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# Stochastic resonance in the hippocampal CA3–CA1 model: a possible memory recall mechanism

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## Abstract

Stochastic resonance (SR) in a hippocampal network model was investigated. The hippocampal model consists of two layers, CA3 and CA1. Pyramidal cells in CA3 are connected to pyramidal cells in CA1 through Schaffer collateral synapses. The CA3 network causes spontaneous irregular activity (broadband spectrum peaking at around 3 Hz), while the CA1 network does not. The activity of CA3 causes membrane potential fluctuations in CA1 pyramidal cells. The CA1 network also receives a subthreshold signal (2.5 or 50 Hz) through the perforant path (PP). The subthreshold PP signals can fire CA1 pyramidal cells in cooperation with the membrane potential fluctuations that work as noise. The firing of the CA1 network shows typical features of SR. When the frequency of the PP signal is in the gamma range (50 Hz), SR that takes place in the present model shows distinctive features. 50 Hz firing of CA1 pyramidal cells is modulated by the membrane potential fluctuations, resulting in bursts. Such burst firing in the CA1 network, which resembles the firing patterns observed in the real hippocampal CA1, improves performance of subthreshold signal detection in CA1. Moreover, memory embedded at Schaffer collateral synapses can be recalled by means of SR. When Schaffer collateral synapses in subregions of CA1 are augmented three-fold as a memory pattern, pyramidal cells in the subregions respond to the subthreshold PP signal due to SR, while pyramidal cells in the rest of CA1 do not fire. © 2002 Elsevier Science Ltd. All rights reserved.

**Keywords:** Stochastic resonance; Hippocampus; Neural network model; Memory recall; Pyramidal cell model; Spontaneous rhythmic activity; Colored noise; Burst discharges

## 1. Introduction

Noise often enhances the detection of subthreshold signals in bistable and monostable nonlinear systems. This phenomenon is known as stochastic resonance (SR). SR of a bistable system was proposed for the first time to explain the periodicity of ice ages (Benzi, Sutera, & Vulpiani, 1981). Bistable systems show switching between two stable states, which is stochastic but somewhat coherent, to a weak periodic signal with the aid of a noise. SR has been studied in many physical systems, for example, Schmitt trigger (Fauve & Heslot, 1983), ring laser (McNamara, Weisenfeld, & Roy, 1998) and Josephson junctions (Hibbs et al., 1995).

SR also takes place in monostable systems with a threshold; where the systems cause transitory excitation when the threshold is exceeded stochastically, and the systems then return to a stable state deterministically. One such well-known monostable system is the neuron. SR has therefore been studied in neuron models and neural networks (Collins, Chow, & Imhoff, 1995; Kanamaru, Horita, & Okabe, 1998; Longtin, 1993; Moss, Douglass, Wilkens, Pierson, & Pantazelou, 1993).

One of the recent attractive issues about SR is the relevance of SR to biological functions. Mechanoreceptor cells (sensory neurons) of the crayfish would detect weak water motions caused by predators using SR where turbulence of water works as noise (Douglas, Wilkens, Pantazelou, & Moss, 1993). In the central nervous system (CNS), it is supposed that people's ability to resolve ambiguous figures may be connected to SR (Riani & Simonotto, 1994). It has also been shown that SR improves

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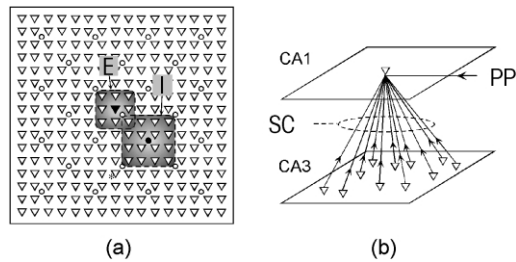


Fig. 1. Network structure of the CA3–CA1 model. (a) Intra-network structure of CA3 and CA1 regions. 256 pyramidal cells ( $\nabla$ ) are placed on  $16 \times 16$  lattice points. Each pyramidal cell in CA3 (CA1) is connected to its nearest and next nearest neighbors through excitatory synapses whose conductance is  $C_{pp\_CA3}$  ( $C_{pp\_CA1}$ ). For example, the pyramidal cell  $\blacktriangledown$  is mutually connected to other pyramidal cells in the area E. 25 interneurons ( $\circ$ ) are placed uniformly among pyramidal cells. Each interneuron in CA3 (CA1) receives excitatory synaptic input from 16 nearby pyramidal cells through synapses whose conductance is  $C_{pi\_CA3}$  ( $C_{pi\_CA1}$ ) and inhibits the same cells through synapses whose conductance is  $C_{ip\_CA3}$  ( $C_{ip\_CA1}$ ). For example, interneuron  $\bullet$  is connected to the pyramidal cells in the area I recurrently. (b) Network structure between CA3 and CA1. Each CA1 pyramidal cell receives excitatory synaptic input from 100 CA3 pyramidal cells randomly chosen out of all the CA3 pyramidal cells through SC connections whose conductance is  $W_{sch}$ . Every CA1 pyramidal cell also receives excitatory synaptic input through PP whose synaptic conductance is  $W_{per}$ .

