

Jitter Effect on the Performance of the Sound Localization Model of Medial Superior Olive Neural Circuit

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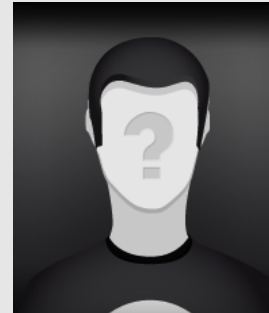
Abstract

Objectives: Additional properties of the stochastic neural circuit model suggested in [1] were studied.

Methods: The performance of the whole circuit when the system employs a different jitter was studied by extensive simulations. By performance we mean the time needed to obtain a reliable estimate of ITD.

Results: It was found that the relation between jitter and performance is nonlinear and we estimated a plausible range of jitter values for the model.

Conclusion: To conclude, there exists an upper bound of the timing jitter since the number of neurons needed to compensate the injected noise grows exponentially and above certain jitter values becomes unrealistically high.



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Keywords

Medial superior olive (MSO), stochastic model, timing jitter, interaural time difference (ITD)

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EJBI 2011; 7(1):51–54

received: September 10, 2011

accepted: October 31, 2011

published: November 20, 2011

1 Introduction

The way mammalian brain localizes sound azimuth remains a matter of discussion. The current textbook view is based on the theory of delay lines proposed a long time ago by [2].

Although there is a strong experimental evidence that delay lines implemented by the branching pattern of neuronal fibers are present in the Nucleus Laminaris in birds [3], experimental evidence for such branching pattern in the Medial Superior Olive (MSO - counterpart of bird's NL) in mammals remain weak [4] and alternative theories have been proposed [5].

In a specific variant of the slope-encoding model [6] proposed in [1] the interaural time difference (ITD) is encoded by the firing rate of the first binaural neuron. This

rate is driven by coincidence detection of the action potentials coming from time locked ipsi- and contralateral inputs shifted by ITD and additional jitter added to the system. Under certain conditions each ITD value corresponds to a unique value of the firing rate, thus the imaginary observer monitoring output of such a neuron is able to estimate ITD only by interpolation from its firing rate.

The role of noise in this model is ambiguous. On the one hand it allows a finer distribution of recognized ITD values, on the other hand higher values deteriorate the estimation performance of the circuit.

This performance decline was indicated in [1] for two circuits with different jitter. The aim of this report is to extend the previous result and show quantitatively how jitter affects performance of the whole range of circuits defined by different jitter values.

2 Methods

The circuit operates at an abstract level of description without explicit membrane potential regarding spikes as single time point events and consists of several consecutive processing stages (see Fig. 1):

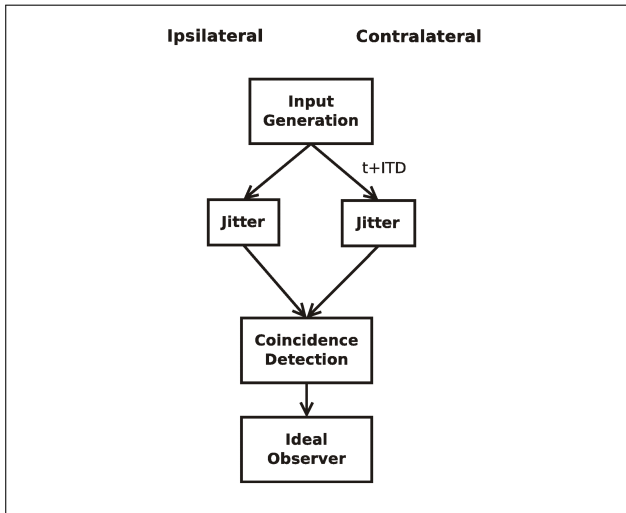


Figure 1: Scheme of successive processing stages of the circuit.

- A generator of action potentials simulates time-locked inputs, impulses from the contralateral side are shifted in time by ITD value. The frequency of generation is set to 140 Hz as in the previous study.
- A jitter generator which represents noise occurring in the circuit during the signal transmission along the auditory pathway. It is parametrized by a single value. It should be noted that each different parameter value defines a different circuit since it changes the characteristic ITD *interpolation curve* used for interpolation. Together with the spike generator they can be considered as a very simplified counterpart to the auditory pathway up to the MSO (where the signal from the left and right ear used for sound localization based on low sound frequencies converges). In this stage each spike is shifted in time by small random jitter Δ which is parametrized by jitter magnitude J , more precisely $\Delta = J(B(2,4) - 0.5)$, where $B(a,b)$ is a random variable from the beta distribution with parameters a, b .
- A coincidence detector representing the first binocular neuron. It generates a new spike only in case two input spikes occur within a short time window and in a specific order when contralateral spike precedes the ipsilateral one.
- An observer which collects output of the previous processing stages and estimates the ITD value computed by the circuit. It can be seen as a counterpart of higher processing stages which measure how much

information can, in principle, be obtained from the rate coded presented by a single binocular neuron.

