Superposed recurrence plots for reconstructing a common input applied to neurons

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In the brain, common inputs play an important role in eliciting synchronous firing in the assembly of neurons. However, common inputs are usually unknown to observers. If an unobserved common input can be reconstructed only from outputs, it would be beneficial to the understanding of communication in the brain. Thus, we have developed a method for reconstructing a common input only from output firing rates of uncoupled neuron models. To this end, we propose a superposed recurrence plot (SRP) comprising points determined by using a union of points at each pixel among multiple recurrence plots. The SRP method can reconstruct a common input when using various types of neurons with different firing rate baselines, even when using uncoupled neuron models that exhibit chaotic responses. The SRP method robustly reconstructs the common input applied to the neuron models when we select adequate time windows to calculate the firing rates in accordance with the width of the fluctuations. These results suggest that certain information is embedded in the firing rate. These findings could be a possible basis for analyzing whole-brain communication utilizing rate coding.

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I. INTRODUCTION

Neural synchronization is ubiquitously observed in the brain during task-relevant activities and at rest [1]. For neural synchronization, common inputs play an important role by eliciting collective behaviors from spatially separated neurons. Transcranial alternating current stimulation has been used to impose electrical common inputs on certain brain areas to activate an assembly of neurons, resulting in enhanced working memory performance [2]. Each neuron exhibits an increased firing rate when it receives a stronger common input. The mean firing rates vary depending on the firing characteristics of each neuron. Subsequently, the responses of collective neurons are robust because they can generate synchronous output.

Apart from experimental situations, common inputs are usually unknown to observers. If an unobserved common input can be reconstructed from output measurements, it would be beneficial to the understanding of how information is conveyed in the brain. Thus, we have developed a method for reconstructing a common input only from the output firing rates. Robustness is also examined to study whether different types of neurons can retain information from a commonly applied input.

Same-class neurons in given layers usually have small individual differences in their firing characteristics [3] while sharing the same membrane dynamics. Such individual differences between neurons may disturb the transmission of common input information by changing the firing timing among neurons.

Moreover, various types of neurons with different characteristics are present in the brain. For example, pyramidal neurons in the cortex exhibit relatively slow (10–60 Hz) periodic and regular spiking, whereas inhibitory neurons exhibit fast spiking (80–140 Hz). Some pyramidal cells in the visual cortex demonstrate chattering spiking, in which intermittent bursts are observed [4]. Although chattering neurons are localized in small areas, different types of neurons coexist in the cortex and in other areas. Thus, different types of neurons usually receive common inputs simultaneously [5].

By consistently identifying a common input by using the firing rates obtained from various types of neurons, we may be able to gain information about communications by using rate coding, which is one of the major neuron coding schemes [6,7]. Thus, in the present study, we develop a method that uses a recurrence plot (RP) to reconstruct common inputs. Eckmann *et al.* [8] introduced the concept of RP to identify the nature of dynamical systems in terms of periodicity, nonlinearity, and nonstationarity. Nonlinear, possibly chaotic, deterministic dynamical systems often return to the neighboring trajectory in a phase space. In other words, nonlinear deterministic dynamical systems exhibit recurrences.

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The RP is a visual expression of the recurrences and is used to describe the characteristics of nonlinear dynamical systems because they can possess multidimensional information, despite providing two-dimensional visualization.

Ten years after Eckmann *et al.* introduced RPs, Casdagli [9] further demonstrated that the RPs of an output time series are similar to those of the input time series obtained from a target dynamical system. Since this discovery, RPs have been used to reconstruct common inputs by utilizing the output time series of a target dynamical system. According to Hirata *et al.* [10], we can reconstruct the common input generated from a nonlinear dynamical system using the following procedure. First, multiple RPs are created using the respective output time series of forced systems that simultaneously receive a common input. Subsequently, to obtain the approximation of an RP regarding the common input, an RP is calculated by taking unions at each corresponding pixel among multiple RPs. Next a coarse-grained RP is created by focusing on the large areas in the RP union because the short lines correspond to the local dynamics of the forced models. The coarse-grained RP is then transformed into a network, each link of which has a weight defined by the similarity between states in multidimensional phase space (see Sec. II). Finally, the amplitude of the input time series is reconstructed by applying a multidimensional scaling method to the network. The scope of this reconstruction method is not limited to specific dynamical systems because RPs use the state information embedded in a high-dimensional space rather than the details of the target system. Thus, we hypothesize that this method might also be useful for forced systems that yield a point process, such as uncoupled neurons that receive a common input.

Neurons are nonlinear dynamical systems that sometimes exhibit chaotic behavior [11,12]. Recurrence plots can represent the nature of nonlinear dynamical systems. Usually, the firing rates of a neuron reflect fluctuations, such as intensity and persistency, in the common input, as well as in the dynamics of each neuron. Therefore, we can hypothetically obtain information about a common input if we can counterbalance the effects of neural dynamics.

