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A dendritic model of coincidence detection in the avian brainstem☆

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Abstract

We have constructed a detailed biophysical model of coincidence detector neurons in the nucleus laminaris (auditory brainstem) which are purported to detect interaural time differences (ITDs). In the model, ITD coding is improved when the inputs from both ears are located on the bipolar dendrites and segregated, over having both inputs on the soma: the model behaves like the in vivo coincidence detectors. The model has enabled us to explore features of the coincidence detector neurons unexplained by a simpler biophysical model (Agmon-Snir et al., Nature 393 (1998) 262–272), including the effect of synapse location and multiple dendrites.

Keywords: Nucleus laminaris; Dendrite; Coincidence

1. Introduction

Neural coincidence detection is essential in sound localization, which (for frequencies below a few kHz) requires the computation of interaural time differences (ITDs). This task is performed by binaural cells in the avian nucleus laminaris (NL), and its mammalian homologue, the medial superior olive (MSO).

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A "coincidence detector" neuron should fire when inputs from two independent neural sources coincide (or almost coincide), but not when two inputs from the same source (almost) coincide. A neuron that sums its inputs linearly would not be able to distinguish between these scenarios. Segregating the inputs on separate dendrites should avoid this problem: post-synaptic depolarization from a synaptic event is reduced if the dendrite is already partially depolarized. This idea was used by Agmon-Snir et al. [1] to model bipolar dendrites as interaural coincidence detectors in NL. This is a more biophysical model of the same system.

The model emulates a single neuron with an axon, soma, and a variable number of dendrites, each with a variable number of equipotential compartments. All geometric, electrical, and channel parameters are adjustable, as are the number of synapses/dendrite (~ 30), the synaptic locations, and the distribution of synaptic locations. Channel types include potassium (high- and low-voltage activated [Kv1.1, 1.2], and delayed rectifier), sodium, and passive. The values used for all the tunable parameters are in agreement with those in the literature [2–6]. The stimulus is a pure tone of adjustable frequency, with variable binaural phase difference (or contralateral monaural stimulus with variable ipsilateral spontaneous activity). More complex stimuli can be easily introduced.

The synapses fire with conductance proportional to an alpha-function, with adjustable time constant, peak conductance, and reversal potential. The synapses fire as individual Poisson processes, with probability rate given by the half-wave rectified sinusoidal input, with adjustable amplitude and base spontaneous firing rate. The fast Kv 3.1 channels of the pre-synaptic neurons are incorporated in a short synaptic time constant.

The implementation is constructed within the NEURON [7] environment and has a graphical user interface for controlling the parameters and running the model. NEURON allows for a real-time display of data and analysis including the potential at various locations, the two stimuli, the synaptic firings, spike counters, period histograms of synaptic firings and the action potentials, and their vector strengths.

2. Potential curves and period stimulus histograms

Fig. 1 shows typical time plots for a pair of cells each receiving the same stimulus probability distributions (with frequency 500 Hz), with the top cell receiving its inputs binaurally in-phase, and the bottom out-of-phase. The black curve tracks the intracellular potential at soma/axon boundary and the nearby light grapy curve at the axon tip. Below these curves are a pair of curves of the presynaptic probability distribution. The bottom eight curves of each graph show synaptic currents (note the Poisson distributed spread of arrival times).

Fig. 2 shows the same pair of cells tracked for 250 ms of the same stimulus. The vector strength (VS), a measure of phase locking, ranges between 0 and 100%. The cell receiving in-phase stimulus has enhanced its VS relative to its input; the out-of-phase cell has substantially reduced it. Note also the number of spikes in each case: the output spike rate in the out-of-phase case is substantially reduced (this demonstrates

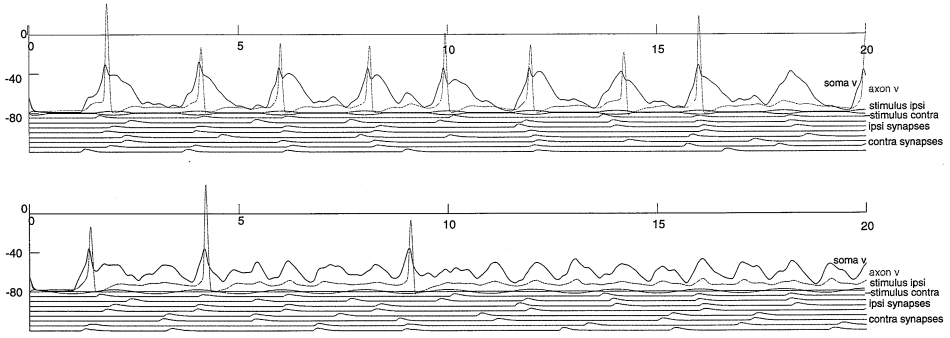

Fig. 1.

