

Neocortical gap junction-coupled interneuron systems may induce chaotic behavior itinerant among quasi-attractors exhibiting transient synchrony

Hiroshi FUJII and Ichiro TSUDA

Kyoto Sangyo University, Kyoto 603-8555, Japan/Hokkaido University, Sapporo 060-0810, Japan

fujii@bacco.kyoto-su.ac.jp

Abstract:

Recent discovery of the massive presence of gap junction couplings among neocortical FS (and LTS) interneurons poses serious questions about their collective dynamical behavior, and their possible cognitive roles. Through theoretical studies, we present the possibility that gap junction-coupled interneuron systems may possess chaotic behavior which is itinerant among quasi-attractors of Milnor's sense, which in turn organizes synchronous cell groups transiently. Some physiological observations from the neocortex, e.g., local field potential (LFP) data exhibiting transient synchrony may provide evidence. We discuss also possible role in the so-called binding problem.

Key Words: gap junction, FS interneuron, transient synchrony, Milnor attractor, perceptual dynamics, dynamical cell assembly, binding problem, class I neuron, saddle-node bifurcation, spatio-temporal chaos, chaotic itinerancy

§.1 Introduction

Recent physiological discovery of ubiquitous presence of gap junctions among FS (and among LTS) interneurons in the neocortex poses serious questions about both their dynamical behavior in *in vivo* neocortex and their role in cognitive functions. It is generally believed that “a (gap junction-coupled) network of FS cells in the neocortex may play a key role in coordinating cortical activity...” (M. Galarreta & S. Hestrin, 1999 [7]), or “interneurons generate a variety of synchronous inhibitory rhythms in the neocortex...” (J. R. Gibson et al., 1999 [8]). Little is known, however, how those interneurons collectively behave when coupled by gap junctions in a massive way. Note that experimental observations of *in vivo* dynamics of interneurons may only be possible indirectly through observations of LFPs (local field potentials), which represent a collective subthreshold activity of pyramidal cells, on which interneuron activity may be reflected.

Charles Gray, on the other hand, found in 1992 [9] that LFP with 40-60 Hz detected in two widely separated regions from cat visual cortex reveals rapid *onset* and *offset* of synchrony with a time scale of

100-900 ms when a light bar is presented. The time development of the rapid transitions of synchrony/desynchrony is nonstationary both within a single trial and among trials. Gray claims that this transitory dynamics is the workshop where *feature bindings* are created in terms of synchrony.

We shall present in this paper a theoretical possibility that gap junction-coupled interneuron systems consisting of class I* neurons may exhibit a chaotic behavior which is itinerant among quasi-attractors of Milnor's sense, characterized as cell groups which dynamically show transitions between synchronous and desynchronous states. One of the coauthors (I.T.) has proposed a conceptual characterization of perceptual dynamics in the neocortex: *perception occurs at the interface between itinerant neural representation and the environment as interacting dynamics* [21]. Along the line of this view, we shall propose a new hypothesis on the physiologically observed data of Gray. Also, we propose the possibility that the dynamical organization of synchronous cell assemblies by the itinerant chaos may play the role of *feature bindings*.

§.2 Emergent chaos in class I* neurons

As Hodgkin has pointed out in 1948, there exist two classes of “neurons” (actually, “axons”) , i.e., class I “axons which are capable of repetition over a wide range of frequencies, varied smoothly over a range of about 5-150 impulses per sec.”, and class II “axons which usually give a train of impulses of frequency 75-150 /sec which was relatively insensitive to changes in the strength of the applied current” (Hodgkin [11]). It is now generally recognized that most of cortical neurons are of class I (Cauli [2]) in the sense of Hodgkin. Mathematically, the difference of behavior between these two classes is attributed to that of generation mechanism of action potentials: *saddle-node bifurcations* (class I), and *subcritical Hopf bifurcations* (class II). Although the concept of “class” of neurons does not depend on the number of variables, we restrict our arguments for a moment to a reduced form of two-variables, where the first variable, say V, may represent the membrane potential, and the second one, R, an activation state of, e.g., some potassium channels in a generalized sense. (Rinzel [14], Rose-Hindmarsh [16], Wilson [24]) With the injected current strength being denoted by I, the single cell equation may be written as:

$$(1) \quad \begin{cases} C \frac{dV}{dt} = f(V, R) + I \\ \tau_R \frac{dR}{dt} = g(V, R) \end{cases}$$

