Representation of auditory signals by neuronal spike trains

Bachelor project report

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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, and the entrainment of response to the stimulus was better with refractory 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.

This project has for purpose to go further in the study of the effects of 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. In [Deger et al. 2010], point processes with refractoriness were studied and mathematical predictions were made for the Fourier coefficients of their response when the stimulus is a modulated pure tone. The second part of the project consisted on trying to see if the results on the model matches these predictions.

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).
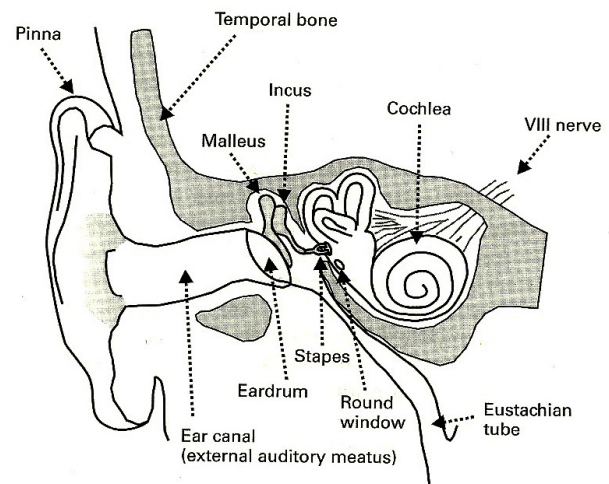

Figure 1. Peripheral auditory system ([Schnupp et al. 2011] p.52)
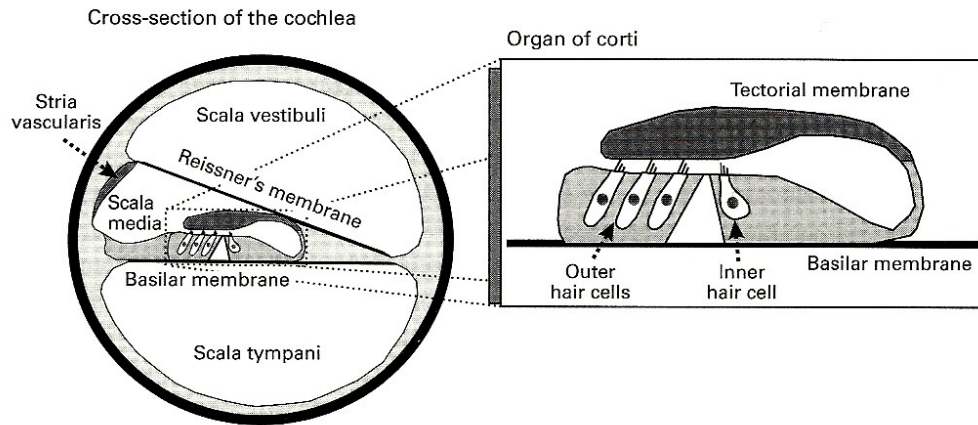
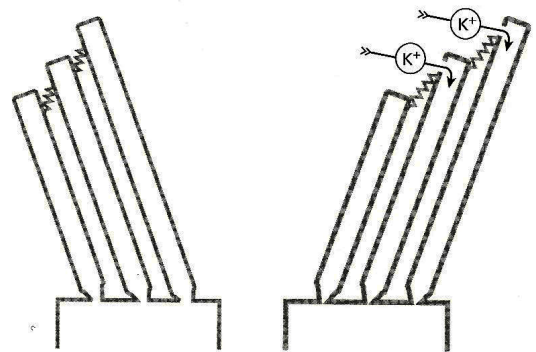**Figure 2.** Organ of Corti ([Schnupp et al. 2011] p.65)

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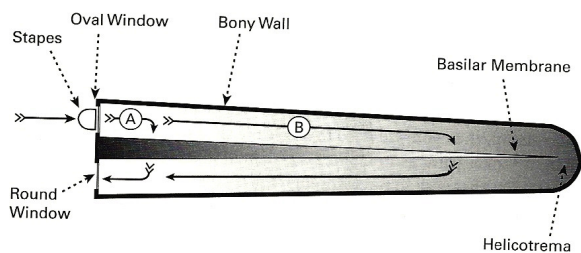
**Figure 3.** Unrolled cochlea ([Schnupp et al. 2011] p.55)