Details of the stages above are identical to those in [1] except for one important feature. Fixed parameters of the circuit define the ITD interpolation curve as seen in Fig. 2. In our previous study this curve was carefully fitted to a fixed sinusoidal function and the inverse of this function was used to interpolate ITD from estimated firing rate.

In Fig. 2 we can see how jitter J dramatically changes this curve. Since we will use the whole range of different jitter values we cannot rely on the fitted function anymore and we shall use directly this interpolation curve. Conceptually, this is not adding anything new, however, it leads to additional computational difficulties - for each jitter value a circuit ITD curve must be recomputed anew and an inverse mapping from firing rate to ITD must use a more elaborate interpolation mechanism since the curve is not locally strictly monotonous.

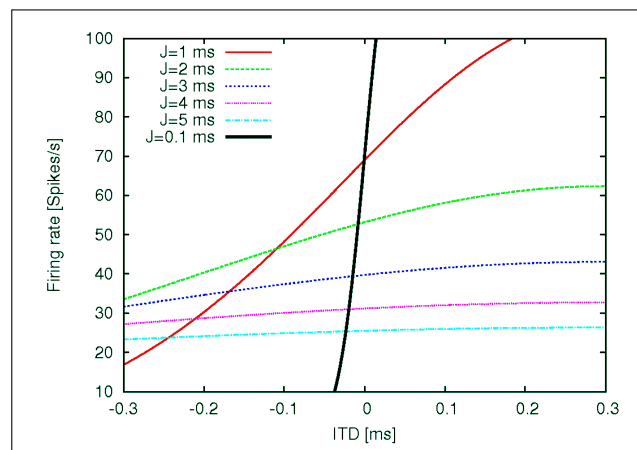


Figure 2: ITD interpolation curves for circuits with a different jitter value. Each firing rate value corresponds to an ITD value and is uniquely determined in case the function is strictly increasing in the ITD values under scrutiny. We see that increasing jitter leads to smaller slopes of the interpolation curve and we expect a deteriorated circuit performance for higher jitter values.

3 Results

Each jitter value defines a new circuit and after computing its interpolation curve we let the circuit estimate a single ITD value while observing how the estimate develops in time. This way we obtain asymptotic behaviour for each circuit, see Fig. 3.

From psychophysical experiments we know that the precision of azimuth estimation in a human is approximately 4° in the head-on direction [7]. We define that the time needed for reliable estimation of ITD is identical with the last-passage-time (LPT) of the 4° precision region, see the area delineated by horizontal dotted lines in Fig. 3.

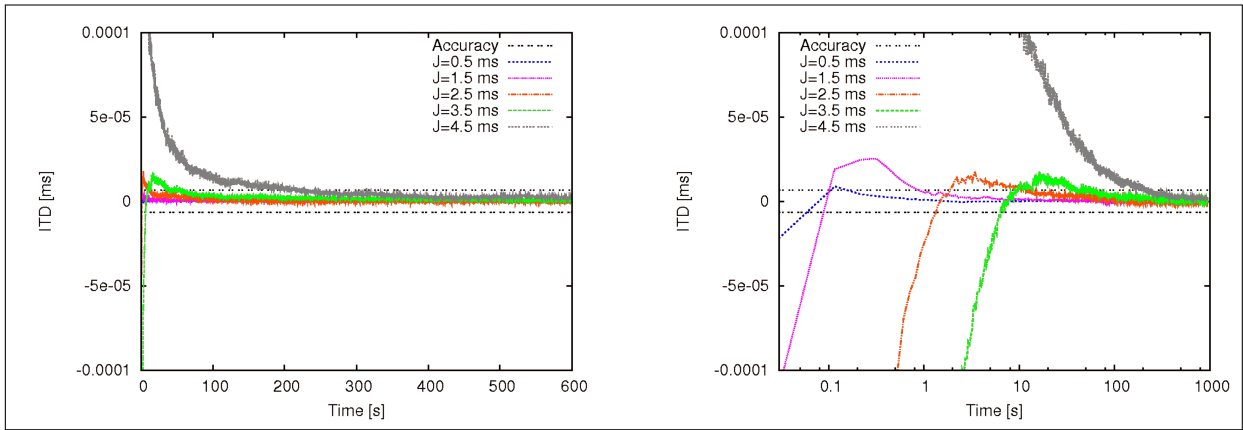


Figure 3: Asymptotic behaviour of ITD estimation produced by observer for selected values of jitter J . The original azimuth was selected as $ITD = 0$. Horizontal lines delineate the region when desired precision of ITD estimate was achieved ($\pm 2^\circ$). For each line we can define the last passage time (LPT) when the function enters the region and remains inside of it. We see that increasing jitter leads to the increase of LPT value. Each line is an averaged function from 1000 simulation runs.