To test our hypothesis, we have developed a superposed recurrence plot (SRP), which refers to an RP where the value of each pixel is summed across the corresponding pixels of multiple RPs and binarized to 1 or 0 depending on whether the summation at each pixel is greater than or equal to 1. Under the conditions of this study, each RP is calculated using the output time series of a neuron receiving a common input. To reconstruct the common input, we set a certain time range in which a point process is used to calculate the firing rates. The accuracy of the reconstruction may depend on the time range because the scale of the firing times may differ from one system to another. Hence, we examine the influence of the time window width w on the firing rate calculations and the accuracy of reconstructing a common input. For the sake of simplicity, we refer to our proposed reconstructing method as the SRP method.

In this study we use the SRP method to reconstruct a common input using the firing rates of the uncoupled neuron models proposed by Izhikevich [13]. We consider the following three cases. In the first case, we reconstruct the common input applied to localized neurons using the firing rates obtained from neurons that share approximately similar firing rates, although they have individual differences depending on the parameters of the models. The change in the parameters bifurcate the states of the neuron model, producing 10–20 ms firing timing variations. In the second case, we reconstruct a general common input applied to mixtures of different types of neurons that coexist in a single brain area, using firing rates obtained from three types of neurons that exhibit different firing characteristics and thus have different baseline firing rates: chattering (CH), regular spiking (RS), and fast spiking (FS) of the Izhikevich neuron model. In the third case, we examine whether the SRP method could also be used to reconstruct a common input for the chaotic response of the Izhikevich neuron model. If useful, even when applied to chaotic neurons, the SRP method may be widely applicable to various types of systems that yield point processes. In these experiments, we aim to demonstrate the possibility of reconstructing common inputs using firing rates. We successfully achieve this goal.

In Sec. II we first explain the method for reconstructing common inputs using an SRP for point processes. We then describe the neuron model in Sec. III. The results of the simulations are reported in Sec. IV. Finally, in Sec. V we discuss the ability and limitations of the SRP method with regard to the reconstruction of a common input applied to uncoupled neurons. We also discuss the potential functions of common inputs in the brain.

II. RECONSTRUCTION METHODS

A. Definition of a superposed recurrence plot

Based on the Takens theorem [14], a one-dimensional time series can be used to reconstruct a multidimensional system by remapping the one-dimensional time series into a state space defined by the time delay coordinates. Suppose that $x(t)$ is a time series measured as the output of the system. We can transform the value of $x(t)$ into a state space using a time delay with a constant interval τ. For instance, if the dimension of state space m is 3, $x(t)$ is transformed into a state vector $\phi_t = (x(t), x(t+\tau), x(t+2\tau))$, in three-dimensional space. Each point in this state space corresponds to the state of a time point. Based on these states, we can calculate a diagonally symmetrical recurrence matrix, in which the pixel (i, j) has a value of unity if the pair of states ϕ_i and ϕ_j are neighbors; otherwise, the pixel has a value of zero. The matrix $\boldsymbol{R}_{ij}$ is defined as [15]

$$\boldsymbol{R}_{ij}(\epsilon) = \Theta(\epsilon - \|\phi_i - \phi_j\|), \quad i, j = 1, 2, \ldots, N, \tag{1}$$

where N is the total number of time points, ϵ is the threshold for detecting neighboring states, and $\Theta(\cdot)$ is a Heaviside step function that returns unity if the L_2-norm $\|\phi_i - \phi_j\|$ is smaller than the threshold; otherwise, the function returns to zero. The RP is a graphical expression of this matrix. In an RP, the pixel (i, j) is filled with black when the corresponding value is unity and in white when the corresponding value is zero. Although RPs are two-dimensional expressions, they can be used to reconstruct a common input because they possess multidimensional information regarding the dynamics behind the original time series.

Membrane dynamics may differ among neurons; hence a point being plotted in an RP depends on the neuron's parameters and thus RPs are different from each other. On the other hand, when the neurons receive a common input, the RPs will resemble each other because the point at the pixel in the RPs consistently reflects the dynamics of the common input. In this case, the point at the pixel in the RPs corresponds to a recurrence in the phase space for joint dynamics between the common input and the target neuron at each time point. A union of these points at each pixel among the RPs would provide consistent information about the commonalities. Hence, we can infer the approximate dynamics of a common input from the union of points at each pixel among multiple RPs [10].