If we denote by $N_V = \{(V, R) \mid f(V, R) + I = 0\}$ and $N_R = \{(V, R) \mid g(V, R) = 0\}$ the nullclines of V and R, respectively, then class I neurons have generally J- (Morris-Lecar model) or U-shaped (reduced Connor model due Rose-Hindmarsh [16]) R-nullclines N_R , while class II neurons have inclined *I-shaped* N_R . Since N_V is essentially cubic, the number of intersections of N_V and N_R changes according to the level of I and there appears a *saddle-node* bifurcation point for Connor neurons, or a homoclinic

(saddle-node separatrix loop) bifurcation for the Morris-Lecar model (with appropriately chosen parameters). The salient property of class I neurons of Connor type is that as injected current I increases, there appears a *narrow channel* between N_V and N_R after the saddle-node bifurcation point. Rogawski [15] and Rose-Hindmarsh [16] emphasized that this is a consequence of the presence of A-current, i.e., a transient, slowly inactivating potassium current, a different ion channel from the Hodgkin-Huxley's rectifying K^+ current. We note, however, that it is still not clear whether this is the case for the FS interneurons in the neocortex.

Our interest is in the study of a system-level behavior of gap junction-coupled neuron systems consisting of class I cells, rather than the dynamics of an isolated single cell. In this respect, we define a neuron class, say I^* , in a more abstract setting, which includes (a part of) the class I neurons of Connor type:

Let I^* denote a subclass of class I neurons, in which there is a certain interval of I (injected current) such that the following conditions hold simultaneously:

1. the presence of a *narrow channel*,
2. the presence of an unstable *spiral*, and
3. the presence of orbits (with positive measure) reentering into the channel.

The last condition prohibits the orbits crossing N_V at points far-from the outlet of the channel. Note that the presence of a saddle-node bifurcation is not required to be of class I^* , although it is a natural situation in most neuron models.

We claim that *class I^* neurons, when coupled by gap junctions, exhibit extensive spatio-temporal chaos in some parameter regions* [6]. Note that they show perfectly regular firings when isolated, hence this chaotic behavior is an *emergent* property of coupled systems.

It is not difficult to construct simple models of class I^* . For instance, the readers can easily see that a model with a cubic N_V and a quadratic N_R can be in the class I^* with appropriately chosen parameters.

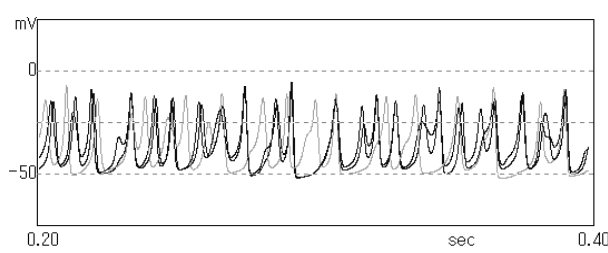


Fig. 1.

*Time series of membrane potentials of 3 neurons
from 10x10 gap junction-coupled class I^* neurons.*

Coupling is among 4-nearest neighbors.

Also, a piecewise linear model with a saw teeth shaped, cubic-like N_V and quadratic-like N_R is possible to satisfy the three conditions for the class I^* [6].

In the following, we show some numerical results showing time series of membrane potentials of three neurons among 10 by 10 neurons coupled by gap junctions with nearest 4 neighbors (Fig.1). The injected current I is constant both in time and space.

The maximum Lyapunov exponent is positive.

(Note: the gap junction couplings are assumed to be of linear diffusion type in this paper. See, [19].)

Fig.2 (a), (b) show snapshots of membrane potential contours made by 80x80 coupled neurons, with increasing gap junction conductance g_{GJ} . This shows *robustness* of spatio-temporal chaos; it appears in a wide range of parameters near the saddle-node bifurcation points, and even for far larger injection currents if g_{GJ} is smaller. Fig.2 (a), (b) are the cases for 4- and 8-nearest neighbor couplings. Also, the size of spatial patterns becomes larger when the coupling g_{GJ} becomes stronger.

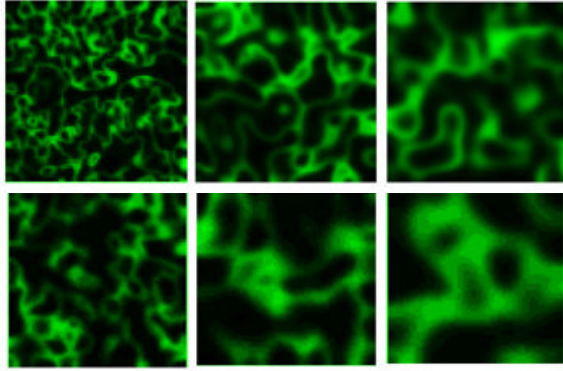


Fig. 2
 Snapshots of contours of membrane potentials of
 80x80 class I* neurons.
 (a) (top) 4-nearest neighbor couplings
 (b) (below) 8-nearest neighbor couplings
 The gap junction strength g_{GJ} is, from left to right, 0.5, 1.5 and 3.

