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Stochastic resonance with differential code in feedforward network with intra-layer random connections

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Abstract

We examined stochastic resonance with a differential coding scheme using a multilayer feedforward neural network which is composed of intra-layer connections. We show that the network, with random synaptic connections in each layer, encodes an input signal into a spike coherence that represents temporal differences among the inputs. We also demonstrate that both internal and external noise enhance the detection of weak signals. Finally, we discuss how the feedforward network with intra-layer random connections is similar to a membrane in its sensitivity to and amplification of a change in stimulus and suggest that the intensity of internal noise may be tuned in a real brain.

Keywords: Feedforward multilayer network; Intra-layer random connection; Differential coding; Stochastic resonance; Hodgkin-huxley model; Noise tuning

1. Introduction

Stochastic resonance (SR) is a phenomenon in which a nonlinear system heightens the sensitivity to a weak signal input (Jung, 1993; Moss, Pierson, & O'Gorman, 1994; Wiesenfeld & Moss, 1995) when noise with an optimal intensity is presented simultaneously. SR in neural systems has been studied using single neuron models (Bulsara et al., 1996; Chapeau-Blondeau, Godivier, & Chambet, 1996; Longtin, 1993; Rudolph & Destexhe, 2001; Sakumura & Aihara, 2002), neural network models (Collins, Chow, & Imhoff, 1995; Wang, Chik, & Wang, 2000), and real neurons including those in the brain (Cordo et al., 1996; Collins, Imhoff, & Grigg, 1996a; Douglass, Wilkens, Pantazelou, & Moss, 1993; Fallon, Carr, & Morgan, 2004; Gluckman et al., 1996; Manjarrez, Diez-Martinez, Mendez, & Flores, 2002).

Neurons and neural networks in the brain are real systems that detect and process signals coming from the outside of the brain. It is unclear, however, precisely how such signals are represented in these systems. In theoretical studies on SR, input signals are assumed to be periodic continuous (sinusoidal) (Longtin, 1993), aperiodic continuous (filtered white Gaussian) (Collins, Chow, & Imhoff, 1995), periodic discrete (pulse current) (Chapeau-Blondeau, Godivier, & Chambet, 1969), or aperiodic discrete (Poisson spikes) (Sakumura & Aihara, 2002). The output signal of an SR system is then evaluated with respect to the same characteristics as the input signals; when an input is periodic, the output is evaluated on the basis of its periodical characteristics (e.g. spectrum), and when an input is aperiodic, the output is evaluated by quantifying its temporal characteristics (e.g. time course of firing rate or spike timing).

Despite this theoretical input-output matching, it is not necessary for real neural systems to express input and output signals in the same way. Signals may be processed rapidly and in parallel, and be treated in various expression schemes in many cortical areas. Experimental studies have reported that spike frequency is high (30–70 Hz) in sensory cortical areas (Eckhorn et al., 1988; Gray, König, Engel, & Singer, 1989) but low (0–10 Hz) when spikes are transferred to the prefrontal cortex (Jung, McNaughton, & Barnes, 1998). These facts suggest that signal representation by neural populations differs between brain areas. Therefore, signal detection mechanisms like SR in the brain should be examined by considering individually the manner of signal expression both for the input and the output.

Signal processing by feedforward networks without intra-layer connections has been studied (Litvak, Sompolinsky,

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Segev, & Abeles, 2003; Masuda & Aihara, 2002; Reyes, 2003; Shadlen & Newsome, 1998; van Rossum, Turrigiano, & Nelson, 2002). In this article, on the other hand, we focus on signal representation and transduction in a feedforward multilayer network with the intra-layer connections. In the model network, neurons in each layer are connected mutually and randomly. In particular, feedback excitation and inhibition in an intra-layer circuit and excitatory synaptic depression are explored. It is shown that the linear transduction of input signal into a spike coherence which represents the differential component of the input is achieved with random synaptic connections among neurons in the intra-layer circuit, and that the detection of weak signals is enhanced by external and internal noise with a moderate intensity in a manner similar to SR.

