Temporal envelope coding in the inferior colliculus.
Evaluation of two computational models of octopus cells

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Introduction

Temporal envelope, also referred as amplitude modulation (AM), is a common feature of sounds like speech, and plays an important role in intelligibility. Its encoding takes place from the inner ear to the auditory cortex: in this area, Temporal Modulation Transfer Functions (TMTF) show strong responses to AM frequencies below approximately 64 Hz [1]. In this communication, we focus on the early processing of AM by examining two computational models of octopus cells in the inferior colliculus, known to be involved in the AM coding. These cells, characterized by onset responses, are respectively based on i) the McGregor point neuron equations, ii) ion concentration gradient and Nernst equation.

Auditory chain

The evaluation is conducted using a global auditory model of AM encoding, simulating processes taking place from the inner ear, then conveyed by the cochlear nucleus (CN), to converge towards the inferior colliculus (IC).

Inner ear

The model of the inner ear is composed of the basilar membrane (BM) modelled by Gammatone filters [2], the inner hair cells (IHC) whose responses are given by Meddis equations [3], and the auditory nerve (AN) whose fibers' discharges follow a geometric law.

Cochlear nucleus

In contrary to the monotype response of the auditory nerve, there are many different responses observed in the CN. Frisina et al. [4] observed that stellate cells in the ventral CN (VCN), characterized by a sustained chopper response, are entrained by specific AM frequencies referred as their best modulation frequency (BMF). Hence, we modelled the VCN as a bank of stellate cells with same or different BMF (see section "Coincidence detection" for details). Chopper responses are provided by Hodgkin-Huxley equations with three ionic channels. The different BMFs were generated by modifying the permeability time constant of the membrane to potassium ions (polarization).

Inferior Colliculus

This nucleus highly participates in the temporal envelope encoding by enhancing the synchronization to the AM frequency. The implicated neurons detect coincident activity in the afferences from CN cells. To mimic the behavior of these neurons, called octopus cells and characterized by short membrane time constant, we used two different models:

- the McGregor point neuron, with one single voltage controlled ionic channel, and a fixed threshold,
- a model proposed by Meyer et al. [5], based on 2 ionic channels: the depolarization one is neurotransmitter controlled, the polarization one is voltage controlled. The opening of the ionic channels modifies the ion concentrations, from which is deduced the potential using Nernst equation.

Coincidence detection

Octopus cells have numerous synaptic connections, ensuring their ability in detecting coherent activity in their inputs. The question is: what sort of afferences receive the IC neurons to increase the synchronization? We investigate two structures referenced in the literature:

1. the choppers of the VCN have same BMFs (with different auditory nerve fibers afferences),
2. the choppers, whose BMFs vary in the interval $[90-300]$ Hz, are grouped together in three subsets according to their BMF ($[90-160]$ Hz, $[160-230]$ Hz and $[230-300]$ Hz), each one converging to a different octopus cell (same characteristics). The detection is achieved by a fourth onset neuron connected to the three previous ones. By limiting the BMF variability among each subset - and so the delays of the choppers responses due to the different time constants - this structure ensures that these responses remain synchronized at the stimulus onset.

Results

The responses of the neurons -choppers and onsets- are characterized by their *mean discharge rate* (spiking rate or SR) indicating the mean activity, and the *modulation gain* (MG) indicating the synchronization of the action potentials on the modulation frequency.

In the VCN, the chopper cells are characterized by a band-pass profile, with a strong synchronization at a given modulation frequency which corresponds to their BMF (see fig.1, top box), whereas their mean activity is almost constant (fig.1 bottom box), whatever the modulation frequency is. Note that the BMFs given in the fig. 1 caption do not exactly correspond to the mean spiking rates.

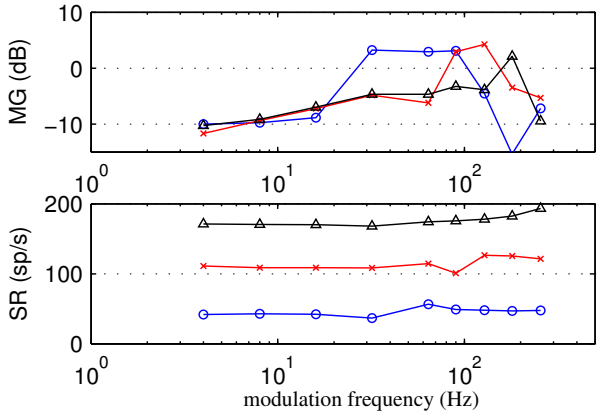

Figure 1: Modulation gain (top box) and mean spiking rate (bottom box) as a function of the modulation frequency, observed for chopper cells with three different BMFs: 60 Hz (circle), 150 Hz (cross) and 250 Hz (triangle).