§.3 Chaotic itinerancy among quasi-attractors which transiently exhibit synchrony states

Chaotic itinerancy is addressed as a transitory and sometimes nonstationary dynamics. (I. Tsuda, 1991 [21]). The dynamical orbits once approach one of "quasi-attractors" (or, "attractor ruins") and stay for sometime with a certain distribution, and escape there and approach to other ruins. This transitory dynamics continues without external perturbations. In chaotic itinerancy, a "quasi-attractor" is defined in the sense of Milnor (Milnor [13]) in which both topological and measure-theoretic concepts play role. The main characteristics of chaotic itinerancy are: (1) the presence of many near-zero Lyapunov exponents, (2) slow decay of correlations/ (mutual) information, (3) history (path)-dependent transition, (4) no ergodicity, (5) nonconvergence of near-zero Lyapunov exponents in some case, (6) the lack of attractor-tracing property as well as the lack of pseudo-orbit tracing property (Sauer [17]). In fact, we generally observe in our numerical data the dimension gap, i.e., the Lyapunov dimension (which may approximate Hausdorff dimension of the chaotic attractor) is bigger than the topological dimension. This dimension gap stems from a large number of negative Lyapunov exponents with a small absolute value. This brings about distributed attractors in phase space.

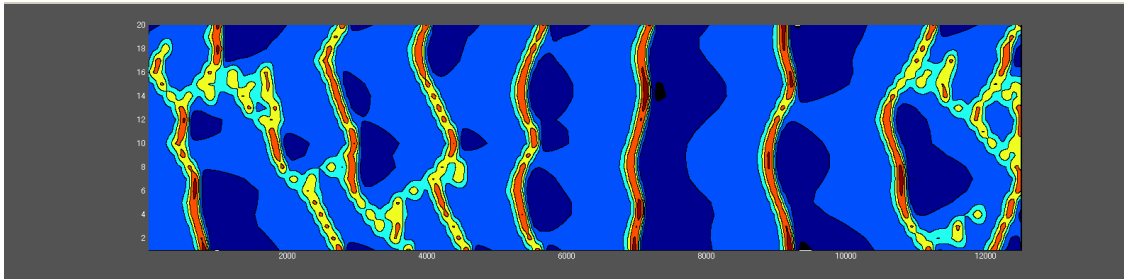


Fig. 3 Contour map of membrane potentials of 20 neurons of class I* (piecewise linear model) neurons coupled with the two neighbors by gap junctions. The vertical and horizontal directions indicates respectively the neuron positions, and the time (0->250 msec). Each neuron receives a constant injected current without any external fluctuations. No structural irregularity exists in this model.

Figure 3 shows a contour map of time series of membrane potentials of the coupled class I* neurons. We observe *metachronal* waves which chaotically repeat creations and annihilations. (A *metachronal* wave is a wave produced by successive phase shifts of neighboring neurons' activity like the movement of centipedes or cilium and flagella.) If a *metachronal* wave is viewed as a *synchronized state*, Figure 3 and other examples of our numerical results may indicate the presence of *transient synchrony* - chaotic alteration of *synchronized* and *desynchronized* states; the alternation is chaotic both in its timing and spatio-temporal patterns.

§.4 Hypotheses – LFP fluctuations and its transient synchrony /binding problem

We proposed in this paper a theoretical possibility that gap junction-coupled interneuron systems consisting of class I* neurons may exhibit a chaotic behavior which is itinerant among quasi-attractors, characterized as cell groups which dynamically show transitions between synchronous and desynchronous states. One of the coauthors (I.T.) has proposed a conceptual characterization of perceptual dynamics in the neocortex: *perception occurs at the interface between itinerant neural representation and the environment as interacting dynamics* [21]. In this regard, we here propose a few hypotheses related to physiologically observed data of cortical dynamics, the concept of dynamical cell assembly and the so called *binding problem*.

