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Synchrony and delay activity in cortical column models

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Abstract

Recent studies have shown that neurons in the visual cortex responding to related features tend to synchronize their activity. Although synchronous oscillations have been observed in associational cortices during visual working memory activity, there has been few modeling attempts to address the process which could simultaneously generate both types of dynamics. We propose a realistic mechanism that accounts for delay activity and synchronous oscillations within and between cortical column models, in a range that is consistent with experimental data. These dynamics result from the interplay between intrinsic cellular bistability and synaptic interactions. © 1999 Elsevier Science B.V., All rights reserved.

Keywords: Working memory; Bistable neurons; Synchronous oscillations; NaP

1. Introduction

During various visual delayed response tasks, some cortical neurons of monkeys were found to exhibit sustained firing activity that persisted across the delay period after the removal of the sensory input. In inferotemporal cortex (IT), this delay period (hereafter called DP) activity has been hypothesized to reflect the short-term storage of the information concerning the immediately preceding stimulus, whereas in prefrontal cortex (PFC), it could act as a selective working memory of the stimulus [5,6].

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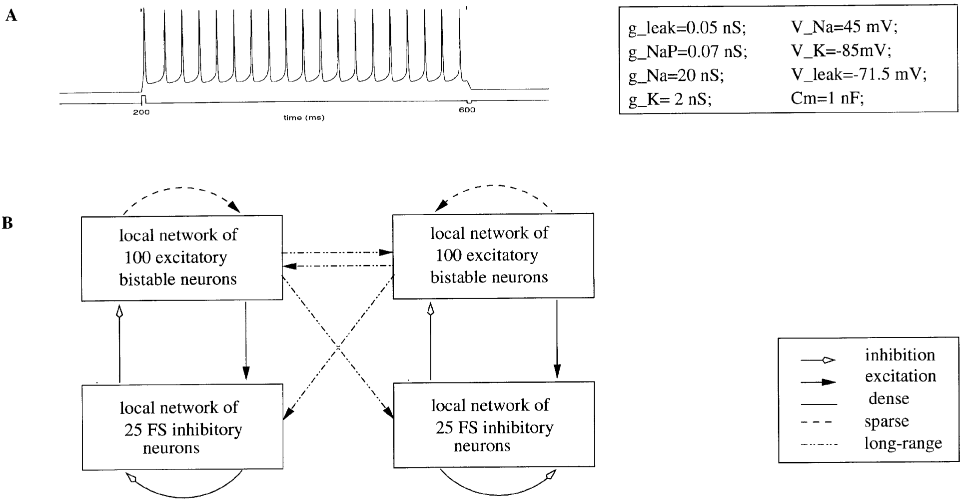
DP activity is usually assumed to result solely from activity reverberations through excitatory loops (e.g. [1]). However, experimental and theoretical evidence suggests that intrinsic cell properties, such as plateau and bistable firing, could participate in generating elevated firing rates after removal of the stimulus [7,3].

In this study, we explore the possibility that synchronous DP activity can be maintained by an interplay between network properties and intrinsic cellular bistability. Realistic bistable neurons were incorporated in models of small cortical columns that capture the relevant architectural details of local cortical circuits. The resulting dynamics were studied, both during external stimulation and during the DP, with a focus on situations of coherent activity within and between columns.

2. Model neurons and columns

The dynamics of excitatory neurons were described by a Hodgkin–Huxley model with an additional persistent Na^+ (NaP) current, as known to exist, for example, in PFC neurons and as shown to be capable of producing a plateau potential giving rise to neuronal bistability. The model excitatory neuron and non-inactivating NaP channel were taken from [4] in the bistable firing domain (Fig. 1A). Inhibitory interneurons possessed only fast Na^+ and K^+ channels and exhibited classical fast spiking behavior.