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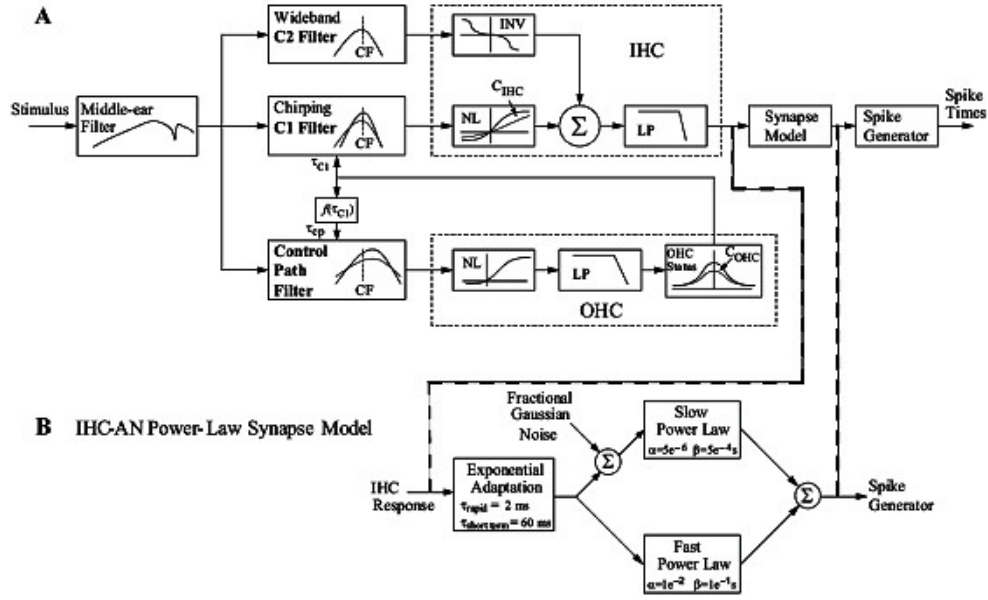
Figure 5. Schema of the model ([Zilany et al. 2009] their fig. 2)

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.

We will not go into the details of the model, but we 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 the power-law functions 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.
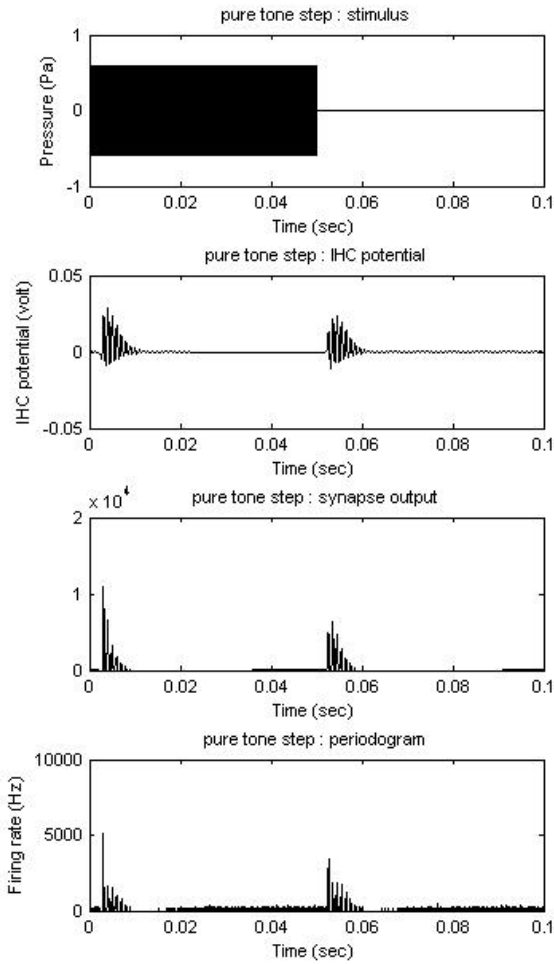
Figure 6. Example of model results ([Zilany et al. 2009])