To extract the information of a common input, we superpose multiple RPs and combine them at each pixel. Thus, a superposed recurrence matrix is defined using the mathematical expression

$$\boldsymbol{SR}_{ij}^{x^{(1,\dots,n)}}(\epsilon_{x^{(1)}},\dots,\epsilon_{x^{(n)}}) = \mathrm{sgn}\left(\sum_{k=1}^{n}\boldsymbol{R}_{ij}^{x^{(k)}}(\epsilon_{x^{(k)}})\right),\quad i,j=1,\dots,N, \tag{2}$$

where n is the total number of systems, $x^{(k)}$ is the kth system that yields each $x(t)$, $\boldsymbol{R}_{ij}^{x^{(k)}}$ is the recurrence matrix for observed variables of the kth system among $x^{(1)}, x^{(2)}, \dots, x^{(n)}$, and $\epsilon_{x^{(k)}}$ is the threshold for $\boldsymbol{R}_{ij}^{x^{(k)}}$. In Eq. (2), $\mathrm{sgn}(\cdot)$ is a sign function that maps positive values to 1, zeros to 0, and negative values to -1. Note that the summation at each pixel in $\boldsymbol{R}_{ij}^{x^{(k)}}$ only takes a positive integer or zero in this study. The SRP is a graphical expression of this matrix. In the SRP, the pixel (i, j) is filled in black when the corresponding value is unity and filled in white when the corresponding value is zero. In this study, $\epsilon_{x^{(k)}}$ for each system is identified as the number corresponding to the lower 10% of the total number of combinations of i and j.

B. Networks and paths

A key concept of reconstruction is the neighboring states of the two time points. To quantify the extent to which the two time points are close to each other, Hirata *et al.* [10] used a relational network created using the information provided by RPs. For two particular time points, if the amplitudes of a common input are similar, the states are close to each other in the state space. This is because a neural system behaves in a similar manner when the common input has a similar amplitude. To transform an RP into a network of states in a multidimensional state space, we use the distance between states. Hirata *et al.* [10] defined the weight for each link in this network by using the ratio of the number of elements in the union of a set to the number of elements in an intersection. The weight $W(i, j)$ of a link between time points i and j is defined as [10]

$$W(i,j) = 1 - \frac{|G_i \cap G_j|}{|G_i \cup G_j|}, \tag{3}$$

where G_i and G_j are the sets of states in the state space that are close to the states ϕ_i and ϕ_j, $\cap$ and $\cup$ represent intersection and union of the two sets, respectively, and $|X|$ denotes the number of elements in set X. If the number of elements in an intersection dominantly occupies the number of elements in the union, that is, if the two time points share many points, we can infer that those two points are neighbors in the state space. However, if there are no elements in the intersection, it means that the time points have no shared points; therefore, we can estimate that the two time points would be separated from each other. In summary, regarding two target time points, the ratio between the number of elements at their union and that in their intersection indicates their similarity. Thus, we can define the distance by subtracting the ratio from unity.

III. RECONSTRUCTING A COMMON INPUT

A. Overview

For the simulation setup, we apply a common input generated by the Duffing equation [16] to an assembly of uncoupled neurons [17]. We then create an SRP from RPs calculated using the output time series, the values of which are the number of firings within a certain time window. Next we apply the method to calculate weight of links [10] to create a network using SRP. Finally, we reconstruct the amplitude of the original common input by applying multidimensional scaling to the distance matrix.

B. Common input

We use the variable x in the Duffing equation as a common input. The Duffing equation is selected in accordance with Ref. [17], which suggested that recurrence plots can be constructed from the output time series of the Izhikevich model. The Duffing equation is defined as follows:

$$\dot{x} = y, \quad \dot{y} = -0.05y - x^3 + 7.5\cos t. \tag{4}$$

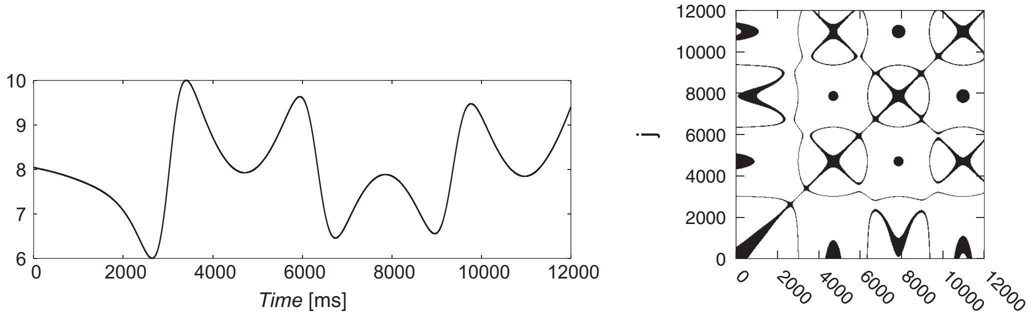
Figure 1(a) depicts the original time series of a common input generated by Eq. (4). This time series is rescaled to 6–10, a range in which the Izhikevich neuron model would fire sequentially. Figure 1(b) presents the RP of this common input. In this RP, the plotted lines and blocks form rounded shapes because the time series varies slowly.

