Sound localization with a model of the medial superior olive

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Introduction

The human auditory system extracts both spectral and temporal features of sound signals, which might be the reason why it still outperforms automatic speech recognition systems in adverse acoustic conditions. In the auditory nerve, rate-place coding transmits spectral features of sound, while fine-grained temporal information (e.g. due to phase locking) is captured by precise timing of the nerve-action potentials. During the last decades, we [1] and others (e.g. [3]) have developed and evaluated auditory models, which provide realistic spike trains of the auditory nerve for arbitrary stimuli (see our review [10]). We can now apply these models to study (temporal) processing in the neuronal auditory pathway by connecting them with model neurons and whole neuronal networks. In this report, we focus on a model of the medial superior olive (MSO), which plays an important role in sound localization.

Modeling the medial superior olive

The MSO is thought to be the first nucleus at which interaural time difference (ITD) information is extracted from the sound arriving at both ears (compare Figure 2). ITD-rate functions of gerbils show a maximal firing rate for ITDs outside the physiological range (compare Figure 2, blue line), suggesting that the slope of the coding function, and not its maximum, is used to decode ITDs. The shift is thought to be caused by inhibitory inputs, as blocking these inputs removes the shift and places the best ITD at 0 ms [4].
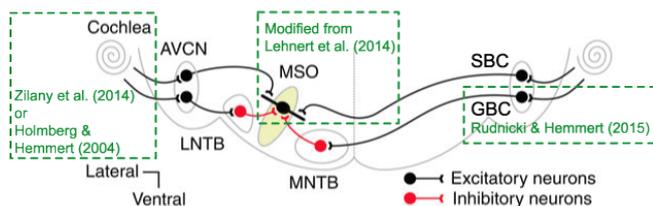

Figure 1: Schematic drawing (modified from [7] of the major stages of the MSO circuit. Our current model included a model of the complete auditory periphery [3] as well as the GBC model developed by [11]. Models for SBCs, LNTB and MNTB were not yet included.

We started to create a Hodgkin-Huxley type neuron model of the gerbils' MSO circuit. The MSO neuron is modeled using the ion channels from [6]. It is directly excited by ipsi- and contralateral auditory nerve fibers [3], bilateral inhibition originates from our GBC model. While previous models required ultra-fast inhibition (e.g. [4]), our preliminary model reproduced a ITD-rate function including the reported shift in maximum firing rate

using only realistic excitatory and inhibitory time constants.

As a starting point for our modeling approach, we apply our recently developed "cochlea" framework [2], which provides a uniform interface to a collection of inner ear models that are easily accessible as Python functions [10]. Here we used auditory nerve spike trains from the Zilany-Carney model [3]. It provides a realistic source of jitter to the excitatory and inhibitory inputs of the MSO. While we currently neglect SBCs in the excitatory input, the GBCs in our model introduce a considerable increase in synchrony in the inhibitory pathway. This increased synchrony seems to be necessary to achieve the shift in best ITD as we were not able to reproduce a large shift in best ITD without GBCs in the inhibitory path. On the other hand, when we improved the synchrony in the excitatory path, we could not achieve such a large improvement in (physiological) ITD shift. This finding is somewhat surprising but also very interesting because it shows that high temporal precision in the inhibitory pathway seems to be more important than in the excitatory pathway. The brainstem contains two identical versions of the MSO circuit, one in each hemisphere. As the time difference seen by these two circuits is sign inverted, we gain two outputs which are symmetric (see Figure 2). Day and Delgutte [5] have evaluated monaural and binaural schemes to decode the ITD (or the position of the sound source). The simplest but also the most precise method is to calculate the difference in firing rate between the two sides (see Figure 3). This approach removes sound level dependent changes in the output firing rate and provides a linearized output. It is interesting to notice that already a simple subtraction of the output of the two MSO circuits can convert ultra-small ITDs into a rate code, which is easy to relay to higher neuronal stages even with "slow" neurons. Whereas the conversion of ITDs into a rate code per se is not debated, the exact mechanisms still need to be elucidated [5].

Whereas the precision of ITD decoding is impressive, it is also fragile and requires precise tuning [7, 8, 9] conducted experiments with acutely, long-term and congenitally deaf cats. In these experiments the auditory nerve was stimulated with bilateral cochlear implants. ITD coding was most severely degraded in congenitally deaf cats, where the number of ITD sensitive neurons in the inferior colliculus was significantly decreased. In long-term deafened cats the best ITDs were broadly distributed around midline, where in normal hearing animals the distribution was more focused and biased toward contralateral leading ITDs. This finding indicates that the underlying neuronal circuit has lost its fine tuning.
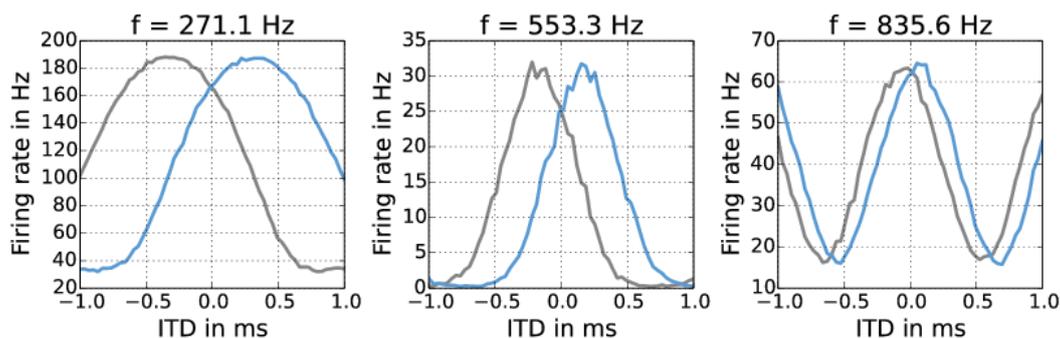
Figure 2: The MSO firing rate plotted as a function of ITD for both ears result in two nearly identical curves. Both are shifted in the direction of the respective contra-lateral leading direction.
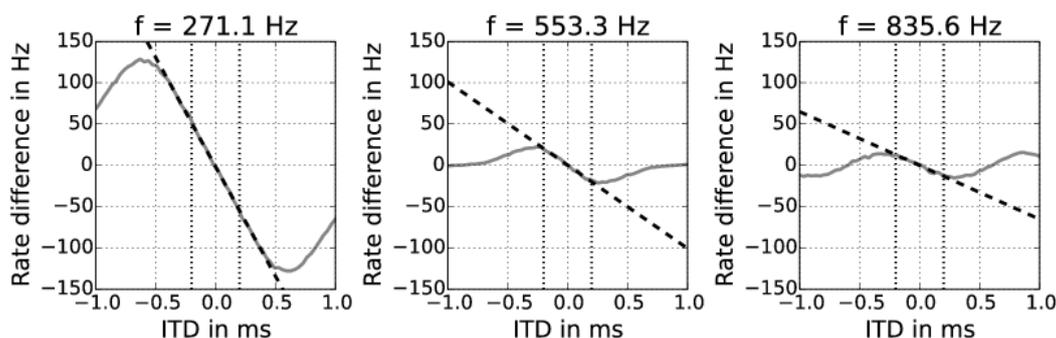

Figure 3: Already a simple subtraction of left and right MSO neurons' firing rates accomplishes an almost linear encoding of ITDs into a rate code.

Acknowledgements

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