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# Memories as bifurcations: Realization by collective dynamics of spiking neurons under stochastic inputs

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## ABSTRACT

How the neural system proceeds from sensory stimuli to generate appropriate behaviors is a basic question that has not yet been fully answered. In contrast to the conventional viewpoint, in which the external stimulus dominantly drives the response behavior, recent studies have revealed that not only external stimuli, but also intrinsic neural dynamics, contribute to the generation of response behavior. In particular, spontaneous activity, which is neural activity without extensive external stimuli, has been found to exhibit similar patterns to those evoked by external inputs, from time to time. In order to further understand the role of this spontaneous activity on the response, we propose a viewpoint, memories-as-bifurcations, that differs from the traditional memories-as-attractors viewpoint. According to this viewpoint, memory is recalled when spontaneous neural activity is changed to an appropriate output activity upon the application of an input. After reviewing the previous rate-coding model embodying this viewpoint, we employ a model of a spiking neuron network that can embed input/output associations, and study the dynamics of collective neural activity. The organized neural activity, which matched the target pattern, is shown to be generated even under application of stochastic input, while the spontaneous activity, which apparently shows noisy dynamics, is found to exhibit selectively higher similarity with evoked activities corresponding to embedded target patterns. These results suggest that such an intrinsic structure in the spontaneous activity might play a role in generating the higher response. The relevance of these results to biological neural processing is also discussed.

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## 1. Introduction

How sensory input is transformed to generate appropriate behaviors in a neural system is critically important to understand neural processing. In the conventional view, it is considered that sensory stimuli drive neural activity in the lower sensory cortex, and that this neural activity, in turn, evokes changes in the neural activity of the higher cortex, as is often represented by information processing on the feed-forward layer network. Extensive theoretical studies have been carried out to elucidate this information processing in such layered networks (Rumelhart & McClelland, 1986).

Recent experimental studies, however, have revealed that the neural activities are not only processed along such feed-forward layered networks, but that there are many feedback projections and internal connections in each cortex. Rich neural-activity dy-

namics is observed, even without sensory input, and is called spontaneous activity, or on-going activity (Luczak, Bartho, Marguet, Buzsaki, & Harris, 2007; Raichle et al., 2001). Neural information processing is a result of the interplay between the intrinsic dynamics of the neural network, and its external inputs.

One often observed characteristic behavior of spontaneous activity is its similarity with the activity evoked by a sensory stimulus (Berkes, Orbán, Lengyel, & Fiser, 2011; Kenet, Bibitchkov, Tsodyks, Grinvald, & Arieli, 2003; Luczak, Bartho, & Harris, 2009). Although there have been theoretical studies for over a decade that attempted to characterize the spontaneous activity (Amit & Brunel, 1997; Destexhe & Contreras, 2006), the relationship between the spontaneous and evoked activities as well as its response against external input has not yet been fully elucidated (Marre, Yger, Davison, & Fregnac, 2009). To analyze this relationship, we have focused on memories of the input/output (I/O) map, one of the principle functions of the neural system, and proposed a novel viewpoint of memory (Kurikawa & Kaneko, 2011), which we have termed “memories as bifurcations”. This view is in sharp contrast to the

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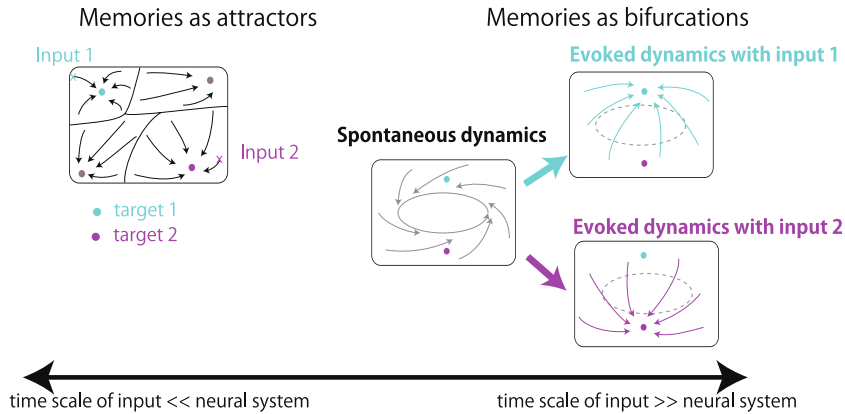


Fig. 1. Schematic representations of the two viewpoints, memories-as-bifurcations and memories-as-attractors.

conventional memory viewpoint (Amit, 1992), “memories as attractors”, as will be briefly reviewed below.

