

A competition between tonotopic neural ensembles underlies pitch-related dynamics of the auditory evoked fields

Alejandro Tabas, Bournemouth University, atabas@bournemouth.ac.uk

André Rupp, Universität Heidelberg

Emili Balaguer-Ballester, Bournemouth University, BCCN Mannheim

Auditory evoked fields observed in MEG experiments systematically present a negative transient known as the N100m, elicited around 100 ms after the tone onset in the antero-lateral Heschl's Gyrus. The exact N100m's latency is correlated with the perceived pitch of a wide range of stimulus (e.g. [3]), indicating that the transient reflects the processing of pitch in auditory cortex. However, the neurophysiological substrate of this relationship remains an enigma. Preceding models of pitch, focused on perceptual phenomena, failed to disclose the mechanism generating cortical evoked fields during pitch processing in sufficient biophysical detail. In this work, we introduce a cortical model of pitch describing, for the first time to our knowledge, how cortical pitch processing gives rise to observed neural responses and why its latency strongly correlates with pitch.

The thalamic input is generated by a delay-and-multiply procedure based on the the principles of the autocorrelation models [2]. A realistic model of the auditory peripheral system is used to to simulate the auditory nerve activity, which is phase-locked to the waveform of the sound and preserves the periodicities contained in the stimuli. A set of $N = 200$ chopper neurons in the ventral cochlear nucleus systematically delay the auditory nerve input by N different lags δt_n , which are compared with the original auditory nerve activity by an array of coincidence detector units in the inferior colliculus. The coincidence detector n spikes when the characteristic delay δt_n is a multiple of a periodicity present in the sound [1]. Coincidence detectors activation is leaky-integrated by thalamic ensembles and forwarded to the cortical model. The typical thalamic activity pattern elicited by a sound with a periodicity T presents peaks of activation in the channels characterising $\delta_n t = kT, k \in 1, 2, \dots$.

The cortical model transforms these harmonic thalamic patterns into tonotopic receptive-field-like representations. Each cortical functional block is characterised by a best period $\delta_n t$ and consist of pyramidal excitatory cells and inhibitory interneurons. Blocks interact with each other through local AMPA and NMDA -driven excitation and GABA-driven selective inhibition [4]. Excitatory and inhibitory ensembles $H_n^{e,i}(t)$ were modelled using mean-field approximations; AMPA/GABA and NMDA dynamics were modelled as leaky integrators with instantaneous and slow rising times, respectively [4]. Values of the parameters were taken from the literature [4] and slightly tuned within the biophysical range in order to achieve a suitable e/i balance. The neuromagnetic fields elicited by the cortical dynamics were computed as a linear function of the activation of the excitatory ensembles $\sum_n H_n^e(i)$.

Excitatory cells in block n receive direct input from the thalamic channel characterised by the delay δ_n . Excitatory ensembles are connected locally to the inhibitory populations, which connect selectively to other blocks in the network. The selective inhibition effectively shunts populations encoding the lower harmonics present in the thalamic input. This circuitry describes a general pitch processing mechanism that explains the N100m deflection as a transient state in the cortical dynamics: The deflection is triggered by a rise in the activity elicited by the thalamic input, peaks after the inhibition overcomes the input, and ends when model dynamics reach equilibrium. The duration of the transient state depends on the encoded pitch of the tone: High frequency tones have more inferior harmonics in the hearing range, eliciting a stronger inhibition along the network and driving the system to equilibrium faster than low pitched tones. This behaviour explains the empirically observed correlation of the N100m latency with the tone's pitch.

Perceptual experiments were performed on pure tones, several different harmonic complex tones, and iterated rippled noises. In all the cases, after 50-100ms, the system reaches an state of equilibrium characterised by an unimodal distribution of the activation centred in the ensemble parametrised by the period of the perceived pitch of the stimulus. Moreover, neuromagnetic simulations computed with pure tones reveal N100m latency predictions that are fully in line with the available experimental data [3].

References

- [1] Balaguer-Ballester et al., E. Understanding pitch perception as a hierarchical process with top-down modulation, *PLoS computational biology* 5 (3) pp. e1000301, 2009.
- [2] Meddis, R and O'Mard, L. P Virtual pitch in a computational physiological model, *JASA* 65 (2) pp. 3861-9, 2006.
- [3] Roberts, T. and Ferrari, P. Latency of the auditory evoked neuromagnetic field components: stimulus dependence and insights toward perception, *Journal of Clinical Neurophysiology* 17 (2) pp. 114-29, 2000.
- [4] Wong, K.-F. and Wang, X.-J. A recurrent network mechanism of time integration in perceptual decisions, *The Journal of Neuroscience* 26 (4) pp. 1314-28, 2006.