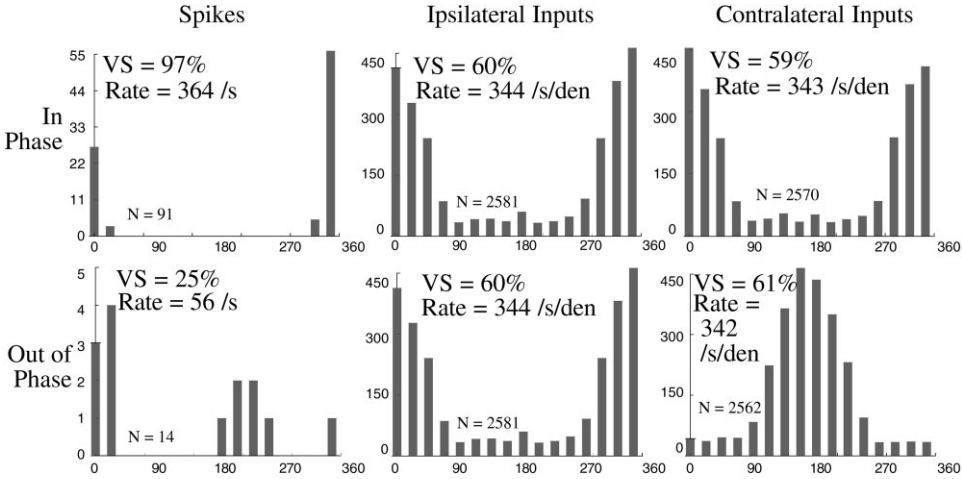

Fig. 2.

that the VS is not a good measure of phase-locking for low spike rates, because it is much more susceptible to noise – the extreme case of a single spike, even if at a random time, give a VS of 100%).

3. Results

Only a small volume of parameter space for this model is biologically relevant, but due to a relative paucity of experimental data, it is not obvious where the relevant subspace lies. Some parameters are known to have values that fall in a particular range, and different parameters, with respective ranges, may be correlated or not. Some parameters may be particularly relevant for certain species but not for others

(e.g. the barn owl can detect ITDs up to 8 kHz, whereas the chicken can detect only up to 2 kHz).

To limit the search, we usually compare the performance of a pair of identical cells receiving identical stimuli, with one set of stimuli in-phase and the other out-of phase. Then we pick "reasonable" values for all parameters, vary the dendritic length, compare firing rates and observe the VS of the in-phase case. Fig. 3 plots the results for 1 kHz stimulus. The output rate of the in-phase case is clearly always higher than the out-of-phase case. The VS of the in-phase case is very close to 100% for all but the longest dendrites.

In the avian NL, the dendritic length varies (roughly) inversely with the best frequency of the cell. By directly covarying the stimulus frequency with the dendritic length, we can attempt to capture a central subspace of the entire parameter space. Covarying the stimulus frequency with the dendritic length gives us a curve that is relatively flat, but by covarying one additional parameter, the maximum dendritic conductance of the high-voltage activated potassium channel (K_{HVA}), we can get a rate curve that matches the nominal rate quite closely (at least at 250 Hz and above). This is justified since the effect of higher K_{HVA} conductance is qualitatively similar to the effect of adding (shunting) inhibition from a feedback loop, and this model does not yet include inhibition. The upper graph of Fig. 4 plots the same values as Fig. 3, but in the case that stimulus frequency is covaried with dendritic length (by a simple inverse relationship) and with K_{HVA} conductance, according to the relationship plotted in the lower graph in Fig. 4.

Typically the synapses might be uniformly distributed along the dendrite. The effect of moving all synapses to the centre of the dendrite is relatively small: the in-phase rate is moderately reduced, worsening at large dendrites/low frequencies. The ratio of in-phase rate to out-of-phase rate remains large in the same range. One might have expected the cell to perform better with all the synapses together, to reduce jitter from the differing travel times of the signals to the soma, but the dendrites are (electronically) relatively compact.

