Autoreferát disertační práce

Modelování prostorového slyšení

Models of binaural hearing

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Contents

1 Abstract (in Czech language)

Disertační práce pojednává o modelu prostorového slyšení a srovnává ho s ostatními modely. Podle nejnovějších výsledků z experimentů na savcích hraje inhibice velkou roli v určení časového posunu signálu mezi levým a pravým uchem. Tento časový posun je pro nižší frekvence klíčem k určení směru, odkud zvuk přichází. Výsledky experimentů vedou k závěru, že prostorové slyšení savců pracuje na jiném principu než u ptáků. Dnes existuje několik teoretických prací, které se snaží tento jev vysvětlit, ale naprostá většina z nich je založena na mimořádně přesném časování v inhibiční části obvodu. Tento předpoklad je však odtržen od dosavadní znalosti fyziologie. Na druhé straně, modely popsané v disertační práci jsou založeny na faktu, že každý neuron reaguje na podráždění s jistým náhodným zpožděním. Pokud je tato vlastnost uvážena v obvodu, ve kterém se objevuje inhibice, zpoždění a detektor koincidence, pak lze ukázat, že výstupní frekvence obvodu odpovídá azimutu binaurálního zvuku na vstupu a současně experimentálně získaným datům. Modely jsou podepřeny analytickými výpočty a numerickými simulacemi zahrnujícími i kochleární implantát.

2 Abstract

In the thesis is presented stochastic model of binaural hearing in context of alternative models. According to latest experimental data on mammals, inhibition plays a role in interaural time difference recognition, which is a key for low frequency sound source localization. The output of experiments may lead to the conclusion, that the binaural hearing works differently in mammals compared to birds. Nowadays there are a few theoretical works addressing this new phenomena, but all of them are relaying on a very precise inhibition timing, which was never proved as physiological valid. On the other hand, models described in the thesis are based on the fact, that every neuron has a random delay when reacting to an excitation. If this time jitter is taken into account and combined with inhibitory signal, delay in the neuronal circuit and coincidence detection, than the output firing rate corresponds to the azimuth of the sound source. In the thesis it is shown, that such a neuronal circuits are giving the same output results compared to experimental data. The models are supported by analytical computations and numerical simulations including simulation of cochlear implant.

3 Introduction

To localize a lower frequency (below 1.5 kHz in humans) sound source, interaural phase difference is used in mammals. To recognize a difference of a few degrees in horizontal plane, the action potential timing precision of tens of microseconds must be used. This is very unique precision, which can't be observed in other parts of the neural system.

Jeffress suggested [Jeffress, 1948], that an array of delay lines with coincidence detectors is used to estimate the interaural time difference (ITD) of the two signals. But this array was never located in the mammalian brainstem. Also newer experiments [Brand et al., 2002] have shown, that inhibition is essential for sound localization in mammals and that there is no tuning to a specific delay as suggested by Jeffress. It seems more probably that the direction of the sound corresponds to output firing rate of the binaural coincidence detectors.

It is not yet clear, how the neural system in medial superior olive (MSO) works. It seems, that some of the published models [Brand et al., 2002], [Grothe, 2003] are expecting, that the inhibition part of the system works extremely fast. These models are omitting limitations like time jitter of the neuronal firing or neuronal refractory phase. But there is no physiological evidence of such extremely precise neurons. Our presented models are based on a different approach. We are aware of quite a lot of limitations of single neurons, yet we are also aware of the strength of massive parallelism in the sound system, which enables a statistical approach in this field.

4 Hypothesis and Goals of the Work

The task to estimate the time delay between two signals is very easy on the mathematical or physical level – it is a simple correlation of these two signals. But if we have specialized neurons as a building blocks for such computation, we have to consider very thoroughly all the properties of the neurons as duration of refractory phase, time jitter on the synapses and other limitations.

For example if the time jitter on the synapses is in the same range as the timing precision of the system, then we can't ignore it, when constructing the model. The massive parallelism in the sound system enables us to ignore single failures of a neuron in the system and to evaluate the output statistically. Whereas the parallelism of the sound system is a multilevel one at each stage of sound processing in the auditory pathway. Also for a pure tone, more neurons are excited and thanks to the periodicity of the sound waves, the evaluation can be done multiple times as well, according to the frequency of the sound.