C. Neuron model

In this study we selected the Izhikevich model as the mathematical neuron model because it can be used to reproduce various firing patterns by changing its parameters. The Izhikevich neuron model is described as

$$\begin{aligned}\dot{v} &= 0.04v^2 + 5v + 140 - u + I_v(t),\\ \dot{u} &= a(bv - u),\end{aligned} \tag{5}$$

and if $v \geqslant 30$ then $v \leftarrow c$ and $u \leftarrow u + d$, where v is the membrane potential, u is the recovery variable, and $I_v(t)$ is a time-varying variable defined as a common input. We generate this common input using the Duffing equation. Other parameters a, b, c, and d determine the firing pattern of the Izhikevich neuron model. In the present study we examine the following three cases. In each case, the neurons are uncoupled to clarify the influence of common input.



(a) (b)

FIG. 1. Original time series of the common input and its RP: (a) the first 12 000 points of variable x in the Duffing equation and (b) the RP of the original common input.

In the first case, we apply the SRP method to the uncoupled chattering neurons. Chattering neurons express a firing pattern comprising intermittent bursts. According to Ref. [3], neurons of the same class have similar firing characteristics, while there may be small individual differences. A typical instance of these neurons in a specific area is the grouping of pyramidal cells in the visual cortex. In the simulations, to create a situation in which a common input is applied to neurons of the same class, we prepare a group of chattering neurons by changing parameters such as $0.018 \leqslant a \leqslant 0.022$, $0.198 \leqslant b \leqslant 0.202$, $c = -50$, and $d = 2$. The results are described in Sec. IV A.

In the second case, we apply our method to three different types of neurons receiving a common input which is a typical occurrence in any given brain area. Thus, we explore whether a combination of different types of neurons and the number of neuronal firings per window influences the accuracy of the reconstructed common input. To create a situation in which there are different types of neurons, we prepare a group of neurons by changing the parameters a and b to the following ranges: regular spiking neurons ($0.018 \leqslant a \leqslant 0.022$, $0.198 \leqslant b \leqslant 0.202$, $c = -65$, and $d = 8$), fast spiking neurons ($0.998 \leqslant a \leqslant 0.102$, $0.198 \leqslant b \leqslant 0.202$, $c = -65$, and $d = 2$), and chattering neurons ($0.018 \leqslant a \leqslant 0.022$, $0.198 \leqslant b \leqslant 0.202$, $c = -50$, and $d = 2$).

We then discriminate between these neurons using a superscripted index to indicate the neurons used in the respective simulations. For instance, the parameters of $\mathrm{RS}^{(9p+q+1)}$ are determined as $a = 0.018 + 0.0005\,p$, $b = 0.198 + 0.0005\,q$, $c = -65$, and $d = 8$, where p ($p = 0, 1, 2, \ldots, 8$) and q ($q = 0, 1, 2, \ldots, 8$) are index variables. Therefore, when $p = 0$ and $q = 0$, $\mathrm{RS}^{(9p+q+1)}$ corresponds to $\mathrm{RS}^{(1)}$: This means that the model has the first combination of parameters a and b, that is, the regular spiking neuron with the parameters $a = 0.018$, $b = 0.198$, $c = -65$, and $d = 8$. Using the same notation, $\mathrm{RS}^{(2)}$ means that the model has a second combination of parameters $a = 0.018$, $b = 0.1985$, $c = -65$, and $d = 8$. Similarly, $\mathrm{FS}^{(9p+q+1)}$ has parameters $a = 0.998 + 0.0005\,p$, $b = 0.198 + 0.0005\,q$, $c = -65$, and $d = 2$ and $\mathrm{CH}^{(9p+q+1)}$ has parameters $a = 0.018 + 0.0005\,p$, $b = 0.198 + 0.0005\,q$, $c = -50$, and $d = 2$. The results are described in Sec. IV B.

In the third case, we apply the proposed method to chaotic neurons. Izhikevich [11] showed that his model, with particular parameters ($a = 0.2$, $b = 2$, $c = -56$, and $d = -16$), exhibited irregular firing patterns when the model received a strong negative input [$I_v(t) = -99$]. A prior study using these parameters [17] revealed that the RPs of the firing rates are similar to those of the input. The authors of that study predicted that, theoretically, the common input can be reconstructed by applying the procedure in Ref. [10]. In this study we explore whether we could reconstruct a common input applied to the Izhikevich neuron model that exhibits chaotic responses. The results are described in Sec. IV C.

D. Firing rates and spikes per window

To reconstruct a common input, we set a certain time range to calculate the firing rates using a point process. The scale of the firing times differs between the systems. We then examine whether the accuracy of reconstructing a common input depends on the width of the time window. Specifically, we assess the number of spikes per window. One possible reason for the width of the time window influencing reconstruction accuracy is that a wider window can contain a larger number of spikes. Therefore, it is necessary to control the baseline firing rates of the different types of neurons.