The first graph is a representation of one period of the stimulus, sampled at 100'000 Hz (so with bins of 0.01 ms size), at 84dB SPL. 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 (ARP) 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.
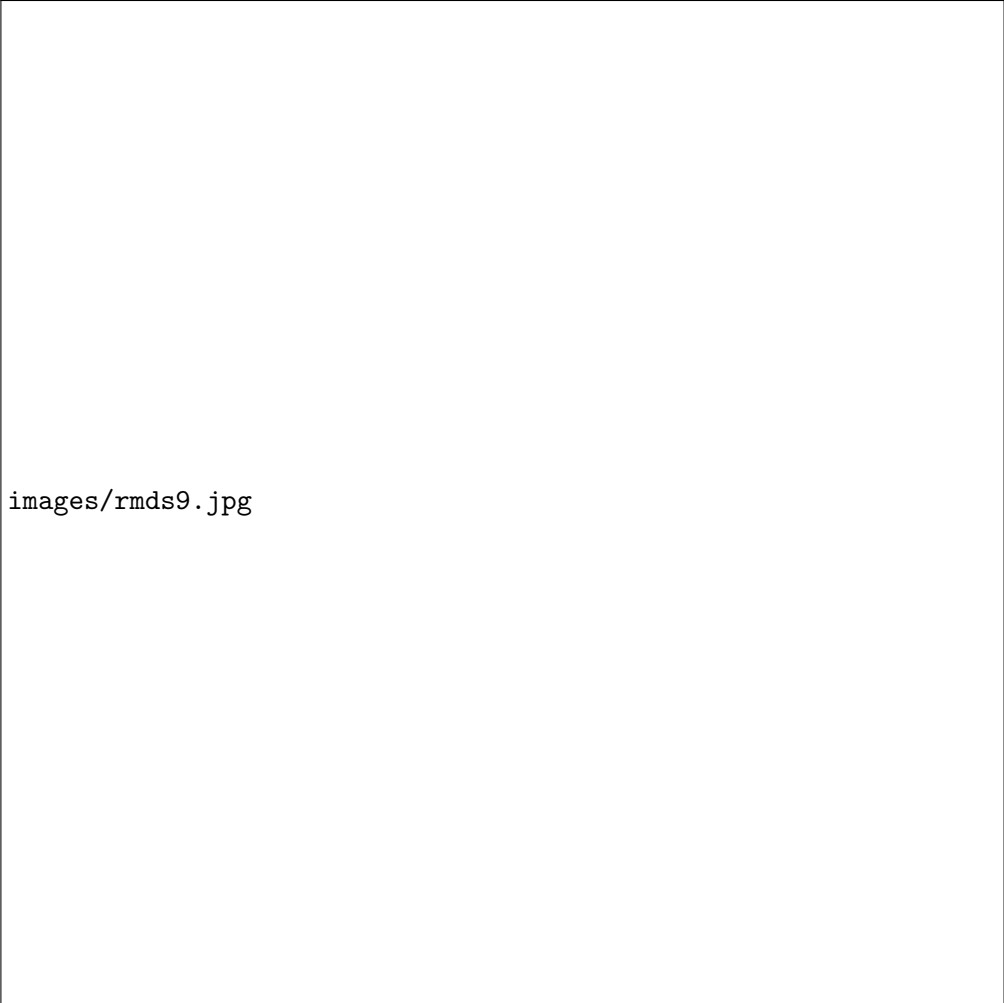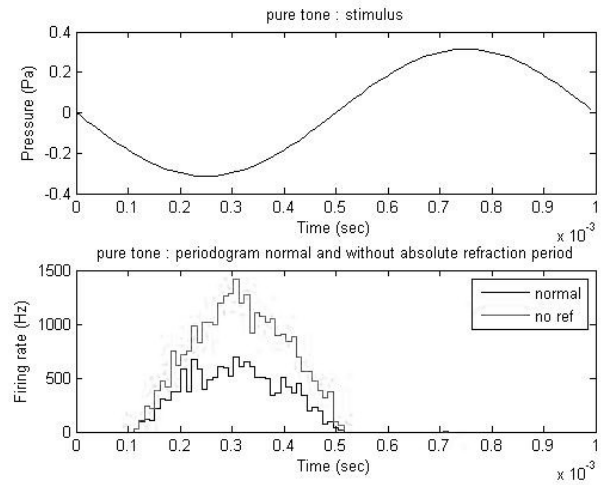

