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Gamma-oscillations support optimal retrieval in associative memories of two-compartment neurons[☆]

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Abstract

Theoretical studies concerning iterative retrieval in conventional associative memories suggest that cortical gamma-oscillations may constitute sequences of fast associative processes each restricted to a single period. By providing a rhythmic threshold modulation suppressing cells that are uncorrelated with a stimulus, interneurons significantly contribute to this process. This hypothesis is tested in the present paper utilizing a network of two-compartment model neurons developed by Pinsky and Rinzel. It is shown that gamma-oscillations can simultaneously support an optimal speed for single pattern retrieval, an optimal repetition frequency for consecutive retrieval processes, and a very high memory capacity. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Gamma-oscillations; Threshold control; Associative memory

1. Introduction

Synchronized gamma-oscillations have been observed in many cortical areas of different species [1,2,8]. Their functional significance in sensory areas has been interpreted by the feature integration or binding-hypothesis stating that cells express their participation in the representation of the same external object by rhythmic synchronized firing in the gamma-range [1,8,11].

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Binding has been repeatedly modelled assuming feature-coding periodically firing neurons that adjust their phases in time such that different objects become segregated into different phases of the collective oscillation (see [11] and references therein). In contrast, we proposed an interpretation that avoids the strong assumptions of phase-coding and strictly rhythmic firing of single neurons [10–12]. In this scheme, gamma-oscillations are interpreted as sequences of fast individual retrieval processes carried by recurrent associative excitatory connections and rhythmically interrupted by inhibitory interneurons.

Theoretical results by Schwenker et al. [7] on iterative retrieval of sparse binary patterns in conventional associative memories suggest that such excitation-inhibition cycles should provide a retrieval mode in networks of spiking neurons that is optimal in several respects: (1) Provided the number of active neurons is controlled by a suitable threshold mechanism, at most three feedback steps suffice for perfect pattern completion [7,3]. This implies that retrieval is fast enough to take place within single gamma periods, say within roughly 10 ms. (2) If retrieval processes are so fast, then different patterns can in principle be processed at a maximal repetition frequency in the gamma-range. (3) Moreover, the results in Ref. [7] imply that synchronous firing of cells within a few milliseconds also supports a very high memory capacity (cf. [11]).

Cortical conditions have been sketched in an associative memory of simple spiking neurons where interneurons realize the necessary threshold control [10,11]. Here, input patterns composed of several stored patterns were completed and segregated into different periods of the collective rhythm. However, the biological relevance of fast rhythmic associative memories has to be substantiated by more realistic simulations. To this end we employ associative retrieval in a network of two-compartment neurons [6]. Unlike models considering asynchronous persistent firing [4], the activity patterns to be completed in our model are coded by synchronized spike-patterns.

2. Methods

Pinsky and Rinzel [6] developed a reduced two-compartment model of a 19-compartment cable model [9] segregating fast currents for sodium spiking into a soma-like compartment and slower calcium and calcium-mediated currents into a dendrite-like compartment. We studied a network of 100 excitatory cells and one inhibitory interneuron. The excitatory subnetwork was exactly the same as in Ref. [6] including all parameter settings with the exception of the external stimulation, inhibition, and the recurrent connectivity matrix.

The connectivity matrix was formed by binary Hebbian learning of 0/1-patterns containing $k = 10$ ones at random positions [5,7]. Excitatory synapses terminated on the dendritic compartment and activated AMPA- and NMDA-currents [6]. Since memory patterns were small, EPSP-amplitudes in response to a single spike had to be scaled to high values of a few mV (cf. Ref. [4]).

The single inhibitory interneuron had a graded output modeling the average firing rate in a pool of interneurons that control the total activity in their neighborhood [3,5,7,11]. The inhibitory cell received input from all excitatory cells, had a threshold-linear rate function and inhibited all excitatory cells with equal weights on their soma-compartment. Inhibitory synapses employed a fast GABA-ergic conductance change. A single spike of an excitatory cell after being transmitted through the inhibitory loop evoked an IPSP on the soma of pyramidal cells somewhat delayed and stronger than the respective EPSP. The decay time of IPSPs (roughly 10 ms) crucially influenced the period of the collective network oscillation [13].

During retrieval, subsets of principal cells belonging to one of the memory patterns receives depolarizing dendritic input (Poisson processes) strong enough to evoke steady firing of these addressing cells.

3. Results

Fig. 1 shows a raster plot of spike trains in a network of $N = 100$ cells where $P = 50$ patterns each containing $k = 10$ ones have been stored. Neurons 1–10 constitute the first memory pattern, all other stored patterns are random. During the first 100 ms only neurons 1–5 receive external input, they represent the first address pattern. Note that the memory pattern is completed in every gamma-cycle, but action potentials (dots) of the first 10 cells are not perfectly synchronized: the spikes scatter over several milliseconds mainly caused by input noise and synaptic transmission times: address neurons 1 ... 5 always fire first and trigger the cells 6 ... 10 after one synaptic feedback step.