To calculate firing rates, we use time windows with widths w of 100, 500, 2500, and 12 500 ms. The baseline firing rates for each firing pattern are approximately 48–60 spikes/s for CH, 15–20 spikes/s for RS, and 80–136 spikes/s for FS neurons. Thus, the average counts in each time window among the firing patterns differ. For instance, when we use RS neurons and a 500 ms time window, the spikes per window are calculated as $15 \times \frac{500}{1000} = 7.5$. The first term 15 corresponds to the baseline firing rate of RS neurons and the numerator 500 represents the width of the time window. In all simulations, we discard the first 2000 ms of the firing rate time series because the neuron models are in a transient state during this period.

E. Evaluation of accuracy

We use the root mean square error (RMSE) as an index of accuracy. The RMSE $\mathcal{E}$ is defined as

$$\mathcal{E} = \sqrt{\frac{1}{n}\sum_{t=1}^{n}[I_r(t) - I_o(t)]^2}, \tag{6}$$

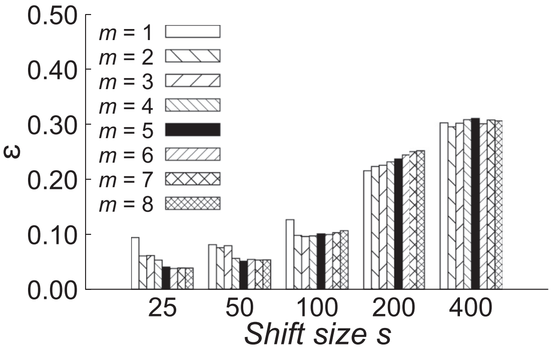


FIG. 2. Influence of shift size s and embedding dimension m on RMSE $\mathcal{E}$.

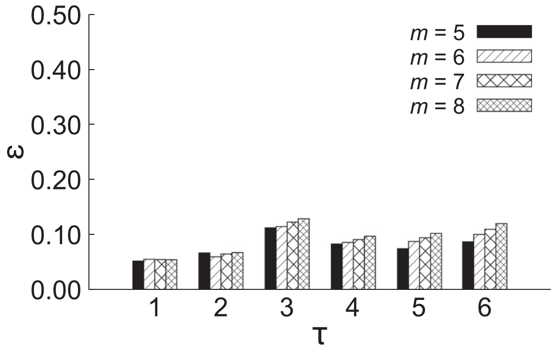


FIG. 3. Influence of time delay τ and embedding dimension m on RMSE $\mathcal{E}$.

where t is a point of discrete time with a unit of τ and n is the total sampled time. In Eq. (6), $I_r(t)$ is the value of the reconstructed common input at t, and $I_o(t)$ is the resampled value of the original common input at t. To obtain $I_o(t)$, we adopt the resample( ) function in MATLAB2021a.

IV. RESULTS

A. Case I: Uncoupled neurons with small individual differences

1. Parameter determination

In this section we reconstruct a common input using an assembly of CH neurons. The neuron exhibits a constant firing rate when it receives a constant common input because there is no dynamical or observational noise. The firing rate provides a fixed point in a time-delayed phase space. Thus, an RP of the output firing rate corresponds to the fluctuations of the common input. Theoretically, the dimension of the state space $m \geqslant 5$ is sufficiently large because the dimension of the input is 2 [18]. However, the reconstruction accuracy may be sensitive to m, whereas the dimension of an unobserved common input is usually unknown to observers. Hence, we first examine the influence of the parameters of shift size s and dimension m using CH neurons.

As shown in Fig. 2, $\mathcal{E}$ between the original common input and reconstructed common inputs become larger when a shift size of more than 100 ms is utilized. Contrary to this trend, $\mathcal{E}$ are smaller when $m \geqslant 5$ when $s = 50$ and 100.

The reconstruction accuracy may also depend on the delay time τ required to transform the time series into states in a state space. Thus, we examine $\mathcal{E}$ by altering τ using CH neurons. In this examination, we adopt the parameters $m = 5$, $w = 500$, and $s = 50$. As shown in Fig. 3, $\mathcal{E}$ became larger when we adopt $\tau = 3$ and a longer time delay. These results suggest that $\tau = 1$, which corresponds to a delay of 50 ms, is suitable for the reconstruction. Overall, we consider that the method using the SRP can reconstruct common inputs with smaller deviations from the original input when we use parameters of $m = 5$ and $\tau = 1$, especially when we take advantage of a shift size narrower than 50 ms. Thus, we adopt a shift size of 50 ms, rather than 25 ms, because it maintains a similar level of accuracy by reducing 50% of the calculation costs. Similar parameter dependences are determined when we reconstruct common inputs using RS and FS neurons with the parameters $m = 5$, $w = 500$, and $s = 50$ (for details, refer to Appendix A). Therefore, we adopt these parameters in the following simulations.