Our first proposal is the *inhibitory chaotic field hypothesis*, which says that the origin of the LFP fluctuations and transient synchrony observed by Gray is the itinerant chaos exhibited in gap junction-coupled interneuron systems consisting of class I* neurons. It is to be noted, however, that chaotic fluctuations of inhibitory interneurons, say of FS cells in cortical layers, are not *directly* reflected in LFP. Rather, the inhibitory influence of FS cells to pyramidal cells affects the fluctuations of membrane potentials of the latter (pyramidal) cells, and the consequences of which may be observed as transitory and synchrony dynamics of LFP, as observed by Gray.

Chaotic itinerancy between metachronal synchrony assemblies may play a role of creating local assemblies, which could be an information component, i.e., the *basic format* of the brain (von der Malsburg, 1981[23]), and transmit information among assemblies by linking these components. By this mechanism of creation of shared information, reorganization of assemblies may proceed smoothly.

This may also be related to the so called *binding problem*. Von der Malsburg [23], Aertsen [1], and Fujii et al. [5] have proposed a dynamical cell assembly hypothesis, where the feature binding problem is assumed to be solved by dynamic formation of cell assemblies via spike coincidence. Our present results present an *alternative* possibility that chaotic itinerancy appears to associate with dynamic change of cell assemblies, and thus feature bindings may not necessarily be established by spike coincidence but possibly by chaotic behavior of background FS (fast spiking) interneurons.

Since many questions, including whether cortical FS cells belong to class I* even in an approximate sense and so on, still remain open, our proposals are speculative in nature. As our conclusion, we may propose the following:

Hypothesis 1: Chaotic and nonstationary transitions between synchrony and desynchrony which have been observed in the neocortical LFP can be explained by chaotic itinerancy yielded by gap junction –coupled interneuron systems.

Hypothesis 2: Not only feature bidding but also binding via category formation ([22]) can be represented by spatio-temporal itinerant chaos of gap junction-coupled systems.

Acknowledgements: The first author is supported by the Advanced and Innovational Research Program in Life Sciences from Ministry of Education, Culture, Sports, Science and Technology, the Japanese Government.

§§. *References*

- [1] A. Aertsen et al., *Physica D*, 75 (1994), 103-128.
- [2] B. Cauli et al., *J. Neurosci.*(1997), 3894-3906.
- [3] J.A. Connor et al., *Biophys.J.*18 (1977), 81-102.
- [4] W. J. Freeman, *Societies of Brains – A Study in Neuroscience of Love and Hate*, Lawrence Erlbaum Associates, Inc., Hillsdale, 1995.
- [5] H. Fujii et al., *Neural Computation*, Vol. 9, No. 8, 1303-1350 (1996).
- [6] H. Fujii and I. Tsuda, in preparation.
- [7] M. Galarreta and S. Hestrin., *Nature* 402 (1999), 72-75.
- [8] J.R. Gibson et al., *Nature* 402 (1999), 75-79.
- [9] C. Gray et al., *Visual Neuroscience* 8 (1992), 337-347.
- [10] S.K. Han et al., *J. Bifurc. and Chaos*, No.4 (1997), 869-876.; *Phys. Rev. Lett.* 75 (1995), 3190-3193.
- [11] A.L. Hodgkin, *J. Physiology* (1948), 107, 165-181.
- [12] L. Kay et al., *Intern. J. Neural Systems* 7(1996), 489-495.
- [13] J. Milnor, *Comm. In Math Physics*, 99(1985), 177-195.
- [14] J. Rinzel., *Fed. Proc.* 44 (1985), 2944-2946.
- [15] M.A. Rogawski. *TINS* 8 (1985), 214-219.
- [16] R.M. Rose and J.L. Hindmarsh. *Proc. R. Soc. Lond. B* 237 (1989), 267-288.
- [17] T. Sauer, *Abstracts for SIAM Pacific Rim Dynamical Systems Conference*, August 9-13, 2000, Hawaii, 51.
- [18] C. A. Scarda and W. J. Freeman, *Behavioural and Brain Sciences* 10 (1987), 161-195.
- [19] N. Schweighofer et al., *J. Neurophysiol.* 82 (1999), 804-817.
- [20] G. Tamas et al., *Neuroscience.* 3 (2000), 366-371.
- [21] I. Tsuda, *World Futures* 32 (1991), 167-185.
- [22] I. Tsuda, H Fujii et al., manuscript.
- [23] C. von der Malsburg, *Internal Report 81-2*, Max-Planck-Institute for Biophysical Chemistry, 1981.
- [24] H. R. Wilson, *J. Theor. Biol.* (1999a), 200, 375-388.