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Dynamical Reorganization of Attractor Structure in Neural Networks with Dynamic Synapses

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Abstract—We investigate the dynamical properties of a neural network with dynamic synapses, whose transmission efficacy is modulated by short-term plasticity, and we use a mean field model that approximates the population dynamics of spiking neurons. In particular, we consider a neural network with recurrent connections via depression and facilitation synapses, and we analyze the influence of synaptic modulation on the dynamics of synaptic activity via slow-fast analysis with time-parameterized bifurcation parameters. The model is described by three variables: one represents synaptic activity, whereas the other two represent modulation in synaptic transmission efficacy. The variables that represent the synaptic modulation can be considered as slow variables that affect the properties of synaptic activity, which can be regarded as the fast variable. The analysis indicates that an attractor in the fast system corresponding to an active state of the neural network appears or disappears according to the activities of the neural network. The concept of dynamical reorganization of the attractor structure can potentially uncover the mechanism of flexible brain functions.

1. Introduction

A population of neurons forms a network with synaptic connections, which transmit electric signals and contributes to various information processing in the brain. The dynamics of a neural population is often characterized by the attractor structure. In the state of a neural network characterized by an attractor, a pattern of neural activity is maintained for a while, even under noise or disturbance. For instance, Hopfield proposed that in a neural network model of memory association, the process of memory retrieval can be considered as a process of convergence to an attractor [1]. Further, the mechanism of the working memory in the brain can be understood on the basis of the attractor structure. The dynamics of a population of neurons connected with a certain type of synapses forms a bistable system [2]; one of the attractors is the state in which neurons maintain their activity by sending excitatory signals to each other, and the other attractor is the resting state of the neurons. Such a neural network that acts as a working memory is able to retain a fragment of information by switching its state. The concept of the attractor structure is crucial to understanding the mechanism of representation and processing of information in the brain.

In the abovementioned studies, the strength of synaptic connections is assumed to be static. However, recent physiological studies have revealed that the transmission efficacy of synapses undergoes dynamic short-term changes with the consecutive activation of presynaptic neurons [3]. This dynamical property of synapses is known as short-term plasticity, and such synapses are called dynamic synapses. The modulation in the synaptic transmission efficacy effectively changes the formation of the network structure. Thus, the attractor structure of the network are also influenced by the dynamic synapses. This concept, referred to as dynamical reorganization of the attractor structure, is useful for understanding the functions of neural networks. For instance, the mechanism of flexible information representation in the prefrontal cortex can be explained on the basis of this concept [4].

The time scales of changes in synaptic modulation with short-term plasticity are longer than those of neural membrane potentials or synaptic activities that represent the ratio of open receptor channels in the synapses. Thus, variables that describe synaptic activity and synaptic modulation can be considered as fast and slow variables, respectively. In other words, slow variables can be considered as bifurcation parameters that influence the properties of a system with fast variables (fast system), and such slow variables reorganize the attractor structure of the fast system.

Slow-fast analysis focuses on the differences between the time scales of dynamical variables, and it is potentially applicable to various biological and neural systems. For instance, the dynamics of a bursting neuron can be explained by this approach [5, 6]. A slow variable in a neuron acts as a bifurcation parameter and switches the properties of a fast system between the resting state and the firing state, which are characterized by a stable equilibrium and a limit cycle, respectively. In previous studies, a single variable has been primarily considered as the slow variable.

In this paper, we analyze the dynamical properties of a neural network with dynamic synapses, including both depression and facilitation synapses, by considering that multiple slow variables are parameterized with the time variable. In the next section, we describe the mean field model, which consists of variables that represent synaptic activity and synaptic modulation. Then, we analyze how the attractor structure in the fast system is reorganized via synaptic modulation by using the abovementioned slow-fast analysis. Finally, we discuss the possible interpretations of the analysis results.

