from this encoding are influenced, among other factors, by the refractory period of the auditory nerve fibers. In fact, for example we learn in [Avissar et al. 2013] that, for the encoding of pure tones, the time-spike precision depends in part on the ratio of the refractory period to the stimulus period. We also know from the research of Berry and Meister described in [Berry and Meister 1998] that the refractoriness of neurons may make their signals more reliable. In [Deger et al. 2010], processes with refractoriness were studied and predictions were made for the Fourier coefficients of response when the stimulus is a modulated pure tone.

This project has for purpose to go further in the study the effects of the refractoriness on the result of the encoding in the peripheral auditory system. First, it studied this effect on an ad-hoc computation made on spike trains, the rate-modulation depth, for four kinds of stimuli. Then, it tried to see if their Fourier coefficients, when the stimulus is a modulated pure tone, match the predictions of [Deger et al. 2010].

For this aim, a model of the peripheral auditory system was used [Zilany and Bruce 2006, 2007; Zilany et al. 2009], in which the refractory period has been be modified. Virtual experiments were run on the two versions of the model and the resulting spike trains were compared to see the influence of the refractory period.

Now, before going any deeper about the model, we should remind us some things about the auditory system.

2. The Auditory System

The "Auditory Neuroscience" book [Schnupp et al. 2011] tells us in the chapter two what is important for us here to know.

The peripheral auditory system has (generally air) pressure as input, and spike trains as output. We will go through the parts of the ear, with help of Figure 1.

Let us consider first the external ear. There the pressure signals come through the ear canal and make the eardrum vibrate. This takes us to the medium ear. The vibration is propagated throughout it by three ossicles: malleus, incus and stapes. The farthest part from the external ear of the stapes touches the boundary of the cochlea, on the oval window, in the inner ear, and makes vibrate the liquid we find in it. The cochlea forms an interface between this mechanical vibration and the neural signal that will go through the auditory nerve (VII nerve on Figure 1).

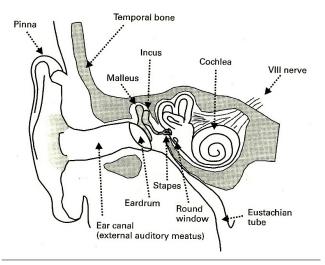


Figure 1. Peripheral auditory system ([Schnupp et al. 2011] p.52)

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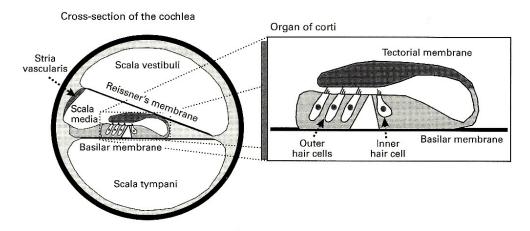


Figure 2. Organ of Corti ([Schnupp et al. 2011] p.65)

We will speak more about this interface below. But first we should see more about the vibration of the cochlea. The cochlea is a tube that has two main compartments which are placed on top of each other and separated throughout the cochlear tube by the basilar membrane, except at the far end of it where they are joined, as you can see on Figure 3.

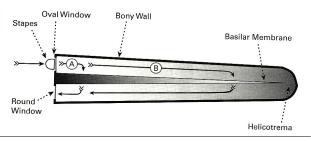


Figure 3. Unrolled cochlea ([Schnupp et al. 2011] p.55)

A vibration that comes will try to propagate through the basilar membrane from the upper compartment to the other. When doing that, it will not make all the parts of the basilar membrane vibrate at the same intensity. In fact, the cochlea is like a "biological Fourier analyzer" according to the book. The frequency content of vibrations is decomposed and each frequency has its "favorite" place in the cochlear coiled tube that it makes vibrate particularily. The part of the basilar membrane that is the first we can see vibrating, when we gradually put on the volume of a pure tone of frequency f, is said to be of "characteristic frequency" f. Near the oval window, the characteristic frequencies are high, and as we go to the tip of the tube, the characteristic frequency becomes lower.

Throughout the cochlear tube, we have the organ of Corti, which is the interface about which an allusion was made above in the text. We will use Figure 2 to illustrate our purpose.

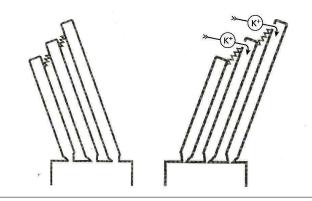


Figure 4. Transduction ([Schnupp et al. 2011] p.66)

The upper compartment of the cochlea is in fact in two parts separated by a membrane. The scala media, where we find the organ of Corti, has a higher concentration of potassium cations. We have as consequence a polarization between the liquid of the scala media and the inner hair cells. When the basilar membrane vibrates, the tectorial membrane does that also and that makes the liquid move. These movements has as consequence the deflection of the stereocili of the inner hair cells, and when this happens, some potassium ions of the scala media go into the inner hair cells (IHC), and we have a depolarization. We can see that in Figure 4. This has as consequence that some glutamate is leaked in synapses between the IHC and the auditory nerve

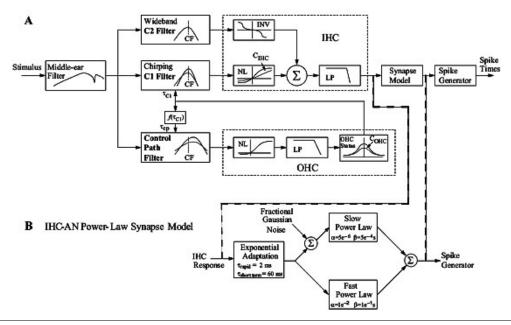


Figure 5. Schema of the model ([Zilany et al. 2009] their fig. 2)

fibers, what excites these fibers and make them perhaps have some spikes.