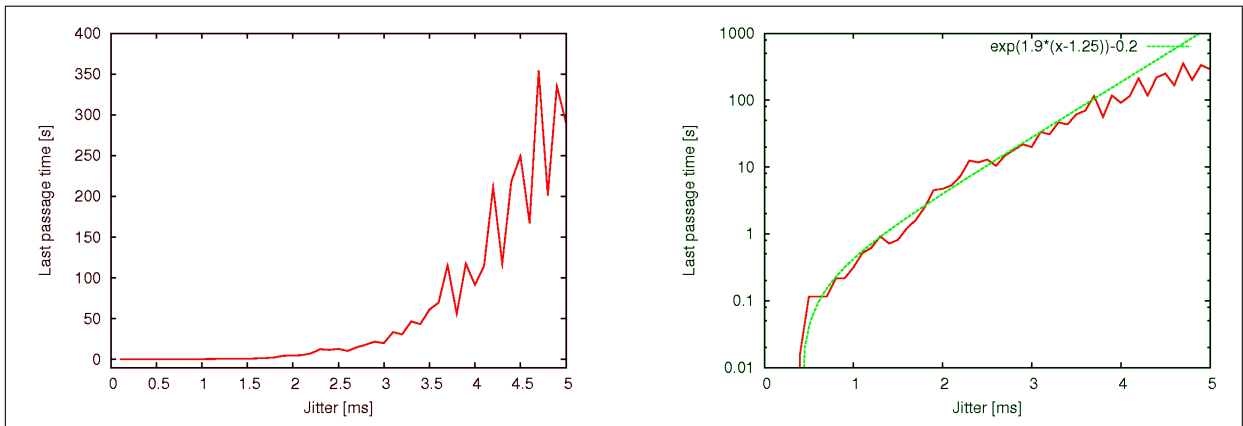


Figure 4: Dependence of last-passage-times on different jitter values. On the right hand side the same plot in logarithmic scale. We fit $f_{fit}(x)$ in such a way to be as close as possible in the interval of 0.1 - 10 s of LPT. This will be subsequently used for relating plausible jitter ranges, see text.

In this way we obtain unique LPT for each circuit with specific jitter value, as plotted in Fig. 4. As we can see, the functional dependence is nonlinear and can be approximately fitted by $f_{fit}(x) = e^{1.9(x-1.25)} - 0.2$.

Obtained circuit's LPT time t_A corresponds to the processing time of a single binaural neuron in MSO needed to estimate ITD. Because the auditory pathway consists of many parallel fibers and processing of the signal is simultaneous, we used the ergodic hypothesis in our previous study.

In short, we assume that when a single neuron of this type requires the time t_A , n neurons working in parallel need the time t_A/n to produce equivalent information subsequently used in higher stages of the pathway (represented by the concept of the observer).

The number of binaural neurons working in parallel is difficult to estimate but does not exceed hundreds of units. Next, we know from psychophysical experiments that the time t_A needed for azimuth estimation ranges around 150 - 300 ms in human subjects [8].

This allows us at least to connect specific jitter value J with the required number of neurons n in order to obtain t_A (let us fix $t_A = 0.2$ s). By employing the ergodic hypothesis we get $t_A = \frac{LPT(J)}{n}$ and from fitting $f_{fit}(J)LPT(J)$, hence

$$n = \frac{f_{fit}(J)}{t_A} = \frac{e^{1.9(J-1.25)} - 0.2}{0.2}. \quad (1)$$

To sum up, we obtain that the physiologically plausible range of simultaneously working neurons $n \in [1; 100]$ corresponds to jitter range $J \in [0.7; 2.8]$, which also implies plausible jitter values for the canonical set of parameters of this model.

4 Discussion

Irregularities in spike timings observed in physiological recordings were originally thought to be the result of neuronal cells unreliability and it was assumed that the

firing-rate neural coding scheme is used because of its robustness against the noise present in neuronal activity. Later decades have shown that what was often considered as erratic behaviour was rather a misunderstanding of the transmitted code [9] and it turned out that neurons are capable of reliable and precise spike timing [10] needed for so-called temporal coding. Coincidence detection of precisely timed input spikes is an important concept in theories of binaural hearing and we suggested one variant of such a model in a stochastic neural circuit in [1].

This time we focused specifically on the role of jitter. In the previous study the jitter parameter was fixed to $J = 1$ ms which is in a good agreement with experimental findings [11]. Here we took a further step and estimated a range of possible values based on circuit performance. We should, however, note that this analysis is bound to the canonical set of basic circuit parameters. For example, the spike generator frequency also has an impact on the overall performance of the circuit; in the previous study we employed a more detailed model of the auditory periphery [12] and we could observe a decrease of overall performance of the circuit. This result cannot be, however, so easily incorporated since one processing stage (bushy cells layer) is missing. There are indications that this layer is able to provide better time locking and consequently improve coincidence detection in binaural neurons — that can be another example of a somewhat unexpected observation that higher processing stages of neural circuitry increase the accuracy of phase locking [13].

Another problematic point is that the number of parallel circuits employed in ITD estimation is not experimentally known. This parallelism would have a strong impact on the overall performance as well, and we have at least shown the correspondence between jitter and the required number of neurons (or vice versa). By employing the ergodic hypothesis we can conclude that due to (1) the number of neurons needed to compensate the injected noise grows exponentially and above certain jitter values becomes unrealistically high. This gives us an approximate upper bound of jitter allowed for this type of circuit.

Acknowledgments

The work was supported by the grant SVV-2011-262 514 of Charles University in Prague.

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