We are addressing this issue and we construct our models according to it. This leads us to a statistically described models. Statistical properties of spike trains average out errors in individual spikes and enable to render neural computation of azimuth at the same time.

5   Materials and Methods

In the core of the model, which is equivalent to a part of mammalian brain stem we are using simple neural circuit operations:

- **coincidence detection** – which can be understood as an operation of the "and" binary logical gate

- **inhibition** – which can be understood as the "not" unary operation

- **delay** – since the speed of the information in the neuronal networks is not infinite

For generation of the signal in auditory nerve we are using:

- **model of a cochlear implant (CI) with SPEAK strategy program** – the incoming sound signal is processed using a bank of 20 filters with center frequencies between 250 Hz and 10 kHz. The strongest signals are selected and transformed to current pulses.

- **model of the transition from CI electrodes to auditory nerve** – based on the work of [Bruce et al., 1999], which studied the transition of the signal form a CI to the auditory nerve of a cat. His model is very precise and enables us with combination of a CI simulator to achieve very precise model of auditory system of a hearing impaired patient subject with CI.

- **leaky integrate and fire neurons.** – simple model of neuron which consists of resistor and capacitor and can be described with equation

$$i(t) = i_R + i_C = \frac{u(t)}{R} + C\frac{du}{dt}. \tag{1}$$

where $i(t)$ is input current, R is resistance and C capacitance of the membrane, $u(t)$ voltage on the membrane and t is time.

6 Results

We have constructed several models using components described in previous section. They mostly differ in complexity of processing of the input. All the output data from the models are well corresponding to the experimentally measured data of [Brand et al., 2002]. Wiring of such a model with cochlear implant is captured in Figure 1. This figure gives the schematic description, how the model works. An output of numerical simulation of this model is in Figure 2. It shows a typical dependence of the firing rate on the interaural delay.

A little simplified model which replaces the complex part of the transition from sound wave to a spike in the auditory nerve with simple detection of the entering edge of the sound signal can be analyzed analytically using Laplace transform.

The output form left respectively right inner hair cells is randomly shifted in time using the beta distribution

$$f(x) = \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} x^{\alpha-1}(1-x)^{\beta-1} \tag{2}$$

with parameters $\alpha_r = 2$ a $\beta_r = 4$ respectively $\alpha_l = 4$ a $\beta_l = 2$, $\Gamma()$ is the gamma function. Let us denote step jump in time t as $H(t)$ (Heaviside function), then we can describe the signal for left $(l(t))$ respectively right $(r(t))$ ear like