2. Window size and reconstruction accuracy of the SRP method

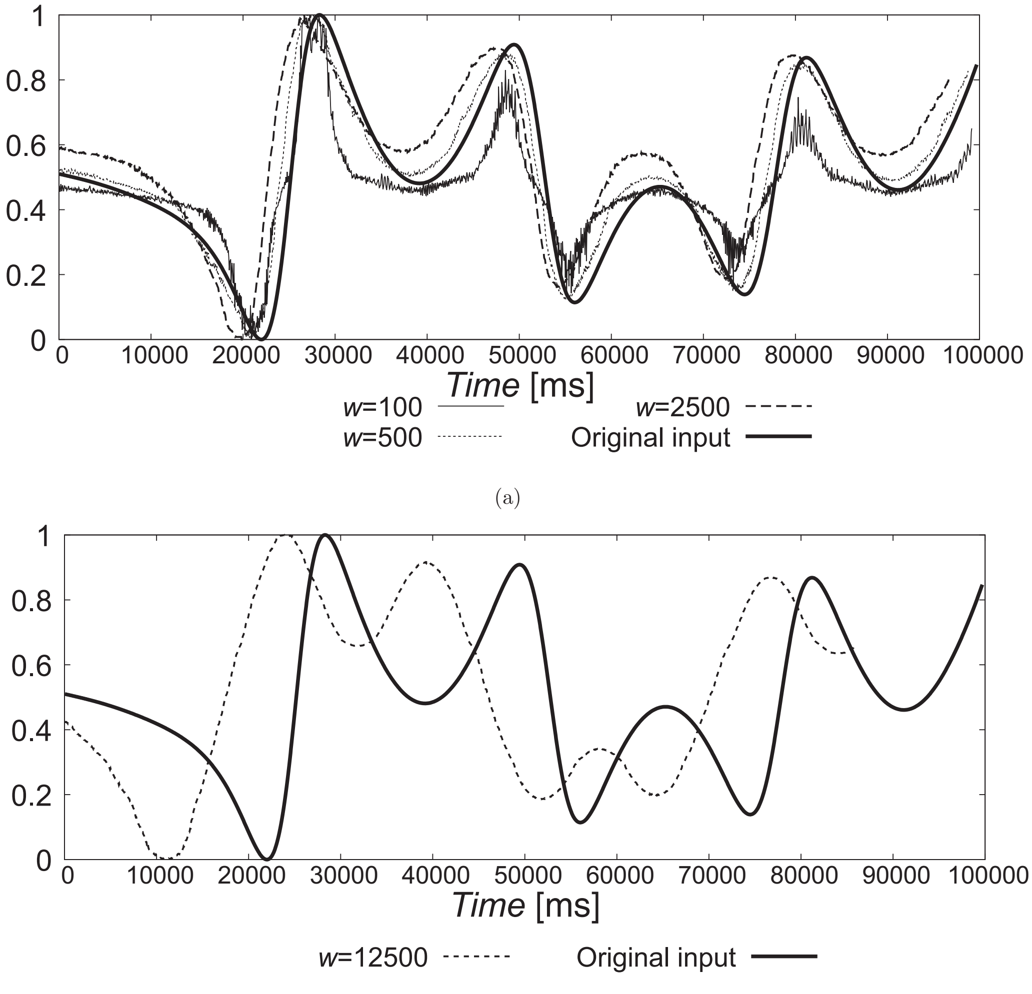
Next we examine the relationship between the width of the time window used to calculate the firing rates and reconstruction accuracy. In these examinations, we adopt CH neurons and window widths $w = 100 \times 5^i$ ($i = 0$, 1, 2, and 3). The other parameters are $m = 5$, $\tau = 1$, and $s = 50$.

As shown in Fig. 4, the reconstructed common inputs when using 12 500 ($w = 100 \times 5^3$) ms deviate from the original common input [the black thick solid line in Fig. 4(b)]. From these results, the RMSE $\mathcal{E}$ increases when we use a time window that is too wide. Corresponding to these results, the RMSE $\mathcal{E}$ is lower when we use the middle range of w, i.e., $w = 500$, as shown in Fig. 5. Similar tendencies are observed when we used RS and FS neurons (for details, refer to Sec. IV B).

To explore the causes of the loss of accuracy, we compare the RPs used for the reconstructions of common inputs. Figure 6 illustrates the RPs when we use a time window width of 100–12 500 ms. As shown in Fig. 6(d), the main islands in the RPs disappear in a time window of 12 500 ms. The disappeared areas correspond to the first 600 units, which are the first 30 000 ms in the timescale of the original common input.

In these instances, the results demonstrate that the time location of the first peak shifts forward by approximately 10 000 ms, compared with the original input [the solid line in Fig. 4(b)]. This may be caused by ignoring fluctuations, because the time window is wider when the initial decrease and subsequent increase in firing rates occur. These results suggest that we must set an appropriate time window width that is narrower than the width of the fluctuations of the original common input. As a technical constraint of the SRP method, the length of the reconstructed time series is shortened to the same length as the established time window. This is another indication that relatively narrow time windows are necessary.

