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Modeling of Binaural Hearing

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The thesis will be available to public at least five working days prior to the defense at the Department of Research and Foreign Relations of the Dean's Office of the First Faculty of Medicine, Charles University in Prague.

Contents

Abstract

The central theme of this thesis is a description of information processing in the sound localization circuit of the auditory pathway. The focus is on principal neurons of the medial superior olive (MSO), the first major convergence point for binaural information. Selected properties and relations of MSO neurons are derived and expressed through models.

In the thesis we present three modeling studies. The first one clarifies a relationship between biophysical parameters of the MSO neuron and its ability to detect coincidental spikes from the left and the right ear. The second study describes the statistical behavior of spike trains on the input and output of the MSO neuron. In the third work, we studied how interaural coherence could guide localization of sound sources in complex listening situations with multiple sound sources in reverberant environments.

The main results are analytical and numerical models describing the aforementioned relations and behaviors. Secondary results include that inhibitory input to the MSO neuron narrows and shifts the time range of coincidence detection, that ergodic assumption from statistical physics and circular statistics are beneficial in the description of spike trains in the auditory pathway, and that interaural level difference of parts of the signal with high interaural coherence could explain human localization performance in complex listening scenarios.

Keywords

binaural hearing, binaural neuron, model, sound localization

Abstrakt

Ústředním tématem této práce je popis zpracování informace v lokalizačním obvodu sluchové dráhy. Důraz je kladen na první místo konvergence binaurální informace, neurony mediální olivy superior (MSO). Vybrané vlastnosti a vztahy neuronů MSO jsou odvozeny a vyjádřeny prostřednictvím modelů.

V disertační práci uvádíme tři modelovací studie. První objasňuje vztah mezi biofyzikálními parametry neuronu MSO a jeho schopností detekovat simultánní signály z levého a pravého ucha. Druhá studie popisuje statistické distribuce vzruchů na vstupu a výstupu neuronu MSO. Ve třetí práci jsme studovali roli interaurální koherence při lokalizaci ve složitých poslechových situacích s více zdroji zvuku v dozvukovém prostředí.

Hlavní výsledky jsou analytické a numerické modely popisující výše uvedené vztahy a chování. Aplikací modelů jsme získali sekundární výsledky: (1) inhibiční vstup do neuronu MSO zužuje a posunuje časový rozsah detekce simultánních signálů, (2) ergodický předpoklad ze statistické fyziky a cirkulární statistika jsou vhodné nástroje při popisu vzruchů v sluchové dráze a (3) hlasitostní rozdíl v části signálu s vysokou interaurální koherencí může vysvětlit přesnost lidské lokalizace ve složitých poslechových situacích.

Klíčová slova

binaurální slyšení, binaurální neuron, model, lokalizace zvuku

1. Introduction

A starting-point for the presented work is the model of binaural hearing developed by a group of people around prof. Marsalek over a period of around ten years (Marsalek and Kofranek, 2004; Marsalek and Lansky, 2005; Marsalek and Drapal, 2008; Sanda and Marsalek, 2012). The main focus of their study was the relationship between probability distributions of input and output spike trains, hence the model is named *"Probabilistic delay model"*. In this model, the principal neuron is reduced to a simple mathematical formulation — spikes are represented by point processes and the neuron detects coincidence if and only if spikes are closer in time than a certain constant (coincidence window). The category of models that do not deal with biophysical properties of neurons are also known as black-box models. Nowadays, there is an ongoing debate about how exactly principal neurons of the MSO are performing coincidence detection and which mechanisms are utilized to tune their function. Many extensive neurophysiological studies have been published recently trying to resolve these questions, but the issue is still not clear (McAlpine et al., 2001; Grothe, 2003; Pecka et al., 2008; Myoga et al., 2014; Franken et al., 2015). From this point of view, it is important to question whether a black-box model has support in recent neurophysiological findings.

Regarding data from psychoacoustic studies, *Probabilistic delay model* was compared to the Mills study (Mills, 1958; Marsalek and Lansky, 2005) to show that the model accounts for a dip in localization performance between low and high frequencies. Confrontation of the model with more complex psychoacoustic measurements including multiple speakers and reverberant environments (Kopco et al., 2010) showed that *Probabilistic delay model* alone is not able to explain localization with concurrent sound sources. A higher level model with the ability to separate cues from individual sound sources (Faller and Merimaa, 2004; Dietz et al., 2011) was needed to explain the results of Kopco et al. (2010).