2. Model

We consider the mean field model that approximates the population dynamics of a spiking neural network with recurrent connections via dynamic synapses [4]. In the mean field model, the firing rate r is given by a firing rate response function $f(g)$ as a function of input conductance g: $r = f(g)$, where $f(g) = r_0(g - g_0)^N/\{\Theta^N + (g - g_0)^N\}$ when $g > g_0$; otherwise, $f(g) = 0$. We set $r_0 = 0.070, g_0 = 8.183$, $\Theta = 2.283$, and $N = 2$ [4]. When the neurons fire, synapses on the axonal terminal of the neurons will be activated. In the present model, the variables s, x, and u represent the synaptic activity, the ratio of releasable neurotransmitters, and the calcium concentration, respectively. The synaptic activity s represents the ratio of open receptors that induce the post synaptic current. We assume that s converges to a certain steady state with a time constant $\tau_s = 90$ [ms],

$$\frac{ds}{dt} = \frac{\bar{s}(r) - s}{\tau_s}, \tag{1}$$

where $\bar{s}(r) = r\tau_s(1 - \exp(-1/(r\tau_s)))$ is the steady state of the synaptic activity as a function of the firing rate. When the synapses are activated, the ratio of releasable neurotransmitters x transiently decreases and the calcium concentration u transiently increases, depending on the firing rate. If the neuron does not fire, x and u recover its steady states $x = 1$ and $u = U$ with the time constants τ_x and τ_u, respectively. This situation can be described by the equations [7, 8]

$$\frac{dx}{dt} = \frac{1 - x}{\tau_x} - uxr, \tag{2}$$

$$\frac{du}{dt} = \frac{U - u}{\tau_u} + U(1 - u)r, \tag{3}$$

where $U = 0.3$ is the steady state of u. The synaptic efficacy (the synaptic modulation) is proportional to the product xu. Differences between depression and facilitation synapses are specified by parameters τ_x and τ_u.

Here, we consider the neurons that are mutually connected with depression or facilitation synapses. The input conductance for the population of neurons is given by

$$g(t) = I_0 + g_R s(t)x(t)u(t)/U + I_e(t), \tag{4}$$

where $I_0 = 8$ is the constant bias input and g_R is the absolute strength of the recurrent connection. The term $x(t)u(t)/U$ is unity in the resting state, and it tends to be larger (smaller) than unity when the synapses are facilitated (depressed). $I_e(t)$ is a time dependent external input. Here, we use $\tau_x = 500$ [ms], $\tau_u = 150$ [ms], and $g_R = 3.2$ for a network with depression synapses, and $\tau_x = 150$ [ms], $\tau_u = 1000$ [ms], and $g_R = 1.9$ for a network with facilitation synapses.

3. Results and Analyses

We analyze the dynamical properties of the neural network according to the following procedure. Suppose that $\mathbf{x}$ is a whole variable in a given dynamical system and that it develops according to the differential equation $d\mathbf{x}/dt = F(\mathbf{x})$. First, the time course of $\mathbf{x}(t)$ is obtained by solving the differential equation with a given initial state. The variable $\mathbf{x}$ is divided into fast variables $\mathbf{x_f}$ and slow variables $\mathbf{x_s}$. Then, we consider the following differential equation with respect to the fast system,

$$\frac{d\mathbf{x_f}}{dt} = F_f(\mathbf{x_f}, \mathbf{x_s}(t')), \tag{5}$$

where F_f returns the part of the fast variables of F. We perform bifurcation analysis on the fast system with respect to the bifurcation parameters $\mathbf{x_s}$ parameterized by the time t'. We denote an attractor on the fast system by merely calling it an attractor.

In the present neural network model, the time scales of changes in variables x and u are relatively longer compared with that in s. Thus, in the following analyses, we regard x and u as slow variables and s as the fast variable.

3.1. Network with Depression Synapses

Figure 1 shows a typical response in the recurrent network with depression synapses when the activation input is applied during $0.3 < t < 0.5$ [s] (Fig. 1d). The neural network is transiently activated by the activation input and its activity decay with a decrease in synaptic efficacy (Fig. 1b). The variables x and u are decreased and increased, respectively; their product xu, which represents the synaptic efficacy, is decreased (Fig. 1c).