However, when using a time window that is too narrow ($w = 100$), most of the pixels in the RP are filled with black [Fig. 6(a)]. This indicates that the time window is too narrow to detect the variations in states at each pixel (i, j) evaluated by the Heaviside step function (neurons than CH neurons are shown in Fig. 15 in Appendix B). Consequently, the



(a)

(b)

FIG. 4. Reconstructed common inputs using uncoupled chattering neurons using (a) 100–2500 ms time windows and (b) a 12 500 ms time window (rescaled for comparison).

reconstructed common input exhibits a distorted shape; thus, the reconstruction accuracy is lower than that when using $w = 500$ or 2500.

B. Case II: Different types of uncoupled neurons

1. Number of firings per window

In this case, we first examine whether the SRP method could be used to reconstruct a common input using different types of neurons. We then explore the conditions under which the SRP method is applicable.

To examine the effect of the window width w, which is adopted for calculating the firing rates, on reconstruction accuracy, we calculate $\mathcal{E}$ by modulating the window widths. In this examination, we use the RS, CH, and FS neurons and window widths of 100×5^i ($i = 0$, 1, 2, and 3). The other parameters are $m = 5$, $\tau = 1$, and $s = 50$.

The results consistently demonstrate that the $\mathcal{E}$ between the original and reconstructed common inputs are larger when $w = 12\,500$ [Fig. 7(a)]. These results suggest that window widths narrower than the fluctuations in the common input exhibit better accuracy. However, the window width that yields the minimum $\mathcal{E}$ varies according to the firing patterns: $\mathcal{E}$ are lowest when $w = 2500$ for RS neurons, $w = 500$ for CH neurons, and $w = 100$ for FS neurons. These results suggest that the number of neuron firings per window may influence reconstruction accuracy because the baseline firing rates differ among these three firing patterns.

Thus, to explore whether the number of spikes per window influences the accuracy of the reconstructed common input, we compare three different types of neurons (RS, FS, and

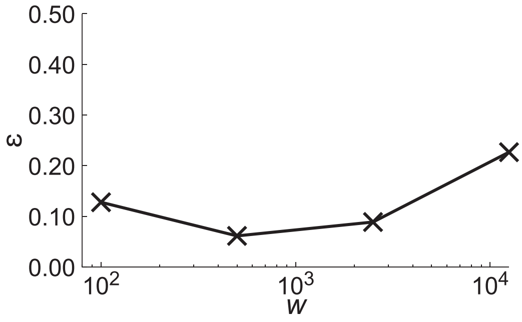
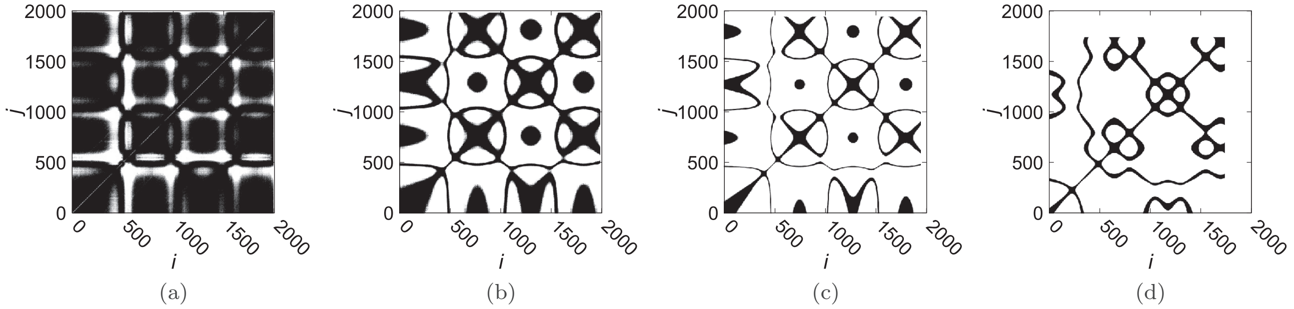


FIG. 5. Influences of window width w on RMSE $\mathcal{E}$: $w = 100 \times 5^i$ ($i = 0$, 1, 2, and 3) were used.



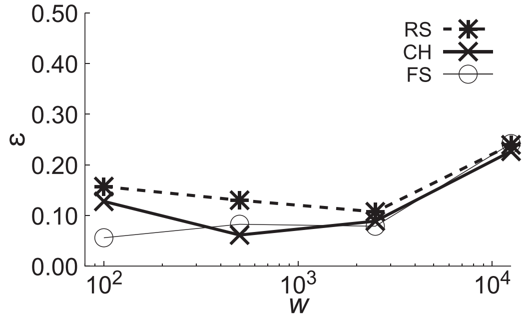
(a) (b) (c) (d)

FIG. 6. Variation of SRPs for chattering neurons depending on the width of the window: (a) $w = 100$, (b) $w = 500$, (c) $w = 2500$, and (d) $w = 12\,500$. Each unit corresponds to 50 ms for i and j depending on the values of τ. The parameter w represents the width of the time window.