subthreshold signal detection in a single hippocampal CA1 pyramidal cell (Stacey & Durand, 2000). Pulse trains that were subject to Poisson processes were applied to a single pyramidal cell through many synapses to cause SR. However, a clear mechanism showing how SR plays a functional role in CNS has not yet been reported. The reason could be that it is more difficult to find what the signal is and what the noise is in CNS than in the sensory neurons.

The hippocampus is a brain tissue essential to learning and short-term memory. The major afferent fibers to the hippocampus are perforant path (PP) fibers from the entorhinal cortex (EC). PP fibers from layer II of EC (EC-II) are projected to granule cells in the dentate gyrus (DG), and axons of the granule cells, namely mossy fibers, are projected to pyramidal cells in the hippocampal CA3 region. On the other hand, PP fibers from layer III of EC (EC-III) are projected directly to pyramidal cells in the hippocampal CA1 region.

The CA3 region spontaneously generates rhythmic activity such as theta, delta and beta activities. These spontaneous activities are quite irregular. Although these activities have their own main frequency components, their power spectra contain broadband frequency components just like colored noise. Each CA3 pyramidal cell projects its axons, namely Schaffer collaterals (SC), to approximately 10,000–35,000 CA1 pyramidal cells (Li, Somogyi, Ylinen, & Buzsáki, 1994). In other words, each CA1 pyramidal cell receives SC fibers from numerous CA3 pyramidal cells, and integrated excitatory postsynaptic potentials (EPSPs) at SC synapses caused by spontaneous activity of CA3 would thus be relatively strong and noisy. Gamma oscillations (40–

100 Hz) have been observed in EC-III and are expected to be projected to CA1 through PP fibers (Chrobak & Buzsáki, 1996). Connections from EC-III to CA1 through PP are almost point-to-point (Buzsáki, Penttonen, Bragin, Nádasdy, & Chrobak, 1995). Moreover, it is known that input to CA1 through PP alone is too weak to cause discharges of CA1 pyramidal cells (Colbert & Levy, 1992).

Therefore, membrane potential fluctuations of CA1 pyramidal cells caused by the irregular activity of CA3 would work as noise, and PP input to CA1 would be a subthreshold signal that could be detected by SR. Since the axons of CA1 pyramidal cells are major efferent fibers from the hippocampus, resulting activity of CA1 pyramidal cells goes back to layer V of EC (EC-V) as an output of the hippocampus.

The purpose of this paper is to examine the hypothesis that CA1 pyramidal cells can be fired by subthreshold PP signals in cooperation with the activity of CA3, using a hippocampal network model. Moreover, we will show that SR is a possible mechanism of memory recall in the hippocampus. We first introduce the CA3–CA1 network model. Pyramidal cells in the CA3 network are connected to pyramidal cells in the CA1 network through SC synapses. The CA3 network causes spontaneous activity, while the CA1 network does not. Secondly, we demonstrate that membrane potential fluctuations of each CA1 pyramidal cell, caused by the CA3 activity, work as noise, and that the amplitude of the noise depends on the SC connection strength. Thirdly, we demonstrate SR in CA1. Subthreshold PP signals can fire pyramidal cells in CA1 in cooperation with the activity of CA3. The signal-to-noise ratio (SNR) of the responses of CA1 pyramidal cells depends on the SC connection strength and shows typical features of SR. Finally, we propose a memory recall model based on SR and discuss the possibility of SR being a mechanism of memory recall in the hippocampus. A preliminary report has been published as a conference proceeding (Yoshida, Hayashi, & Ishizuka, 2000).

## 2. CA3–CA1 neural network model

The hippocampal CA3–CA1 model consists of two networks that correspond to the CA3 and CA1 regions (Fig. 1(b)). The CA3 network model developed by Tateno, Hayashi, and Ishizuka (1998) was adopted and modified to develop a CA1 network model. Each network contains 256 pyramidal cells and 25 inhibitory interneurons (Fig. 1(a)).

### 2.1. Cell models

The CA3 pyramidal cell model is a single-compartment model developed by Tateno et al. (1998). The equations of

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