The present paper is organized as follows. In Section 2, we introduce our novel viewpoint “memories-as-bifurcations” and review our earlier study based on a rate-coding model. Here, chaotic spontaneous behavior shows similarity to evoked activities. We then study whether this viewpoint can be realized by using the leaky integrate-and-fire neuronal network. A specific neural model, as well as the organization of the neural network required to achieve the viewpoint is introduced in Section 3. Results from extensive simulations of the model are described in Section 4, which demonstrate that the memory of a sufficiently large number of I/O mappings is indeed stored, while apparently irregular spontaneous activity is observed, in which collective neural activity showing similarity with the memorized patterns is embedded. Finally, in Section 5, we discuss the possible interpretation of our results and make some predictions to be checked experimentally.

## 2. Memories as bifurcations

In the memories-as-attractors viewpoint (Fig. 1), each memory is embedded as one of the attractors in a unique neural dynamical system. An input specifies an initial condition of the dynamical system, and from that initial state, the neural activity reaches an attractor that matches the target corresponding to the given input. Thus, the initial states are determined by the given inputs, but the neural activity in the absence of inputs is not examined. Many neural network models have been extensively studied according to this viewpoint (Amit, 1992; Ben-Yishai, Bar-Or, & Sompolinsky, 1995; Hopfield, 1984). In particular, it is widely considered that persistent activity, observed after a cue for a delay-response task (with working memory) is applied (Miyashita, 1988; Wang, 2001), results from attractor dynamics in a recurrent neural network (Amit & Mongillo, 2003; Brunel, 2003; Durstewitz, Seamans, & Sejnowski, 2000). This viewpoint, however, does not fit with the analysis of spontaneous activity, where the explicit input does not exist. Indeed, in spite of a few theoretical studies about the possible role of spontaneous activity (Destexhe & Contreras, 2006) and the similarity of spontaneous and evoked activity (Marre et al., 2009), the relationship between spontaneous activity and embedded patterns has hardly been investigated.

In contrast to this conventional viewpoint of memory, we have proposed a novel memory scheme quite recently (Kurikawa & Kaneko, 2011), in which neural activity shows bifurcation upon an input, i.e., an input modifies the neural dynamics as a parameter, and the flow structure of the neural activity is changed from the state it is in without an input. In the absence of an input, the neural activity evolves and corresponds to spontaneous activity. In the presence of a learned input, the flow structure of the neural dy-

namics changes and an attractor that matches the requested target corresponding to the applied input emerges. With an increase in the input strength, the flow structure changes via a sequence of bifurcations in terms of dynamical systems theory. Here, the flow structure can be changed substantially by applying different memorized inputs. Thus, for this viewpoint, termed as memories-as-bifurcations (Fig. 1), memories are embedded in the flow structure of the neural dynamics such that appropriate bifurcations occur upon the application of input.

In this viewpoint, input is clamped during the recall process, whereas the input is applied instantaneously to set the initial condition in the memories-as-attractors. Our viewpoint might be helpful for understanding information processing, for instance, in the olfactory system (Bathellier, Buhl, Accolla, & Carleton, 2008; Mazor & Laurent, 2005; Niessing & Friedrich, 2010) or place cells in the hippocampus (Foster & Wilson, 2006; Leutgeb et al., 2005; O’Keefe & Dostrovsky, 1971). In the olfactory system, the response of neural activity to an odorant, which is applied for a long time, is studied with regard to how the response is changed depending on the administration of different odorants and their concentration. Here, the concentration corresponds to input strength in our model, so that our theory is applicable. Place cells show selective firing when experimental mice pass through a specific place in the experimental field. This firing is achieved by an input depending on the spatial information of the environment or integrated information of a path achieved through the motion of the mice. The input is sustained during the motion of the mice and can be interpreted as a clamped stimulus from the viewpoint of memories-as-bifurcations. These applications will be discussed again in detail in Section 5.

In Kurikawa and Kaneko (2012), we adopted a rate-coding neural network model to demonstrate how the memories-as-bifurcations framework works for storing I/O ( $\mathbf{H}/\mathbf{E}$ ) mappings. Here, we consider a recurrent network with  $N$  neurons each of which receives one incoming input and the temporal evolution of the firing rate  $u_i$  of the neuron  $i$  is given by

$$du_i/dt = \tanh\left(\sum_j J_{ij}u_j + H_i\right) - u_i, \quad (1)$$

where  $H_i$  is an input term added when it is applied. Here,  $u_i$  is rescaled so that it takes the value  $-1$  for non-firing and  $1$ , for maximum firing. The connection matrix giving the network is designed so that in the application of  $\mu$ th input  $\mathbf{H}^\mu$ , the corresponding target  $\mathbf{E}^\mu$  is generated, where  $\mathbf{H}^\mu$  and  $\mathbf{E}^\mu \in \{\pm 1\}$  are chosen randomly with equal probabilities. To memorize  $M$  I/O mappings ( $\mu = 1, \dots, M$ ), the connection matrix  $J_{ij}$  is designed as

$$J_{ij} = \sum_{\mu} (\mathbf{E}_i^\mu - H_i^\mu)(\mathbf{E}_j^\mu + H_j^\mu)/N. \quad (2)$$

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