The thesis is our original work consisting of three modeling studies. The first two extend *Probabilistic delay model* of the MSO neuron: The first one clarifies a relationship between biophysical parameters of the MSO neuron and its ability to detect coincidental spikes from the left and the right ear. The second study describes the statistical behavior of spike trains on the input and output of the MSO neuron. In the third work, we studied how interaural coherence could guide localization of sound sources in complex listening situations with multiple sound sources in reverberant environments.

2. Goals

In our study of information processing in the auditory system, we focus on the sound localization circuit as it shows remarkable computational properties. Based on previous work in the field, we formulated several questions grouped into three research projects:

Analytical description of coincidence detection. In the black box model developed by our research group (Marsalek and Kofranek, 2004; Marsalek and Lansky, 2005), MSO neuron acts as a coincidence detector that reports coincidence if and only if excitatory inputs from both sides are closer in time than a constant Δ, or, excitatory input follows inhibitory input in a time shorter than Δ. This constant forms a time window called a coincidence window. However, the nature of a coincidence window is more complex, as was shown by recent physiological studies that explored the role of inhibition in mammalian MSO (McAlpine et al., 2001; Grothe, 2003; Pecka et al., 2008) and its importance in tuning of coincidence detection (Myoga et al., 2014; Franken et al., 2015). The research questions were:

- What is the relationship between biophysical neuronal parameters and the size and position of the coincidence window?
- How can inhibitory input influence parameters of the coincidence window?

Ergodicity and statistical properties in auditory circuits. One of the characteristic traits of low-frequency auditory nerve fibers is the periodicity of spike trains: neuronal discharges are phase-locked, i.e. the probability of spike is a function of the sound phase. As we measure spike timing on an angular scale, it is beneficial to use circular statistics to describe the stochastic processes in the auditory pathway. Another characteristic trait of the auditory nerve is high redundancy, as a large number of neurons carry information about the same sound feature. It was shown that a large number of auditory neurons converging in a subsequent nucleus resulted in increased precision (Joris et al., 1994;

Marsalek et al., 1997). The precision in the auditory pathway also increases with a longer duration of stimulus. We borrowed the concept of ergodicity from statistical physics. It states that an average taken over a smaller set of units and longer time should equal to average of a larger set of units and shorter period of time. With the help of circular statistics and ergodicity concept, we ask:

- Can we calculate a vector strength of neural spike timing and spike train variability?
- How is the output spiking density of MSO neuron dependent on interaural time delay?

Sound localization in complex acoustic scenes. A psychoacoustical study showed that human localization is quite precise even in the presence of five concurrent talkers and reverberation (Kopco et al., 2010). In such complex environments, multiple sound waves reaching ears simultaneously result in unreliable binaural cues. One theory states that parts of the signal that are dominated by only one sound source have high interaural coherence. The auditory system thus can pick binaural cues from parts of the signal with high interaural coherence for precise localization of multiple sound sources (Faller and Merimaa, 2004; Dietz et al., 2011). Although a recent study claimed good results with the model based on interaural time difference (ITD) that utilized interaural coherence in complex scenes (Josupeit et al., 2016), it did not explore the contribution of interaural coherence per se. A clarification of the following is needed:

- Could models that select binaural cues based on interaural coherence explain the level of precision of human sound localization in complex acoustic scenes with several concurrent talkers and reverberation?
- Could interaural level differences be more reliable than interaural time differences in complex acoustic scenes?

3. Methods and models

To describe the relationship between biophysical neuronal parameters and the coincidence window, we used a simplified version of the formal biological neuron model called the Spike response model Gerstner and Kistler (2002). The model is formulated using linear summations of the membrane potential responses on synaptic inputs and does not use differential equations for the description of the course of the neuronal membrane potential. Postsynaptic potential was modeled as a subtraction of two exponentials. We created two models, excitatory model (ECD) having one excitatory input from each side and inhibitory model (ICD) with one additional contralateral inhibitory input.