Figure 7. Periodogram with and without refractory period for the stimulus of period above

On the first graph, you can see one period of the stimulus, a 1 kHz pure tone, at 84dB SPL. The second graphs shows you the periodogram with and without absolute refractory period. We can see phase-locking for the two periodograms, so we see that the phase characteristics of nerve seems not to change when the refractory period changes. 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

4.1 Rate modulation depth

For the first part of the project, an ad-hoc calculation called rate modulation depth (RMD) was used to see difference between encoding of acoustic signal with and without absolute refractory period (ARP).

Figure 8. RMD values for different SR fibers and intensities

Four kinds of experiments where run and the means of RMD was calculated for each of them, with each type of nerve fiber, and three different intensities : 49dB SPL, 84dB SPL and 120dB SPL to have an overall view of effects. For every experience, the bin size was 0.01 ms, the characteristic frequency was 1 kHz, there was no damage on IHC or OHC, and we told the model to use approximations for power-law function calculations. No noise was added to the stimuli.

The four experiments were clicks, pure tones, noise steps and pure tone steps. The clicks were rarefaction clicks of 0.1 ms and sufficient time was waited between two of them to avoid influence from one to the other. The two steps stimuli had a period of 100 ms and in the first half of the period there was noise or pure tone signal, and in the second half there was 0 Pa as pressure. The noise for the noise step was composed of

random normal variables divided by the square root of the bin size (gaussian white noise). The pure tone of the pure tone step was of 10kHz frequency.

We computed then RMD like that :

$(max - baseline)/baseline$,

where max was the maximum of the periodogram of the encoded sounds when converted in 2 ms bins. The meaning of the baseline depended on the stimulus. For the clicks it corresponded to the response of a 0 Pa pressure signal, for the noise step it was the value of the periodogram just before the second half of the period, in 10 ms bins. The baseline for the pure tone step was the mean of value of periodogram of a response to a pure tone of the frequency used for the stimulus (10 kHz), after the IHC were saturated and have no time to be depolarized. It was seen in experiments that 0.02 ms were sufficient to attain saturation, so for the baseline

the first 0.02 ms were not used. For the pure tone, the baseline was chosen as the mean of the periodogram. When baselines for clicks and for pure tone step where computed, we took attention to the fact that the number of repetitions of stimulus for the used periodogram should correspond to the one for the periodogram used for calculating the maximum. It gives then an equivalent RMD as if we had divided each periodogram by their own number of repetitions.

As you can see on Figure 8, for each type of nerve fiber and each decibel value experimented we have similar values in this sense : for clicks, pure tone steps and noise steps, the RMD without absolute refractory period is bigger than the normal case, and it is the opposite for pure tones.

We probably can explain the first fact because first, we are in presence of a highly non-linear system and, secondly, the three stimuli for which the RMD without ARP is bigger than with ARP are stimuli with sudden changes. In fact, the click can be seen as an approximation of a delta function, and for the steps we have suddenly a signal for some time and suddenly, we have no more of it, and that repeatedly.

The second fact, the fact that RMD is lower for pure tones without ARP, corresponds to what can

4.2 Response according to frequencies of modulated pure tones

In [Deger et al. 2010], predictions are done for norm and angle of Fourier coefficients of response of processes with refractory period. In fact, the mathematical link between $1/d$, d being the absolute refractory period and the modulation frequency f is of first importance according to the predictions.

5. Conclusion

References

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