In Figure 1b, the blue curves indicate the emergence of equilibrium in the fast system; the solid and dashed curves represent stable and unstable equilibrium, respectively. The emergence of equilibrium changes with time. In the initial state, there exists an unstable equilibrium (UE) point and two stable equilibrium (SE) points. One of the SE points corresponds to the active state (SEa) with a relatively large value of s ($s \approx 0.9$), and the other corresponds to the resting state (SEr) with a smaller value of s ($s \approx 0$). The synaptic activity s initially remains in the resting state (SEr).

By applying the activation input, UE and SEr disappear, and the synaptic activity s increases toward the active state

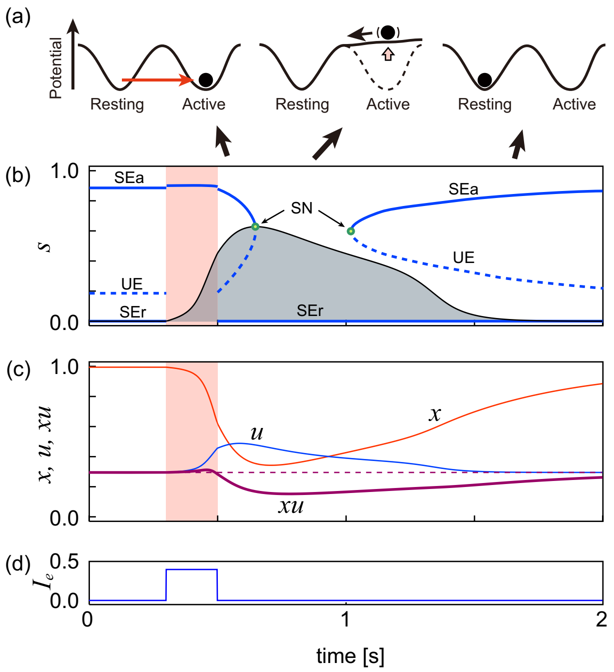

Figure 1: Response in the network with depression synapses. (a) Schematic attractor landscapes. (b) Time course of s (shaded black curve) and sets of equilibrium point. Stable equilibrium (SE) and unstable equilibrium (UE) are indicated by solid and dashed blue curves, respectively. The SE that corresponds to the active and resting state is denoted by SEa and SEr, respectively. The points of saddle-node (SN) bifurcation are indicated by circles. The red area represents the period of the activation input. (c) Time course of x, u, and their product xu, which represents the synaptic efficacy. The steady state of xu is indicated by the dashed line. (d) Time course of the external input.

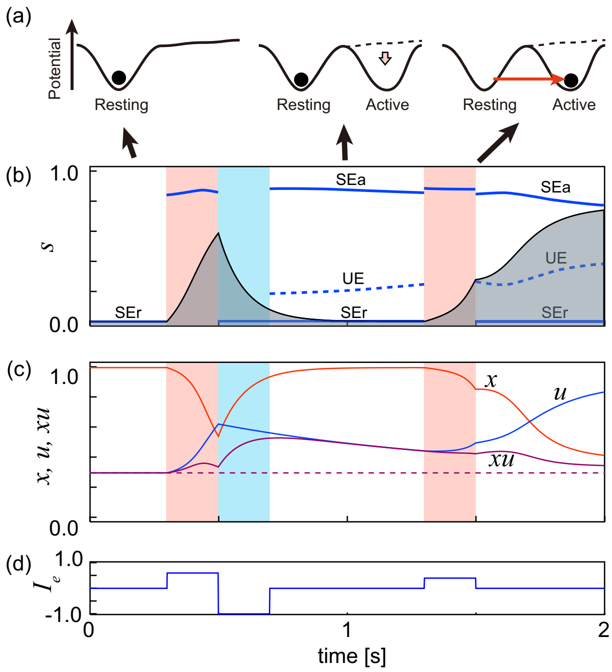

Figure 2: Response in the network with facilitation synapses. The format is the same as that of Figure 1. The blue area indicates the period of the deactivation input.