The analytical description of the relationship between neuron parameters and the coincidence window was constructed through analyzing the local extremes of summed postsynaptic potentials. A numerical approach was used to explore the coincidence detection outside the restricted range of parameters posed by our assumptions and inherent limitations of the Spike response model. The coincidence window size was determined by evaluating the model equation across the range of parameters and ITDs and subsequently comparing this to the action potential threshold.

A formula for vector strengths of spike trains was derived for spike trains approximated with the circular beta distribution and a compound distribution that was a mixture of uniform and sine distribution.

The output spike density of MSO neuron dependent on the time delay between the right and left side was based on a difference of the two random variables. The resulting probability density function was calculated as a convolution of probability densities of random variables. The operation of convolution was used under the ergodic assumption and the assumption that the resulting spikes form a renewal process, meaning that all the interspike intervals have the same probability distribution, and all are mutually independent.

Complex acoustic scenes were modeled by convolving speech samples with binaural room impulse responses measured in a slightly reverberant room. Auditory model utilized a gammatone filterbank to model the frequency analysis of the basilar membrane followed by envelope filtering, rectification and low-pass filtration. The binaural processor that computed interaural time differences, interaural level differences and interaural correlation was implemented as in Faller and Merimaa (2004). Only interaural time differences (ITD) and interaural level differences (ILD) of bins with interaural coherence (IC) higher than the threshold were selected for azimuth estimation. Target cues were distinguished by a binary target mask that marked time-frequency bins in which the target was expected to have some minimal energy. We developed another model that searches for a target in the temporal domain of both the left and right signals and estimates target sound source location from ITD as a difference of target timing between the left and the right signal. Modeling work was realized in MATLAB with the AM toolbox.

Four types of model were tested: 1. low-frequency (LF) ITD only IC-based model with an ideal target mask, 2. high-frequency (HF) ILD only IC-based model with an ideal target mask, 3. HF ILD only IC-based model with a generalized target mask, 4. target-search based model. The first three models were tested for a range of IC threshold settings.

In each simulated trial, speech samples were presented from a subset of eleven evenly spaced loudspeakers ($-50°$ to $50°$ with $10°$ separation). Target sound could be presented from any of the loudspeakers, and maskers were arranged in one of five possible patterns. Maskers were presented either at the same level as the target or 5 dB louder, yielding target-to-masker ratio (TMR) of 0 dB, or, respectively, TMR of -5 dB. The target word was word "two" uttered by one of the female voices. Masker words were four different randomly drawn nondigit words spoken by four different male voices. Fifty different combinations of masker words were generated ensuring that individual variability in masker words combinations would not bias overall behavior.

4. Results

We have developed the analytical relations that determine the two boundaries and the center of the coincidence window as a function of the relative threshold of a neuron with given membrane time constant and the time constant of postsynaptic membrane conductance exponential decay function (Fig. 4.1). Numerical model was used to retrieve values outside of the domains of analytical relations.

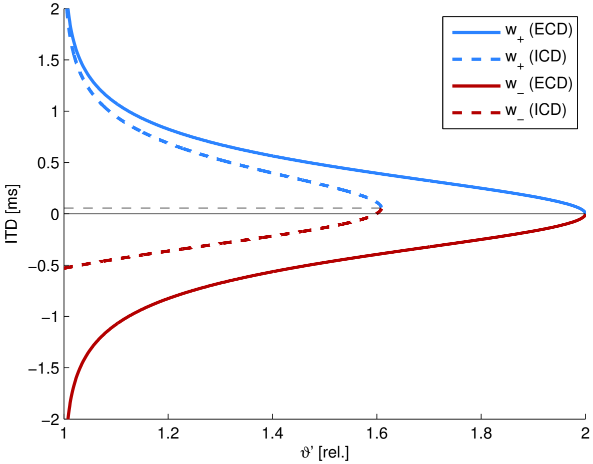

Figure 4.1: Analytical functions determine the boundaries (upper shown in blue, lower shown in red) of coincidence windows for the given relative threshold and neuron parameters. ECD model is shown by thick solid lines and ICD model is shown by thick dashed lines

We derived vector strength of spike trains distributed according to the circular beta distribution with the lowest natural number non-trivial parameters $a = b = 2$ and according to the compound uniform and sine distribution.