We also varied the location of the "concentrated" synapses. With all synapses at the base, the coincidence detector performs poorly for large dendrites/low frequencies,

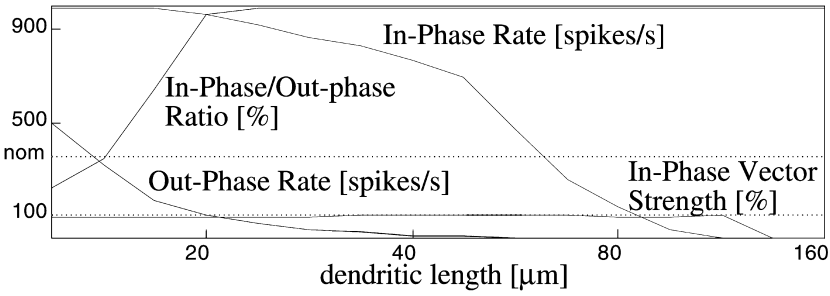

Fig. 3.

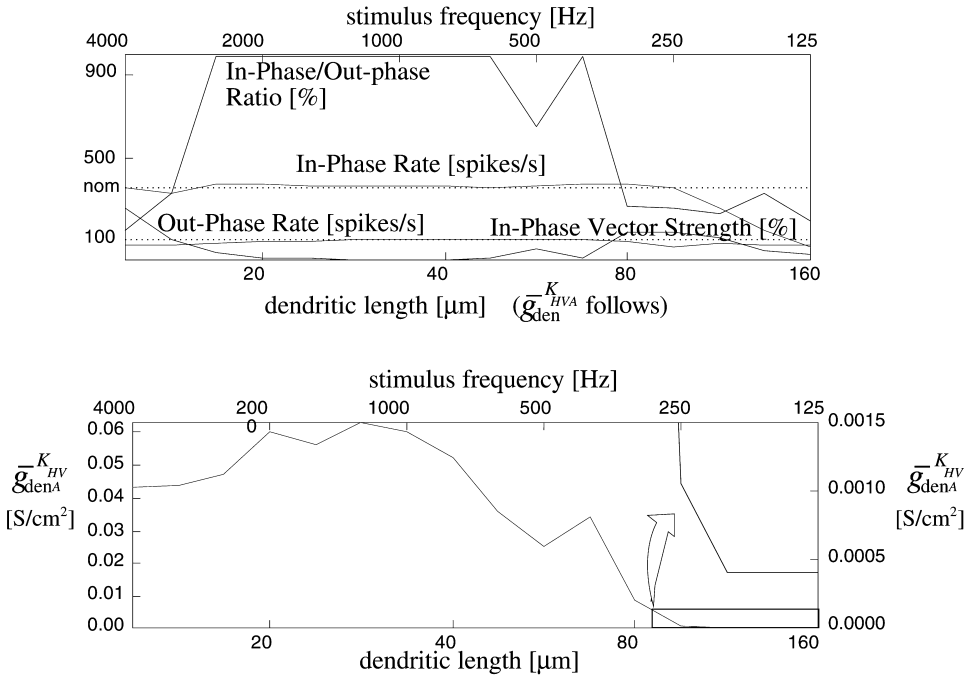

Fig. 4.

giving many false positive. The advantage of inputs adding sublinearly in the dendrites (which are much smaller compartments than the soma) is lost.

The benefit of sub-linear addition of the synaptic inputs can also be seen by varying the synaptic reversal potential. When the reversal potential is artificially raised, the sub-linear addition of the inputs is suppressed, and the coincidence detectors become effective over a smaller range of frequencies/lengths.

This model supports the claim that dendrites are aiding in neural computation. How well does it perform compared to the same model without dendrites? In the previous trials, where the synapses are located at the dendrite/soma boundary, the performance is compromised, but the dendrites are still present and can still act as current sinks, which can increase coincidence detection ability. When the dendrites are removed, the firing rates rise dramatically, but they do so for both the in-phase and out-of-phase cases. The ratio of the rates is near 1, however, indicating poor discrimination.

Coincidence detection is robust against varying the number of synapses/dendrite from 20 to 40. Real NL Neurons vary in dendritic diameter from 2 to 4 mm. Changing the model's dendritic diameter from 4 to 2 μm decreases the input impedance to the synaptic current and increases the electrotonic length (it also decreases the transmission coefficient from the dendrite to the soma, but this is negligible here). Since it increases the firing rate in both the in-phase and out-of-phase cases, the decrease input impedance outweighs than the electrotonic lengthening.