(SEa). After the application of the activation input, the pair of unstable and stable equilibriums re-emerges and s converges to SEa. This situation is shown in the schematic attractor landscape (Fig. 1a left). As time goes by, UE and SEa approach each other and disappear via saddle-node bifurcation in the fast system. s increases until this bifurcation point and then decreases and converges to the resting state (Fig. 1a middle). Then, the pair of UE and SEa reappears, and the network recovers its initial state (Fig. 1a right).

The reorganization of the attractor structure illustrates the changes in the functions of a neural network. This initial bistability of the resting and active states characterizes the mechanism of the working memory, in which neurons send excitatory signals to each other and maintain their activity in the brain [2, 8]. With this bistability, the network acts as an element of short-term memory, which stores a fragment of information in its active state. This active state is triggered by the activation input, but as time goes by, the network loses its stability, i.e., its ability to hold information. Finally, the network returns to the resting state and recovers the ability of short-term memory.

3.2. Network with Facilitation Synapses

Figure 2 shows the response of the network with facilitation synapses when we applied the activation, deactivation, and perturbation input. Here, we set the absolute strength of recurrent connection g_R to be relatively small; thus, in the initial state, SEa does not appear (Fig. 1a left). Instead, SEa appears because of the facilitation of synapses. By applying the activation input, the synaptic efficacy is increased, and SEa appears even after the deactivation of neural activity (Fig. 1a middle).

Because of this facilitation of synaptic efficacy, the network tends to be easily activated by a perturbation input (Fig. 1a right). Figure 2b shows that a network with facilitated synapses can be easily activated by the perturbation input during $1.3 < t < 1.5$ [s]. We confirmed that the network cannot be activated by the perturbation input without the facilitation of synaptic efficacy caused by the activation input. If the perturbation input is not applied, the pair UE and SEa disappears via saddle-node bifurcation.

In a network with facilitation synapses, the attractor is newly formed in the fast system by the activation input. The response of the network for a given external input is influenced by the formation of the attractor. This indicates that the ability to hold information in the neural network is transiently induced by the activation input. In other words, this situation can be interpreted as a context-dependent property of neural activity.

4. Discussion

We analyzed the dynamical properties of a neural network with depression and facilitation synapses by considering the modulations in synaptic efficacy as slow variables or bifurcation parameters. The analyses show the dynamical reorganization of the attractor structure, which characterizes the functions of the neural network. In a network with depression synapses, the attractor that corresponds to the active state of the neural network is destabilized because of synaptic depression. The destabilization of the attractor indicates the loss of the ability to hold information. In a network with facilitation synapses, the attractor is newly formed by the activation input and influences the subsequent neural response.

We emphasize that the roles of a neural network can be manifested by knowing the formation of the attractor structure and that the dynamical reorganization of the attractor structure describes changes in the network function. The state of the neural network will converge to one of attractors in the neural system. Each attractor may represent a piece of information or a certain mental state. Dynamical reorganization of the attractor structure leads to a remapping between an attractor and a piece of information and changes the roles in information representation [4].

In the ordinary framework of dynamical system theory, the dynamics of the present neural network model is merely characterized as a transient process of convergence to an equilibrium state. Although slow-fast analyses provide a clear-cut view for a system including fast and slow variables, only one variable is considered to be the slow variable in most conventional slow-fast analyses. However, in general, multiple variables can be considered as slow variables. In the present analysis, variables were divided into fast and slow variables, and the slow variables were regarded to be parameterized by time. Slow-fast analysis with time-parameterized bifurcation parameters allows us to extend it to systems consisting of many more slow variables.

Although we applied this method to a simple neural network model with two slow variables that represent synaptic modulation, it can be applied to a more complex neural network that may be a more functional network. Furthermore, this approach can be applied to other neural systems or biological systems that include different time scales of dynamics. Our approach should be evaluated on such systems in the future studies.

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