For the output of MSO neuron, we derived the probability density function of the interspike intervals (ISIs) dependent on the time delay between the right and left side. We showed main characteristics of the resulting probability density function and coefficient of variation and vector strength of output spike trains.

Simulations of sound localization in complex acoustic scenes revealed that high-frequency ILD model has significantly lower errors than low-frequency ITD model or target-search based ITD model (average root-mean-square errors re. control at IC = 0.98 are around 5° (TMR 0) and around 9° (TMR -5) for HF ILD model, versus 27° (TMR 0) and 32° (TMR -5) for LF ITD model; target-search-based ITD model had errors of 9° (TMR 0) and 17° (TMR -5)). For HF ILD model, errors were lower with higher IC threshold, although very high IC thresholds led to significant failure rates (Fig. 4.2)). The performance of HF ILD model is comparable to that of human subjects.

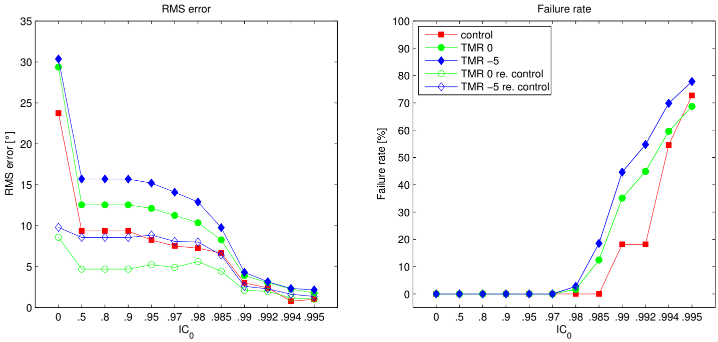

Figure 4.2: Root-mean-square error (left column) and failure rate (right column) of high-frequency ILD model with generalized target mask as a function of IC threshold. Control runs are plotted with red squares, TMR 0 masker runs are plotted with green circles, and TMR -5 masker runs are plotted with blue diamonds. For masker runs, absolute errors are plotted with full marks and errors relative to control run are plotted with empty marks.

5. Discussion

The Spike Response Model was chosen after the consideration of specific properties of the MSO neuron and its function as a coincidence detector. The simplicity of the model allowed us to derive analytical relations for a restricted set of parameters. The most restrictive was the fixed ratio of time constants. Numerical simulations showed that the ratio of time constants has an influence on the coincidence window, but the general results obtained with analytical relation have universal relevance regardless of the specific ratio of time constants.

One of the aims of this study was to explore the role of inhibition in MSO neurons and validate an asymmetric rule for coincidence detection in the probabilistic delay model. Our results showed that inhibitory input narrows and shifts the coincidence window. However, the possible values of these effects are limited and some relations, for example, as in the asymmetric rule for coincidence detection, where inhibition halves and shifts the whole coincidence window to positive values, are excluded.

In our computations we sought a simple description of spike trains following a sound phase. The candidate functions were circular beta and a weighted sum of uniform and sine functions. For the beta distribution we showed derived vector strength only for parameters $a = b = 2$. For any given natural a and b, vector strength can be expressed with the use of hyper-geometric function, however, a formula for all arbitrary values of a and b does not exist. When we use compound density, a weighted sum of uniform and of sine density, we arrive at an arbitrary value of vector strength.

The output spike density of the MSO neuron was calculated under the assumption that spikes are mutually independent and have the same probability distribution. This demonstrates the concept of ergodicity - under this assumption, the readout from one MSO neuron over the time should be equal to the readout of population of MSO neurons.

Simulations revealed that the IC-based model failed in our complex localization task using low frequency ITD cues. This is in accordance with original papers presenting models, showing there was a possibility to localize two sound sources in a reverberant environment with some error (Faller and Merimaa, 2004) and concluding that localization of more sound sources in a reverberant room was not possible (Dietz et al., 2011). Josupeit et al. (2016) used an IC-based model using low frequency ITD cues for the same localization task and reported good results for TMR 0 condition. However, they combined the IC-based model with target masks that ensured certain minimal instantaneous target-to-masker ratio, meaning that target masks alone selected time-frequency bins having the target as a dominant sound source. In our study we explored the ability of the IC-model to select bins having one dominant sound source from a set of all target bins independent of instantaneous target-to-masker ratio.

