How imprecise is neuronal synchronization?*

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Abstract

We investigate the contribution of single cells to collective gamma-oscillations in a network of spiking neurons subject to an inhibitory activity control. In contrast to many earlier studies emphasizing a high precision in spike timing, cell firing is rather unreliable in our model. Nonetheless, we qualitatively reproduce many experimental findings, some of them previously unexplored in modeling studies.

Keywords: gamma-oscillations; synchronization; spike timing; computer model

1 Introduction

The stimulus-dependent synchronization of gamma-oscillations in visual cortex has been proposed as a solution for the feature-binding problem of sensory processing [1–5]: if two cells in visual cortex fire synchronized, then both cells are assumed to participate in the representation of the same external stimulus; if the cells represent different stimuli, then they fire uncorrelated. The hypothesis has been substantiated by experimental studies mainly utilizing cross-correlograms of local field potentials (LFP) or multiple unit activity (MUA); only a few studies report results from single unit activity (e.g. [2]). Such correlograms represent temporal statistical averages over several hundred milliseconds. MUA and LFP furthermore average neural or synaptic activity from within a certain spatial surrounding of the recording electrode. Inasmuch as correlograms are averaged quantities they say little about the occurrence and temporal precision of individual spikes. In the present work we present simulations that reproduce many experimental findings about gamma-oscillations, particularly those derived from single-unit correlograms [2]. Nonetheless, cell

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firing is extremly imprecise and unreliable in our model. This suggests that, if spike timing is utilized for coding in the visual system, then on the base of a population code (cf.[6,7]).

2 Model Network

We consider a local patch of cortical tissue of roughly the size of a column in a primary visual area. We assume that cells in this patch can be ordered by their orientation preference and that similarly oriented cells have a higher probability to be connected. Other tuning properties and the laminar cortical structure are neglected. As a rough approximation of the cortical situation we simulate a one-dimensional topographically ordered model of $N = 128$ excitatory spiking neurons similar to integrate-and-fire cells [6]. Here, topography is meant to represent different orientation tuning. Connectivities are restricted to neighborhoods of cells. The probability for a synapse decays with cell-distance in a Gaussian manner (halfwidth $N/4$). Additional interneurons receive input from excitatory cells in a neighborhood of halfwidth $N/8$ and inhibit the excitatory cells accordingly. Inhibitory cells are graded response neurons with threshold-linear rate-function. They represent local pools of interneurons. PSPs have transmission delays of $1ms$, a rise time of t_r and fall time of t_f, where $t_r = 1ms,\ t_f = 3ms$ for excitatory and $t_r = 2ms,\ t_f = 5ms$ for inhibitory synapses. Axonal conduction delays are not included. A bar-stimulus is modeled as input current to the excitatory cells which is centered at some orientation (say neuron $N/2$) and falls off in a Gaussian way (cf. Fig.1). In addition, each neuron receives a Gaussian white noise input.

All phenomena demonstrated in the sequel are robust against changes in network details and come out of a single exemplary simulation run (5 seconds realtime) not tuned for any particular effect. Crucial are the following details: inhibition must be stronger and somewhat slower than excitation, and the noise level must be so large that the collective oscillation is almost unstable.

3 Results

Figure 1 displays spike activity in response to a bar-stimulus of "vertical" orientation. "LFP" in the figure represents the ensemble average of EPSPs over all cells. The LFP signal clearly reveals gamma-activity, although in a waxing and waning manner similar to physiological recordings. Diamonds above the LFP indicate spiketimes of neuron 49. Apparently, the neuron is not rhythmic, but emits spikes only in some periods of the collective rhythm. Periodicity and spike-timing of the other cells is similarly unreliable.