2. Models

2.1. Neuron model

In this study, an excitatory neuron is modeled by a Hodgkin–Huxley-type ionic conductance model composed of a single compartment (Hodgkin & Huxley, 1952). The membrane potential V (mV) is expressed as the following differential equation:

$$C_{\mathrm{m}} \frac{\mathrm{d}V}{\mathrm{d}t} = -\sum_{j=Na,K,l} g_j \cdot (V - V_j) + I_{\mathrm{syn}}, \tag{1}$$

where C_{m} ($=1.0$ (μF/cm^2)) is the membrane capacitance, g_{Na} ($=120.0\ \mathrm{m}^3\ \mathrm{h}$ (mS/cm^2)) is the fast sodium conductance, g_{k} ($=36.0n^4$ (mS/cm^2)) is the delayed rectifier potassium conductance, and $g_l(=0.3$ (mS/cm^2)) is the leak conductance. Variables m, h, and n obey the differential equation $\mathrm{d}x/\mathrm{d}t = (\alpha_x(1-x) - \beta_x x)\cdot 3^{((15-6.3)/10)}$, where $x=m,h,n$, and voltage-dependent functions α_x and β_x are as previously described (Hodgkin & Huxley, 1952). Reversal potentials (mV) are as follows: $V_{Na}=50.0-E_r$, $V_K=-77.0-E_r$, and $V_l=-54.4-E_{\mathrm{r}}$, where E_r ($=-65.0$ (mV)) is the resting potential. Synaptic current l_{syn} is the sum of excitatory and inhibitory synaptic currents (reversal potentials $V_{\mathrm{exc}}=0.0-E_r$ and $V_{\mathrm{inh}}=-70.0-E_{\mathrm{r}}$ (mV)).

The conductance induced by the ith synaptic event is defined by an α function (Jack, Noble, & Tsein, 1975; Rall & Segev, 1987):

$$g^i_{\mathrm{syn}}(t) = r_i \cdot \frac{g_{\mathrm{peak}} \cdot (t - t_i)}{t_{\mathrm{peak}} \cdot S} \mathrm{e}^{1-(t-t_i)/t_{\mathrm{peak}}}, \tag{2}$$

where r_i is the synaptic efficacy (see below), S is the surface area of a soma represented as a sphere with radius 20 (μm), t_i (ms) is the occurrence time of the ith synaptic event and t_{peak} (ms) is the interval between t_i and the time at which the conductance reaches its peak value of g_{peak}/S (mS/cm^2).

2.2. Network architecture

A model neural network is composed of 100 parallel feedforward multilayer networks, each of which is illustrated in Fig. 1a. We performed simulation runs for the same architecture (Fig. 1a) a hundred times, providing different intra-layer connections for each simulation run.

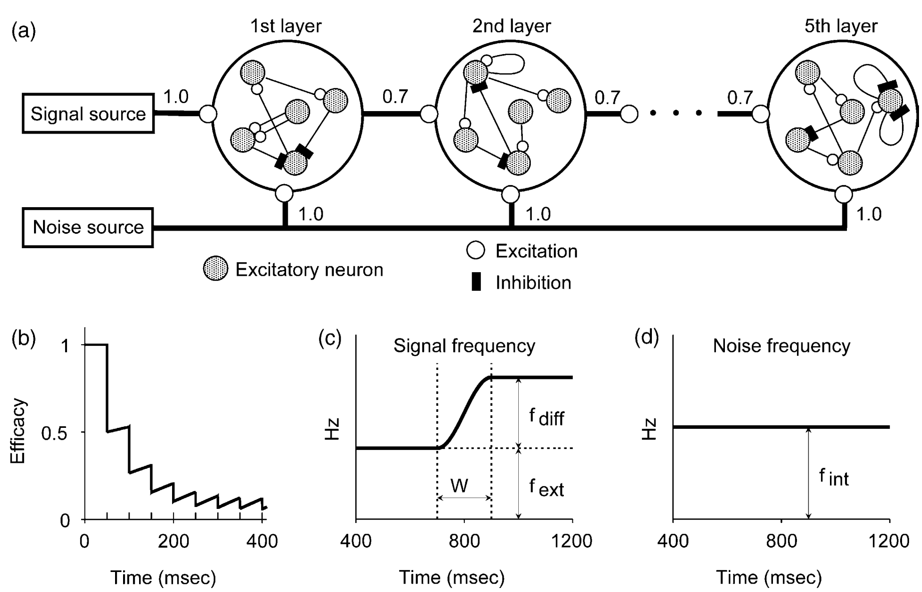

Fig. 1. Schematic diagrams of the model. (a) One processing path is modeled as a feedforward multilayer network. There are 100 excitatory neurons in each layer in which the single neuron has N_E excitatory depressing synaptic connections directly with neurons including itself. The neuron also gives inhibitory effect to N_I neurons. It is assumed that this inhibition comes indirectly from an inhibitory gap junction network. The numbers 1.0 and 0.7 represent connection probabilities (see text). (b) Sample of depressing transmission efficacy of excitatory synaptic events that occur periodically (depressing fraction $\delta=0.5$, period 50 ms). (c) The signal frequency (Hz) changes from $f_{\mathrm{ext}}(t<765)$ to $f_{\mathrm{ext}}+f_{\mathrm{diff}}(805<t)$ in a sinusoidal manner (change interval $W=10$ ms). (d) The noise source has a constant frequency f_{int}.