The network modeled a few interconnected columnar modules (Fig. 1B). Each module was composed of 80% excitatory cells and 20% inhibitory interneurons,



g_leak=0.05 nS;	V_Na=45 mV;
g_NaP=0.07 nS;	V_K=-85mV;
g_Na=20 nS;	V_leak=-71.5 mV;
g_K= 2 nS;	Cm=1 nF;

Fig. 1. **A**. Membrane potential of the Hodgkin–Huxley model of neuron with NaP conductance used, in the bistable firing domain. Persistent 50 Hz rhythmic discharge is provoked by a brief pulse of depolarizing current (10 μA), and stopped by a brief pulse of hyperpolarizing current (− 3 μA). The firing frequency depends on g_{NaP} and g_{leak}. **B**. Sketch of the architecture of a two-column model.

which expressed visual input preferences and responded to similar (presumably high-level visual) features. Within a column, every excitatory cell contacted an average of 10% of all other excitatory cells. Connections between excitatory cells and inhibitory cells were assumed to be dense (60–100%).

Between columns, interactions were mediated by excitatory horizontal connections only and were much sparser than within a column (2.5% and 10–20% onto excitatory and inhibitory cells, respectively). Synaptic conductances were modeled using an α-function conductance change. Postsynaptic potential amplitudes were varied in the range 1–2 nS and 1–6 nS for excitatory and inhibitory conductance changes, respectively. Transmission delays were varied from a few milliseconds within a column up to 15 ms between columns, to account for long-distance lateral interactions. An analog of the local field potential (LFP), defined by the running average of all membrane potentials of all excitatory cells in a column, was computed for each simulation and was used to evaluate the presence of correlated activity.

3. Results

3.1. Oscillatory delay activity within one column

All cells were injected with external uncorrelated spike train inputs at a mean frequency of 100 Hz for a period of 100 ms and the following second of simulation was studied. Fig. 2 shows an example of column dynamics. Here, as in large regions of the parameter space, activity was high during stimulation and persisted long after the end of the external input, although at low firing rates (27 spk/s). It exhibited coherent oscillations at 18 Hz, which would spontaneously cease and reappear. The oscillatory behavior could not be observed in individual pyramidal cell spike times, but was clearly visible in the LFP. It was also observed in the inhibitory cells traces. The main parameter that affected the oscillation frequency and the mean firing rate was the amount of inhibition in the network. Variations of the synaptic conductances $g_{e \to i}$ and $g_{i \to e}$ could shift the frequency and firing rate between 20–50 Hz and 15–60 spk/s. The oscillation frequency was neither determined by synaptic delay time variations nor equal to the intrinsic oscillation frequency of the bistable isolated cells. The mean firing rate and oscillation frequency were also insensitive to variations in the intensity and duration of the stimulus.

3.2. Oscillatory delay activity between columns

Intercolumnar synchrony during DP was studied in a model consisting of two distant columns which were stimulated simultaneously with optimal feature stimuli. When connections were made only between the pyramidal cells of each column ($E \to E$), internal synchrony within each column was not degraded but no stable inter-columnar synchrony could be observed. On the contrary, excitatory onto inhibitory ($E \to I$) long-range connections alone were found to be able to efficiently mediate zero phase-lag synchronization that was not disrupted by up to 15 ms mean