$$l(t) = H(t) \cdot H(1-t) \cdot 20t(1-t)^3 \tag{3}$$

$$r(t) = H(t) \cdot H(1-t) \cdot 20(1-t)t^3. \tag{4}$$

The probability of activity on output of the coincidence detectors for all possible delays is a convolution of these signals. We can use the property of Laplace transform and get the result of a convolution by reverse transform of the product of the equations (3) and (4). The output from this reverse transform is even for low integer values of input density parameters α and β a polynomial of higher degree with many coefficients, but when plotted, we are getting the same mono-phasic curve as in Figure 2.
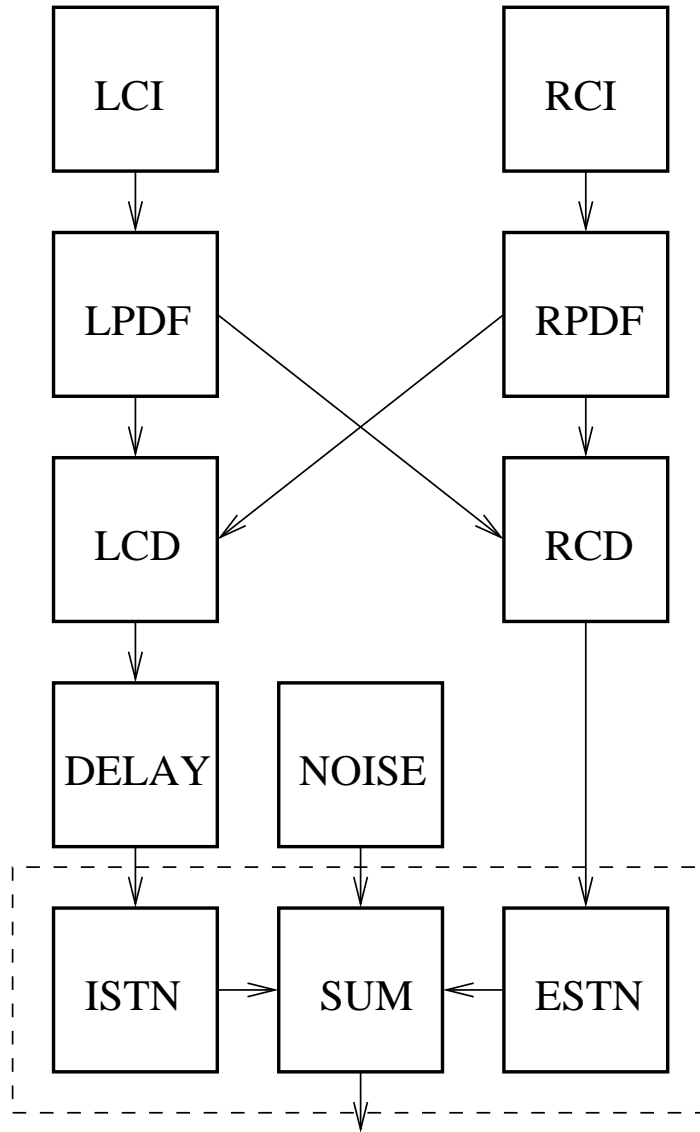
Figure 1: **Model circuitry**
L and R CI are left and right cochlear natural or cochlear implant inputs. L and R PDF are analogously left and right probability density functions of spike generation times. L and R CD are coincidence detector neurons. This is an analogue to the processing at the first binaural neuron. DELAY is the axonal conduction delay and is shown only for the inhibitory branch. I and E STN are inhibitory and excitatory synaptic transmissions, which are summed as the SUM of synaptic inputs together with NOISE. It can be shown that this circuitry is equivalent to the simplified wiring of the mammalian sound localization circuit, as described for example in [Grothe, 2003].
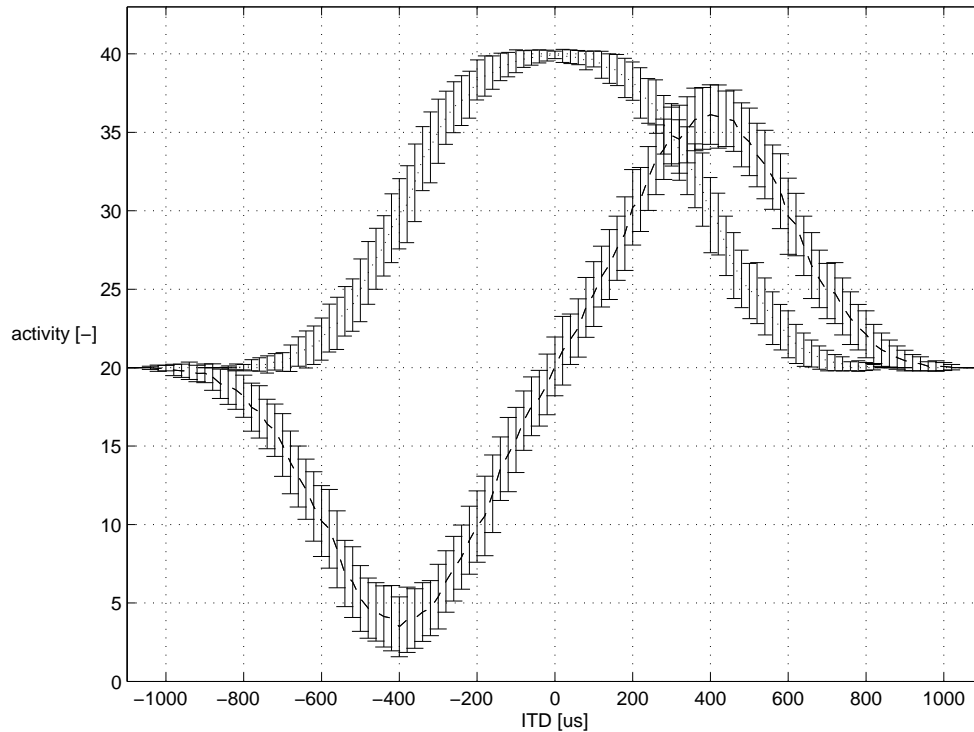
Figure 2: **Output of binaural model neuron**
The model neuron is connected to the whole CI simulation package. ITD is on the x-axis in microseconds. Neuronal output activity is plotted on the y-axis. The dashed bi-phasic curve is the output of the full model with both excitation and inhibition. The dotted mono-phasic curve is the model without inhibition. Only one period of the output is shown on this picture for clarity, but the output is periodic, hence the x-axes could be easily converted to the interaural phase difference. The error bars are sample standard deviations obtained numerically in simulations. In both curves they are the result of 100 trials. In other words, these error bars do not show the level of the noise in the system. Instead, the noise is introduced into the system via the randomness of the random variables and the magnitude of the timing jitter.