IC-based model using high frequency ILD cues showed surprisingly good performance, comparable to that of humans. The precision of localization increased monotonically with IC threshold for control run and masker runs. RMSE of masker runs relative to control run shows the contribution of maskers presence to degradation of localization performance. ILD localization has very low values of RMSE re. control for any IC threshold setting compared to ITD localization, suggesting that the level of masking is much lower at high frequencies than at low frequencies. Moreover, RMSE re. control is relatively constant up to $\mathrm{IC}_0 = 0.98$ suggesting that for $\mathrm{IC}_0 \leq 0.98$ all the improvement in localization is based on target echo suppression.

6. Conclusion

We have presented three modeling studies of binaural hearing.

The first study describes a relationship between biophysical parameters of the MSO neuron and its ability to detect coincidental spikes from the left and the right ear. The most important of these parameters are membrane time constants, conductance decay constants, relative action potential threshold, and relative synaptic strengths. Analytical relation enables better understanding of possible parametrizations of coincidence windows for neurons with known biophysical properties. Comparison of coincidence windows of neurons with excitatory and inhibitory inputs and of neurons with excitatory inputs only shows the major impact of inhibition on the duration and position of the coincidence window. The presence of inhibitory inputs results in a shift of the coincidence window outside the axis of symmetry of ITD and in shortening its duration. Precise value of the threshold potential relative to the EPSP size is essential for a narrow coincidence window. This is achieved also by adjusting the strength of the inhibitory input.

The second study presents models of output spiking densities of the MSO neuron and provides formulas for vector strengths for various density functions of spike trains.

In the third study we model localization of sound sources in complex listening situations with multiple sound sources in a reverberant environment. We conclude that: highly correlated parts of the signal, if available, provide reliable ILD estimates sufficient for precise target localization comparable to that of human subjects; low frequency ITD cues of highly correlated parts of the signal alone are not sufficient to explain human performance; and localization based on ITD is possible in combination with accurate target template.

7. Souhrn

Představili jsme tři modelovací studie binaurálního slyšení. První studie popisuje vztah mezi biofyzikálními parametry neuronu MSO a jeho schopností detekovat simultánní signály z levého a pravého ucha. Nejdůležitější z těchto parametrů jsou membránové časové konstanty, konstanty poklesu vodivosti, prahová hodnota relativního akčního potenciálu a relativní synaptické síly. Analytický vztah umožňuje lepší pochopení možných parametrizací koincidenčních oken pro neurony se známými biofyzikálními vlastnostmi. Srovnání koincidenčních oken neuronů s excitačními a inhibičními vstupy a neurony s pouze excitačními vstupy ukazuje zásadní vliv inhibice na trvání a polohu koincidenčního okna. Přítomnost inhibičních vstupů má za následek posun koincidenčního okna mimo osu symetrie ITD a zkrácení doby jeho trvání. Přesná hodnota prahu vzhledem k velikosti EPSP je nezbytná pro úzké koincidenční okno. Toho se dosáhne také úpravou síly inhibičního vstupu.

Druhá studie představuje modely pravděpodobnostní hustoty výstupního neuronu MSO a poskytuje vztahy pro vektorovou sílu pro různé pravděpodobnostní rozdělení vzruchů.

Ve třetí studii jsme modelovali lokalizaci zdrojů zvuku ve složitých poslechových situacích s více zdroji zvuku v dozvukovém prostředí. Došli jsme k závěru, že: vysoce korelované části signálu, pokud jsou k dispozici, poskytují spolehlivé odhady ILD dostatečné pro přesnou lokalizaci srovnatelnou s lidskými subjekty; nízkofrekvenční ITD klíče vysoce korelovaných částí signálu samy o sobě nestačí k vysvětlení lidského výkonu; a lokalizace založená na ITD je možná v kombinaci s přesnou cílovou šablonou.

8. List of publications

List of publications related to the thesis:

Toth, P., and Marsalek, P. (2015). Analytical description of coincidence detection synaptic mechanisms in the auditory pathway. *Biosystems*, 136: 90-98.
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List of publications not related to the thesis:

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