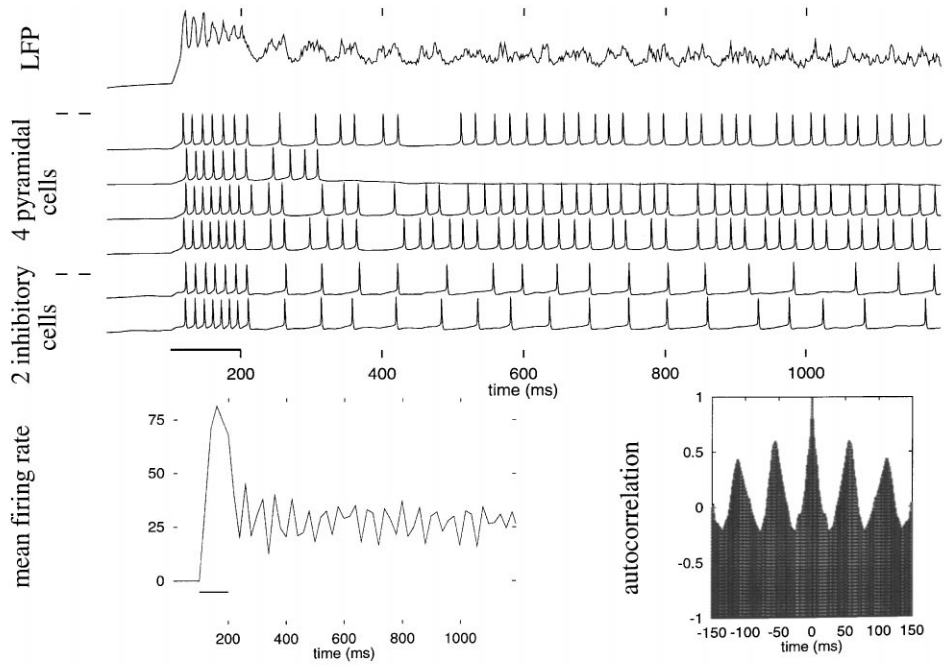


Fig. 2. Delay activity of a model column: synchronous oscillations at 17.7 Hz (CA = 0.6) and mean firing rate of 26.7 spk/s. Autocorrelations and correlation amplitude (CA) were computed from the LFP. $g_{e\to e} = 0.4$ nS (10%), $g_{e\to i} = 2$ nS, $g_{i\to e} = 4.1$ nS, $g_{i\to i} = 1$ nS.

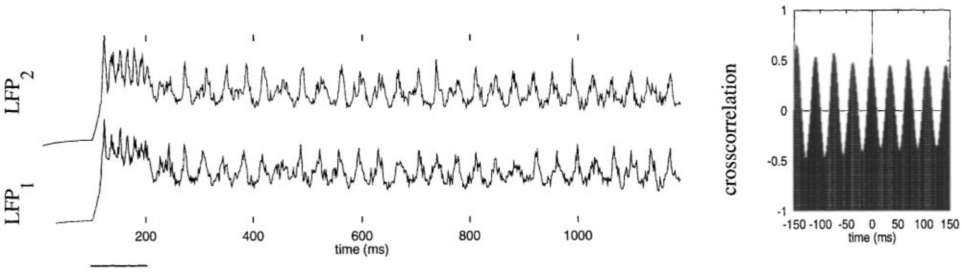


Fig. 3. Cross-correlation between two columns connected with E → I synapses with a density of 10% and mean delay of 15 ms. The columns oscillate in phase at 27.8 Hz (CA = 0.52 at − 1.5 ms). Mean DP activity: 33 spk/s in both columns. $g_{e\to i_{lat}} = 2$ nS.

synaptic delay (Fig. 3). Interestingly, the resulting inter-columnar synchrony was in general more robust to synaptic delay times than when both E → E and E → I connections were included.

With the same type of inhibitory connectivity, inter-columnar synchronization was also observed when the stimulation of the two columns was delayed, that is when one column was externally activated after the other had reached a coherent DP activity state. However, when the $g_{\mathrm{i}\to\mathrm{e}}$ synaptic efficacy was increased, the synchronization was not altered but a competition process between the columns was observed. In such cases, the DP activity of the first column was reset to a lower level and only the last stimulated unit remained active.

4. Discussion

Our model presents a possible mechanism, resulting from the interaction between synaptic strengths and intrinsic cell properties, that simultaneously generates delay activity and synchronous oscillations in a range that is consistent with experimental data [8,9].

We plan on extending our model in several ways. In particular, a more realistic and flexible description of the cellular properties that are responsible for the generation of bistability will be investigated. The influence of spontaneous activity and of prior learning, which are the basis of alternative explanations for delay activity dynamics (e.g. [1]), can then be addressed.