Concerning the responses observed in the IC, the onset neurons, with the same BMF choppers as inputs, exhibit the same behavior as cells of the VCN (see fig. 2): they discharge at a constant rate, whatever the modulation frequency is and exhibit a band-pass profile in terms of modulation gain. Note however that the Meyer model tends to synchronize at low frequencies yielding a roughly low-pass profile for high BMF choppers inputs (see fig. 2.b, triangle marker curve). This is due to the different membrane time constants used for the two onset neurons.

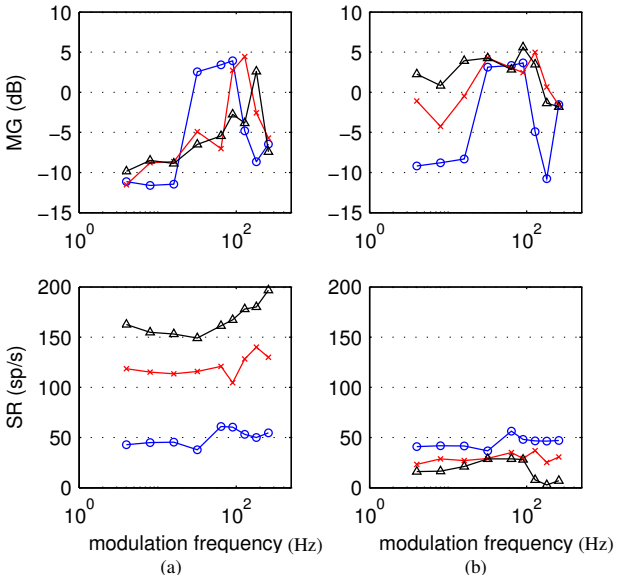

Figure 2: Modulation gain (top boxes) and mean spiking rate (bottom boxes) observed for (a) McGregor neuron, (b) Meyer neuron, for chopper inputs with same BMF: 60 Hz (circle), 150 Hz (cross) and 250 Hz (triangle).

The results concerning the second structure (choppers with different BMFs) are depicted on fig. 3. As observed for *in vivo* cells, the overall synchronization is greatly increased, even though the octopus cells characteristics are identical: the modulation gain remains close to its optimal value (6dB), whatever the modulation frequency is, depicting a quasi low-pass profile. Moreover, the two neurons show an enhanced activity around a particular modulation frequency: about 64 Hz for the McGregor neuron (fig. 3.a), 30 Hz for the Meyer neuron (fig. 3.b). The difference in the two activity regions is once more due to the membrane time constants.

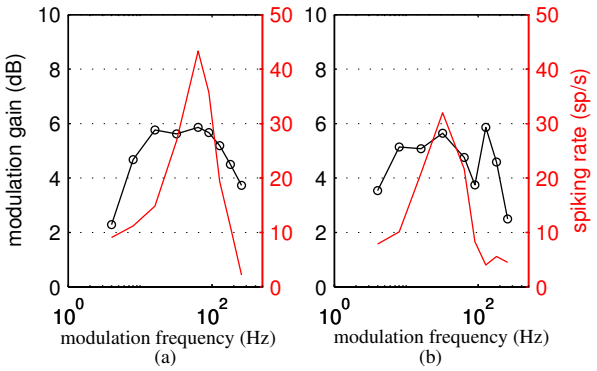

Figure 3: Modulation gain (circle) and mean spiking rate (no marker) observed for (a) McGregor neuron, (b) Meyer neuron, for chopper inputs with different BMFs.

Conclusion

Two models of octopus cells of the IC have been associated to two structures of the VCN. Simulations show that the hypothesis of same BMF choppers in the VCN leads to high variability in the synchronization observed in the IC: the results depend on the onset model as well as parameters (time constant). On the contrary, the VCN structure with different BMFs yields comparable results in terms or synchronization and spiking rate, for the two onset neurons. Moreover, this behavior corresponds to those observed *in vivo*. This tends to affirm that the variability confirms the robustness of the AM coding.

References

[1] N. F. Viemeister, "Temporal modulation transfer functions based upon modulation thresholds", *Journal of Acoustical Society of America*, **66**, no. 5, (1979), 1364-1380.

[2] R. Patterson et al., "Complex sounds and auditory images", in *Auditory Physiology and Perception*, K. H. Y. Cazals, L. Demany, Ed., Oxford (1992), 429-446.

[3] R. Meddis, "Simulation of mechanical to neural transduction in the auditory receptor", *Journal of Acoustical Society of America*, **79** (1986), 702-711.

[4] R. D. Frisina, R. L. Smith, and S. C. Chamberlain, "Encoding of amplitude modulation in the gerbil cochlear nucleus: I. A hierarchy of enhancement", *Hearing Research*, **44**, no. 2-3 (1990), 99-122.

[5] G. Meyer et al., "A computational model of the auditory nerve and cochlear nucleus", in *Fourth European Simulation Multiconference*, Nuremburg, Germany (1990), 573-578.