In this model, the input VS is determined by the spontaneous activity. When there is no spontaneous activity, the stimulus probability function is proportional to a half-wave rectified sinusoid, giving VS = $\pi/4 \approx 79\%$. Our nominal spontaneous activity gives VS $\approx 60\%$, and saturating spontaneous activity gives VS = 0%. In the chick NL, VS varies from the above 90% at the lowest frequencies, decreasing to below 50% above 1 kHz, and losing all phase-locking by 2 kHz. The model is robust against increasing the spontaneous activity (and so decreasing the VS of the inputs), but there is a decreased in-phase firing rate at the highest frequencies/shortest dendrites. This explains why the model above outperforms the chick at high frequencies.

The NL contains arrays of coincidence detectors tuned to a wide range of phase differences, more than just 0° and 180° presented above. Fig. 5 shows responses to a 360° range of phase difference. The firing rate and VS are both strong functions of phase difference, but the firing rate is more sharply tuned (and the VS is not reliable at low rates).

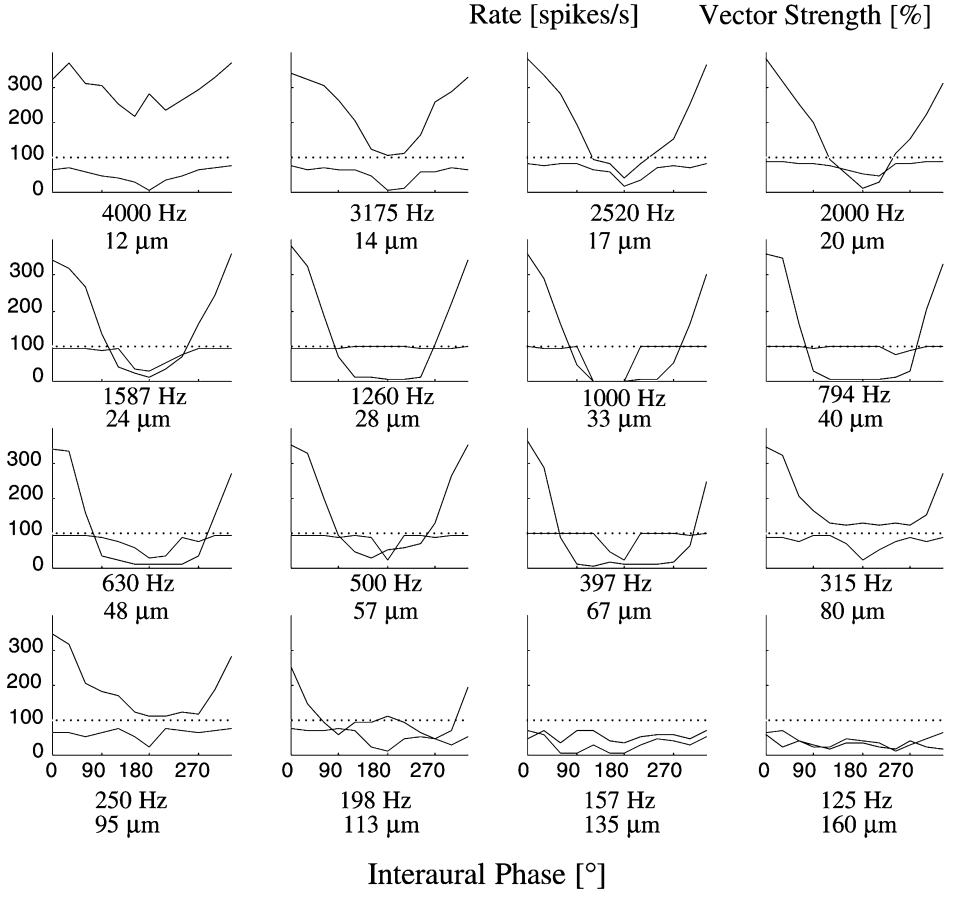

Fig. 5.

Real NL neurons also respond to periodic stimuli presented only in one ear. Presumably this is due to coincidence detection between the monaural stimulus one side and the spontaneous activity on the other side. The model cell locks well to this monaural input, with a VS of near 100% for a broad range of inputs, though its firing rate is well below the nominal best rate for binaural input.

4. Conclusions

The model has parameter ranges that give behavior corresponding to the behavior of real NL neurons. The dendrites aid in the ability of the cell to perform coincidence detection, especially from sublinear addition and dendritic current sinks. The high-voltage activation potassium channels are important for coincidence detection at high frequencies. Coincidence detection is robust against the number of incoming synapses. The model predicts that vector strength is very robust (at fast firing rates), but is not as sharply tuned as firing rate as a function of phase difference. The model locks well to monaural stimulus.

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