The existence (or absence) of cellular short-term memory properties in cortical areas such as PFC and IT remains to be determined. Although other mechanisms have been proposed for the generation of cellular bistability, NaP current has been shown to be a possible candidate. Its role in DP dynamics could be tested experimentally using a specific antagonist. Moreover, bistability is likely to depend on neuromodulatory influences [7]. In this respect, it is interesting to relate the effects of NaP conductance to its modulation by dopamine which has been shown to be involved in short-term memory processes [6].

We have shown that in such a cellular bistability scenario (as opposed to the attractor scenario), strong inhibitory interactions are fully compatible with the production of sustained firing rates after removal of the stimulus. Indeed, in the present model, synchronization is mediated both within and between columns by an inhibitory mechanism in ways similar to what has been suggested *during* external activation in previous modeling studies [2]. On the contrary, most models that have described oscillations and synchronization *after* external activation (i.e. in a memory period) consist of densely connected networks in which firing is synchronized with the periodicity of the delay time (e.g. [10]). Such an inhibitory mechanism is also consistent with recent evidence showing that pyramidal/non-pyramidal interactions are critical for the formation of memory fields [6].

References

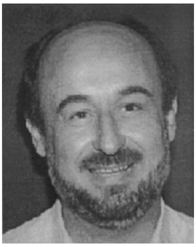
[1] D. Amit, N. Brunel, Global spontaneous activity and local structured (learned) activity during delay periods in cortex, Cerebral Cortex 7 (1996) 237–252.

[2] P. Bush, T. Sejnowski, Inhibition synchronizes sparsely connected cortical neurons within and between columns in realistic network models, J. Comput. Neurosci. 3 (1996) 91–110.

[3] M. Camperi, X. Wang, A model of visuospatial working memory in prefrontal cortex: recurrent network and cellular bistability, J. Comput. Neurosci. 5 (1998) 383–405.

[4] B. Delord, A. Klassen, Y. Burnod, R. Costalat, E. Guigon, Bistable behaviour in a neocortical neurone model, NeuroReport 8 (1997) 1019.
[5] R. Desimone, Neural mechanisms for visual memory and their role in attention, Proc. Natl. Acad. Sci. USA 93 (24) (1996) 13 494–13 499.
[6] P. Goldman-Rakic, Regional and cellular fractionation of working memory, Proc. Natl. Acad. Sci. USA 93 (24) (1996) 13 473–13 480.
[7] E. Marder, L. Abbott, G. Turrigiano, Z. Liu, J. Golowash, Memory from the dynamics of intrinsic membrane currents, Proc. Natl. Acad. Sci. USA 93 (1996) 13 481–13 486.
[8] K. Nakamura, M. Akichika, K. Kubota, Oscillatory neuronal activity related to visual short-term memory in monkey temporal pole, NeuroReport 3 (1992) 117–120.
[9] C. Tallon-Baudry, O. Bertrand, F. Perronet, J. Pernier, Induced gamma-band activity during the delay of a visual short-term memory task in humans, J. Neurosci. 18 (1998) 4244–4254.
[10] M. Usher, H. Schuster, E. Niebur, Dynamics of populations of integrate-and-fire neurons, partial synchronization and memory, Neural Comput. 5 (4) (1993) 570–586.

Peggy Seriès graduated in Computer Engineering (ISEP, Paris) and Artificial Intelligence (M.Sc., University of Sussex) in 1996. The present work originates from research she pursued at the AnimatLab. She is currently a Ph.D. student at the LPPA, in collaboration with the LIMSI. Her research interests include temporal coding, neuronal dynamics and lateral interactions in visual cortex.



Philippe Tarroux studied biology at the University P.&M. Curie in Paris and USTL in Montpellier, and Computer Science at the Ecole Normale Supérieure in Paris. He received a Ph.D. degree from the University of Paris. He is an associate professor at the Ecole Normale Supérieure. His current research interests include the modeling of visual processes and attentional mechanisms, and the elaboration of biomimetic computer vision models.