3. Model

Let us speak now about the model of the peripheral auditory system from [Zilany and Bruce 2006, 2007; Zilany et al. 2009], used to run experiments in this project.

I will not go into the details of the model, but I will speak more about the use of it. You can see in Figure 5 the schematic of the model.

From the user point of view, the model consists of two main functions that are called "catmodel_IHC" and "catmodel_Synapse". Their prototype is

vihc = catmodel_IHC(pin, CF, nrep, tdres,
reptime, cohc, cihc);

and

[synout, psth] = catmodel_Synapse(vihc, CF, nrep, tdres, fibertype, implnt);

like specified in the "catmodel.m" file of the model. Let us go deeper into what each parameters and return value of these functions mean.

The first function, catmodel_IHC, takes as parameters a stimulus vector (pin, in Pa), sampled at some sampling rate that corresponds to the bin size tdres (i.e. is the inverse of it), and the characteristic frequency (CF, in Hz) of the IHC and for which we want to know the potential (vihc, in Volt) when stimulated.

This last thing (vihc) is what is returned by the function. reptime is the time for one repetition of the stimulus, and nrep is the number of repetions we want to be run. cohc and cihc represents the damages on respectively the outer hair cells and inner hair cells in the simulation. vihc will contain the IHC potential for every repetition after the function has been run.

The second function, catmodel_Synapse, takes the IHC potential returned by catmodel_IHC, with the same sampling rate, so the same tdres, which is also here the bin size of the PSTH returned by the function (psth). The PSTH will be computed according to the specified number of repetitions (nrep). The synapse output of the IHC (synout) is also returned by the function. The fibertype parameter is used to tell the model which nerve fiber type we "test" with the stimulus, distinguished by their spontaneus rate (SR): low, medium or high (low: < 1 spike/s, medium: < 18 spike/s, high: 20-50 spike/s, according to [Schnupp et al. 2011]). Finally, implnt is used to indicate the precision we want in the simulation for some calculations in the model.

As an example of what kind of result the model can give, in Figure 6 you can see some graphs that represents the steps of a simulation of a pure tone step stimulus. A nerve fiber with high SR with a 1 kHz characteristic frequency was chosen.

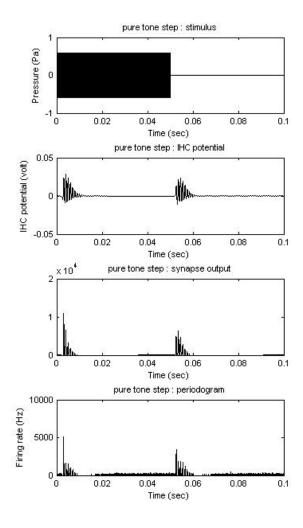


Figure 6. Example of model results ([Zilany et al. 2009])

The first graph is a representation of one period of the stimulus, sampled at 100'000 Hz (so with bins of 10ms), at 84dB. What was given to the model as pin was this period of 100 ms repeated 800 times. The frequency of the pure tone is so high here (10 Hz) that we cannot see its sinusoid. On the second graph, you can see the IHC potential from the first function in response of the last period of the stimulus (with dependencies on the preceding periods included). The third graph shows you a part of the synapse output given by catmodel_Synapse, for the same period as for the potential of IHC. The fourth graph represents the periodogram for the entire stimulus, computed with

help of the PSTH given by the second function of the model.

For the project, the code of the model has been modified to put to zero the absolute refractory period of nerve fibers. This transformation was done in the spike generator part of the model (see in Figure 5 the last step on the right). After that, the spike trains with and without this refractory period could be compared.

In Figure 7 you can see an example of a graph where are drawn two periodograms, calculated from the PSTH given by the model (either modified or not), for another stimulus as before, a pure tone which is not modulated.

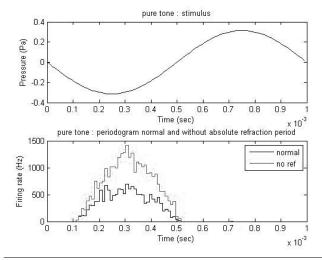


Figure 7. Periodogram with and without refractory period for the stimulus of period above

On the first graph, you can see one period of the stimulus, a 1 kHz pure tone, at 84dB. The second graphs shows you the periodogram with and without absolute refractory period. We can see phase-locking for the two periodograms, as expected for a pure tone. The simulation was done here with a medium SR nerve fiber, with 1 kHz characteristic frequency and 100 ms bin size. We will see now the results of the project.

4. Results

5. Conclusion

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