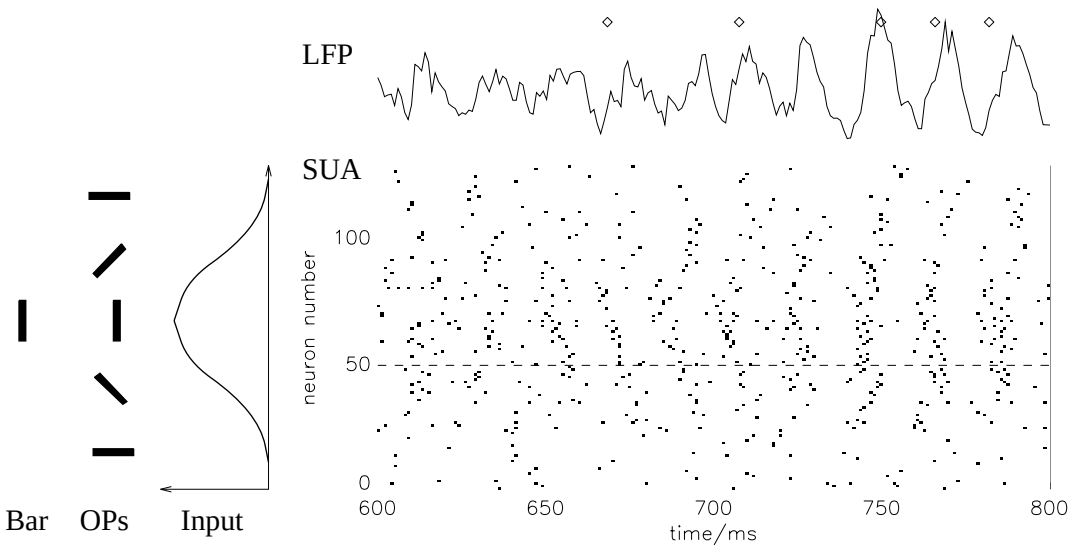

Fig. 1. Typical simulation showing strong LFP-fluctuations and unreliable spike timing. (OP = orientation preference)

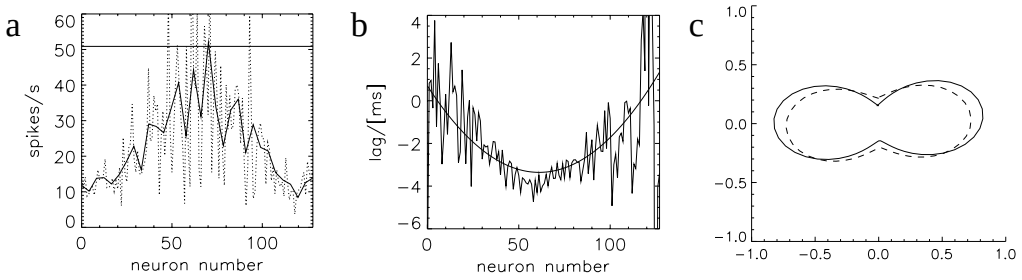

Fig. 2. Tuning properties of different neural variables.

As a consequence of this unreliability, the firing frequencies in our model change with stimulus orientation (tuning). In Fig.2a, firing rates of single neurons are displayed (dashed line) together with a further average over local neighborhoods (thick line, average over 8 neighbors, roughly equivalent to cortical MUA). The horizontal line at 51/s indicates the frequency of the collective oscillation derived from the power spectrum peak of LFP. Most cells have lower rates in accordance with experimental results by Kreiter and Singer in area MT [5]. Although tuning is one of the most basic properties of cortical neurons, it cannot be observed in many comparable network simulations. Those often operate in parameter-regimes, where single cells almost perfectly synchronize and fire periodically at rates equal to the collective oscillation frequency (cf.[6]). Tuning curves are flat in this *tight-binding* situation (data not shown).

König et al. [3] investigated how sub-optimally driven cells lock into the collective rhythm. They found, that sub-optimal cells reveal a systematic phase-lag relative to optimally stimulated cells. Their results suggest that the lag of cells

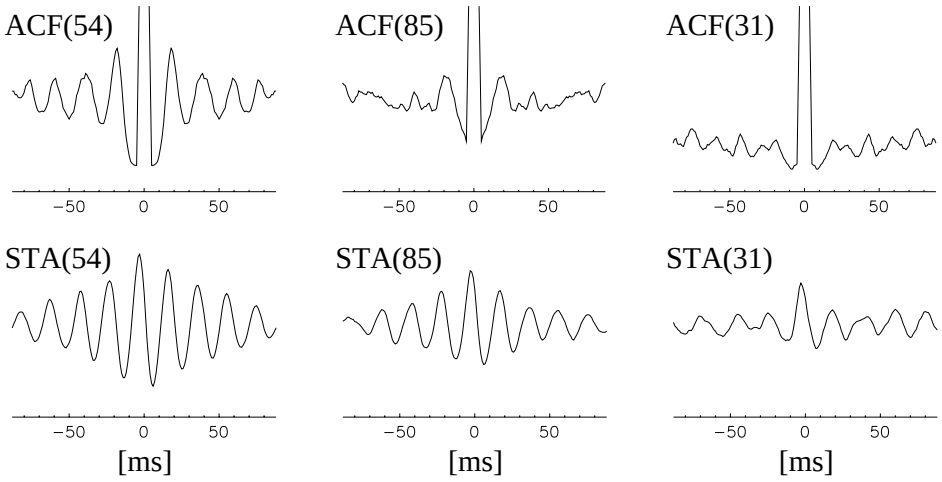

Fig. 3. Rhythmic (left, cell no. 54), lock-in (middle, 85), and unlocked cells.

