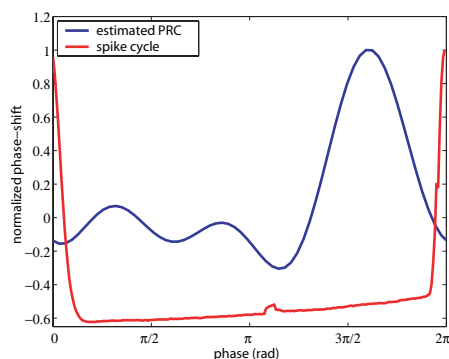


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1. Introduction

The dynamics of complex neural networks can be largely reduced to simple models of coupled phase oscillators. To do so, the phase-response (or **phase-resetting**) curve (PRC) of the neurons must be determined. The PRC quantifies how much the period of the oscillator changes in response to a perturbation occurring at any phase. In mathematical neural models, like the Hodgkin-Huxley equations, the PRC can be calculated from the dynamical equations. However, a reliable estimation of the PRC in real neurons presents difficulties that have impaired neuroscientists from systematically taking advantage of the information PRC provides.



Combining theory, computer simulations and electrophysiological recordings (whole-cell patch-clamp) we have developed an approach for the efficient estimation of PRCs in real neurons¹. This has allowed us to construct a reduced model of the **olfactory bulb**, and to study its dynamics. Using this technique we have determined:

- 1) The estimated PRC of olfactory bulb **mitral cells** has partially positive and partially negative domains, suggesting that they behave as **resonators** or type II neurons.
- 2) The PRC is not purely sinusoidal but possesses higher order harmonics, a necessary condition for the formation of synchronized neural assemblies².

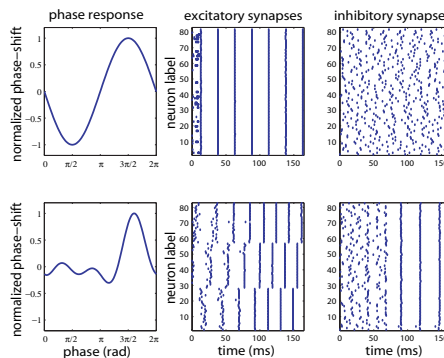
A mathematical analysis of networks of phase oscillators reveals that if the synapses are purely excitatory or purely inhibitory, the network dynamics will organize into **synchronized neural assemblies** if, and only if the Fourier expansion of the PRC contains at least one sine coefficient² with opposite sign (positive or negative) to the synapses' sign. In particular, for the PRC of a mitral cell, a network with purely inhibitory interactions rapidly develops a global oscillation and can therefore act as a **clock** for downstream networks. In the case of mixed excitatory and inhibitory interactions the network displays complex **spatiotemporal activity patterns** that are different for different initial conditions. This property represents an efficient way of encoding information.

2. Excitatory vs. Inhibitory Networks

Studies of neural phase-models reveal a new qualitative behavior when the higher order harmonics of real phase-response curves are considered: namely, the formation of synchronized neural assemblies. Starting with random initial conditions a network of *artificial* neurons with a sinusoidal PRC develops full synchrony with excitatory synapses, whereas it remains asynchronous with inhibitory synapses (top panels). However neurons with mitral cell-like PRCs connected through excitatory synapses converge to three synchronized assemblies, because of the positive coefficient of the third order sine in the Fourier expansion of the PRC. In the case of inhibitory synapses, the first and the second order sine harmonics have negative coefficients. Thus, the homogeneous initial state breaks into synchronized assemblies again.

The simulations show that two assemblies emerge, one of them sparsely populated, with a small relative lag. These results indicate that a **network of real neural resonators** can generate global oscillations through inhibitory rather than excitatory synapses. In the figure (lower right corner), the network predominantly oscillates in the **gamma frequency** band. This network type can therefore act as a **clock** for neighbor networks.

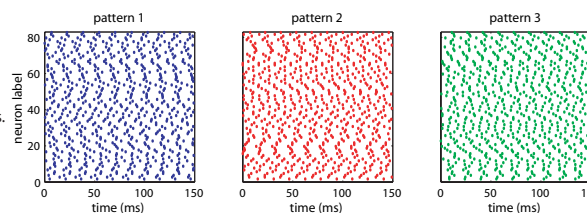
In the olfactory bulb, mitral cells interact through excitatory synapses with other mitral cells in the same glomerulus and also via disinaptic inhibition with mitral cells in other glomeruli. Therefore, to model the neural dynamics in the olfactory bulb in a more realistic manner we consider both, excitatory and inhibitory interactions between mitral cells.



3. Networks with Mixed Connectivity

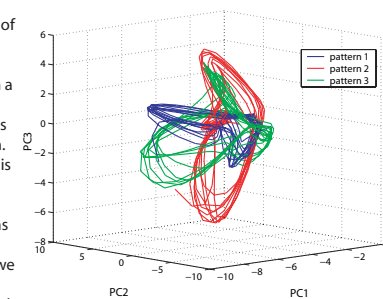
For a given connectivity matrix with random excitatory and inhibitory synapses, the initial stimulus-specific latencies of the neural responses determine the steady-state phase differences between neurons. Thus, the network remaps latency differences to phase differences (**latency code**). This general property of networks with mixed excitatory and inhibitory synapses can be used to **encode information** in spatiotemporal patterns of neural activity.

In the figure, three different activity patterns emerge from the same network for three different initial conditions. The initial conditions represent latencies of the neural responses to an arbitrary stimulus.



4. Low-dimensional Representation of Spatiotemporal Patterns

The spatiotemporal patterns of the network dynamics associated with different stimuli can be represented in a **multidimensional space**, where each dimension stands for the activity of one neuron. For visualization purposes, this high-dimensional space can be projected down onto the three most relevant directions (first three principal components). By doing this, we obtain **trajectories** that are reminiscent of those observed in the neural dynamics of the olfactory system in insects^{3,4}. Finally, a downstream neural network can read out the spatiotemporal patterns with a perceptron-like configuration of coincidence detectors⁵.



5. Conclusions

- * Our method to estimate phase-response curves in real neurons permits us to construct highly reduced, but realistic models of real neural network dynamics.
- * These models are computationally efficient and allow for analytical treatment.
- * Mitral cells in the mammalian olfactory bulb are type II neurons (resonators).
- * In general, the network dynamics of purely excitatory or purely inhibitory neurons display synchronized neural assemblies.
- * Inhibitory networks of resonators can act as clocks in the gamma band.
- * Neural networks with mixed excitatory and inhibitory synapses can encode sensory information in spatiotemporal patterns of neural activity.

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