At time $t \approx 100$ ms the input switches to a second set of $l = 5$ neurons addressing one of the randomly generated patterns. The network immediately follows this switch. Thus, very quick responses to changing stimuli are possible.

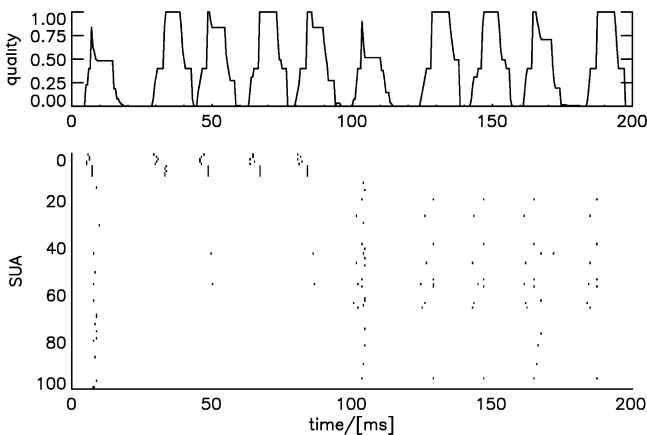


Fig. 1. Raster plot of spikes and retrieval quality in a network storing 50 patterns.

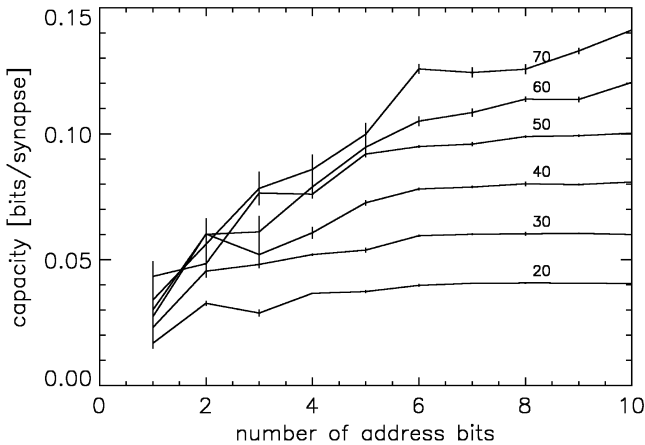


Fig. 2. Completion capacities for increasing memory load, $P = 20, 30, \dots, 70$.

Since the memory load is already high, retrieval is impaired by cross-talk occasionally observable as erroneously firing cells beside the 10 cells constituting the memory pattern. Wrong cells respond especially when the input is switched to a new input pattern ($t = 0$ and 100 ms). A closer investigation of the erroneously firing cells reveals that these typically belong to memory patterns that have considerable overlap with the addressed memory pattern.

Retrieval quality in Fig. 1 is defined as the normalized information about the addressed memory pattern contained in the spike raster binned over the previous 7 ms. The quality often assumes a sharp maximum in the first part of a retrieval period. Apparently, correct cells respond earlier than spurious cells and could be segregated in further processing stages by coincidence detection.

Memory capacities for varying numbers of active address neurons (l) and stored patterns (P) are shown in Fig. 2. Capacities are derived from the transinformation in spike patterns about memory patterns, averaged over 10 retrieval periods for 10 randomly selected addresses. Strikingly, the compartment neuron network loaded almost to the theoretical optimum where 50% of the synapses have been increased [5], still achieves high memory capacity with considerable input fault tolerance. The theoretical optimum of 0.69 bits/synapse could even be approached more closely with optimized pattern activity which is lower than $k = 10$ for networks of only 100 neurons [5].

4. Discussion

Our results support an interpretation of synchronized gamma-oscillations by fast and rhythmic associative processes [10,11]. We have shown that in networks of realistic neurons synaptic association during gamma-oscillations can be restricted to

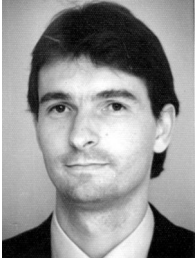
population bursts of cell pools in single periods. Our network operates close to the theoretically expected capacity and, simultaneously, at the maximally possible retrieval speed.

Cell firing in our model is characterized by avalanches of activation spreading from highly excited cells to less excited ones mediated by associative excitatory connections. Inhibition rhythmically interrupts these processes before most of the patterns correlated most strongly with the input can respond. Afterwards a new retrieval process is started by the input.

For future research more plausible interneuron models should be examined. In particular, the finding by Whittington et al. [13] that inhibitory subnetworks produce synchronized oscillations by themselves may influence the retrieval.

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