7 Discussion

Since there is no exact schematics how the auditory signal is processed in the brainstem, we are facing the "black box" problem. Presented models are trying to solve this issue using neurons with as most as possible of standard (physiological) properties. The wiring of our models is in agreement with known theory. All the design is hence subject of the known biological properties.

It may seem that the presented models are very sensitive to the tuning of their parameters like length of time window, type and parameters of the distribution and alike. But the contrary is true. All the presented models are very robust and give acceptable results in most of the variation of the parameters.

8 Conclusion

The models presented in the thesis were designed to be biologically valid, robust in all the parameters and, of course, complying with the experimental data. All these properties of the model were proven as valid. The use of an model of the CI is not purposeless. We would like to focus in this field more deeply, since it was shown for example in [Laback and Majdak, 2008], that the jitter introduced in the system influences the precision of the spatial hearing at patients with an CI.

References

[Brand et al., 2002] Brand, A., Behrend, O., Marquardt, T., McAlpine, D., and Grothe, B. (2002). Precise inhibition is essential for microsecond interaural time difference coding. *Nature*, 417(6888):543–547.

[Bruce et al., 1999] Bruce, I., Irlicht, L., White, M., O'Leary, S., Dynes, S., Javel, E., and Clark, G. (1999). A stochastic model of the electrically stimulated auditory nerve: Single-pulse response. *IEEE Transactions on Biomedical Engineering*, 46(6):617–629.

[Grothe, 2003] Grothe, B. (2003). New roles for synaptic inhibition in sound localization. *Nature Reviews Neuroscience*, 4(7):540–50.

[Jeffress, 1948] Jeffress, L. (1948). A place theory of sound localization. *Journal of Comparative & Physiological Psychology*, 41:35–39.

[Laback and Majdak, 2008] Laback, B. and Majdak, P. (2008). Binaural jitter improves interaural time-difference sensitivity of cochlear implantees at high pulse rates. *Proceedings of the National Academy of Sciences*, 105:814–817.

9 Publications of the candidate with co-authors

Publications with IF

[Drapal and Marsalek, 2010] Drapal, M. and Marsalek, P. (2010). Stochastic model shows how cochlear implants process azimuth in real auditory space. *The Chinese Journal of Physiology*, 53(6). In press. **IF(2008) = 0.698.**

[Drapal and Marsalek, 2011] Drapal, M. and Marsalek, P. (2011). Stochastic model explains role of excitation and inhibition in binaural sound localization in mammals. *Physiological Research*, 60(3). In press. **IF(2008) = 1.430.**

Another publications

[Marsalek and Drapal, 2007] Marsalek, P. and Drapal, M. (2007). Mechanisms of coincidence detection in the auditory brainstem: Examples. In Deutsch, A., Bravo de la Parra, R., de Boer, R., Diekmann, O., Jagers, P., Kisdi, E., Kretzschmar, M., Lansky, P., and Metz, H., editors, *Mathematical Modeling of Biological Systems*, volume 2, pages 255–264. Birkhaeuser.

[Drapal and Marsalek, 2008] Drapal, M. and Marsalek, P. (2008). Model prostorového slyšení. In Kelemen, J., Kvasnička, V., and Pstružina, K., editors, *Kognice a umělý život VIII*, pages 93–96. Slezská Univerzita v Opavě.

[Marsalek and Drapal, 2009] Marsalek, P. and Drapal, M. (2009). Neural coding in sound localization pathway, roles of timing jitter and random delay. *Neuronal Coding, 8th International Workshop*, pages 105–109.