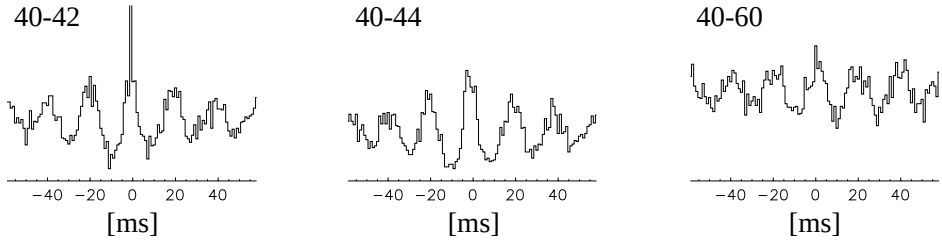

Fig. 4. Cross-correlations between neuron 40 and nearby cells.

with orientation ϕ relative to the best matching cells depends quadratically on ϕ. This is what is clearly seen in Fig.2b, where phase lags obtained from peaks of spike triggered averages of the LFP signal are displayed together with a quadratic fit. Of course, the strong spike scatter visible in Fig.1 shows that this "systematic" lag is only an average property of cell firing and by no means implies deterministic delays between individual firings of two neurons.

Eckhorn and Frien [1] report that oscillatory components in MUA-signals are often sharper tuned than the MUA-activity itself. The same is shown for our data in Fig.2c in form of polar plots (for comparison with Fig.2 in [1]). The dashed curve represents a Gaussian fit of the MUA curve (thick) in Fig.2a; the second profile is obtained similarly from power spectrum peaks of the MUA-signals. Both curves are mapped symmetrically to $[0, 2\pi]$ and scaled to arbitrary units. The higher aspect ratio of the plot for the oscillatory component indicates a sharper tuning in comparison with MUA-rates.

Investigating auto-correlation functions (ACFs) of single neuron spike trains and spiketriggered averages (STA) of LFPs derived from the same electrode, Eckhorn and Obermüller [2] classified single neurons into three categories: (i) *rhythmic cells* with oscillatory ACFs and pronounced correlations in the LFP-STA, (ii) *lock-in cells*, which are coupled to the LFP but are not rhythmic

by themselves (flat ACF), and (iii) *non-participating cells* which are neither rhythmic nor significantly coupled to the global oscillation, although they are driven by the stimulus and fire significantly. As shown in Fig.3 (cf.Fig.1 in [2]), the same celltypes appear in our simulated data. However, the residual correlations for non-participating cells in our simulations are still larger than in experiments. This suggests that experimental spike-trains are perhaps even more noisy than the data in Fig.1.

Figure 4 finally displays cross-correlations between neuron 40 and nearby cells. In some cases we find tight correlations (1-3 ms) on top of an oscillatory correlogram (central peak width 5-10ms). The tight peaks are exclusively due to common input by a third cell and the oscillatory component is a consequence of the network oscillation. We never find tight correlations between neurons more distant than the excitatory coupling width. König et al. describe the same phenomena in the spatial domain in experimental recordings [4].

4 Discussion

The presented simulations reveal many properties well in accord with experiments but not with tight-binding theories: there is a pronounced (and strongly fluctuating) global gamma-oscillation, but single cells may be rhythmic or not. If they are rhythmic, they may or may not fire within individual periods. As a consequence firing frequencies cover a broad range that can differ from the frequency of the collective oscillation, showing that both quantities are independent entities. Because the firing frequencies reflect the external excitation they can be employed for rate coding in the usual sense.

Regarding coding by spike timing, the unreliable firing implies that synchronicity and shifts between differently tuned cells can only be signaled on the population level where averages over many neurons are possible; temporal averaging over hundreds of milliseconds (as in correlograms) is unlikely to take place in cortex. When two cells receive common input from a third cell correlations can be tight (1-3ms), but more typically are damped oscillatory correlograms corresponding with a considerably lower precision (peak width). Such oscillatory correlograms reflect the collective oscillatory network behavior; they arise due to mass action in contrast to the tight peaks.

Oscillatory sidepeaks in correlograms decay quickly on a timescale of several ten to less than 100 milliseconds (1 to 4 gamma-periods). This suggests that any information processing possibly supported by gamma-oscillations does not need long periodic and coherent wavetrains. Instead, only short epochs of the signals seem to be relevant in accordance with an interpretation of gamma-oscillations as an optimal associative retrieval mode in cortical networks [6,7].

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