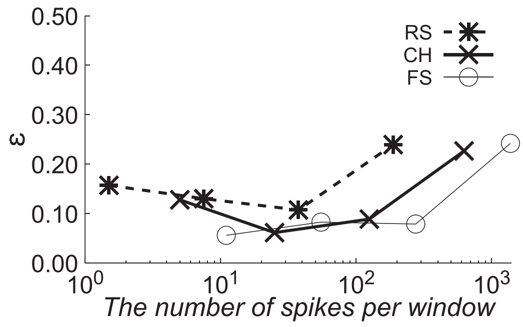
CH). Figure 7(b) shows the relationship between the number of spikes per window and $\mathcal{E}$. The results demonstrate that the number of spikes per window is not proportional to $\mathcal{E}$; however, even 22.5 spikes per window exhibited by the RS neurons realize the reconstruction of the common input with good accuracy ($\mathcal{E} < 0.075$). Thus, in this case, the neurons fire sufficiently to realize the reconstruction of the common input.

2. *Combinations of different types of neurons*

Next we compare three conditions. For the first condition, we reconstruct a common input using a distributed mixture of the three types of neurons, i.e., 27 RS ($\mathrm{RS}^{(1)}$–$\mathrm{RS}^{(27)}$), 27 CH ($\mathrm{CH}^{(28)}$–$\mathrm{CH}^{(54)}$), and 27 FS ($\mathrm{FS}^{(55)}$–$\mathrm{FS}^{(81)}$) neurons (hereinafter called the mixed-distributed condition). For the second condition, we reconstruct a common input using a centered mixture of three types of neurons: 27 RS ($\mathrm{RS}^{(28)}$–$\mathrm{RS}^{(54)}$), 27 CH ($\mathrm{CH}^{(28)}$–$\mathrm{CH}^{(54)}$), and 27 FS ($\mathrm{FS}^{(28)}$–$\mathrm{FS}^{(54)}$) neurons (hereinafter called the mixed-centered condition). We compare these results with the results obtained from 81 CH ($\mathrm{CH}^{(1)}$–$\mathrm{CH}^{(81)}$) neurons reported in Sec. IV A as the control conditions. For all these experiments, we use a 500 ms time window.



(a)



(b)

FIG. 7. Relationship between (a) window width ($w = 100$, 500, 2500, and 12 500 ms) and RMSE $\mathcal{E}$ and (b) the number of spikes per window and RMSE $\mathcal{E}$. Regular spiking, chattering, and fast spiking neurons were used.

If the accuracy of reconstruction depended on the range of parameters regardless of neuron type, we would expect the reconstructed common input to produce a smaller $\mathcal{E}$ under the mixed-distributed condition than under the mixed-centered condition. By contrast, if the accuracy of reconstruction is sensitive to the bifurcation of firing patterns, the opposite result would be observed.

Figure 8 demonstrates the original common input and the reconstructed common inputs under each of the above three conditions. As shown in Fig. 9, we are able to reconstruct the common input with high accuracy ($\mathcal{E} = 0.051$, i.e., 5.1% error in terms of absolute value) when we use an assembly of uniform neurons, i.e., $\mathrm{CH}^{(1)}$–$\mathrm{CH}^{(81)}$. The accuracy is at a similar level under the mixed-distributed ($\mathcal{E} = 0.100$) and mixed-centered conditions ($\mathcal{E} = 0.131$).

3. *The number of neurons*

To examine the effect of the number of neurons on the reconstruction accuracy, we calculate the $\mathcal{E}$ by modulating the number of RS, CH, and FS neurons. In these calculations, we use central 3^i ($i = 1$, 2, 3, and 4) neurons in the range of parameters. For example, we use $\mathrm{RS}^{(39)}$–$\mathrm{RS}^{(41)}$ for three neurons, $\mathrm{RS}^{(36)}$–$\mathrm{RS}^{(44)}$ for nine neurons, $\mathrm{RS}^{(27)}$–$\mathrm{RS}^{(53)}$ for 27 neurons, and $\mathrm{RS}^{(1)}$–$\mathrm{RS}^{(81)}$ for 81 neurons. We use these number of neurons to examine the other two firing patterns as well.

As shown in Fig. 10, regarding RS neurons, $\mathcal{E}$ decrease as the number of neurons increases. However, when we use CH and FS neurons, the RMESs are approximately constant regardless of the number of neurons (for the dependence of dimension, refer to Appendix C). The results suggest that reconstruction accuracy depends mainly on firing patterns rather than the number of neurons used to reconstruct a common input.

Through the examination in case II, we confirm that common inputs can be reconstructed using the SRP method with

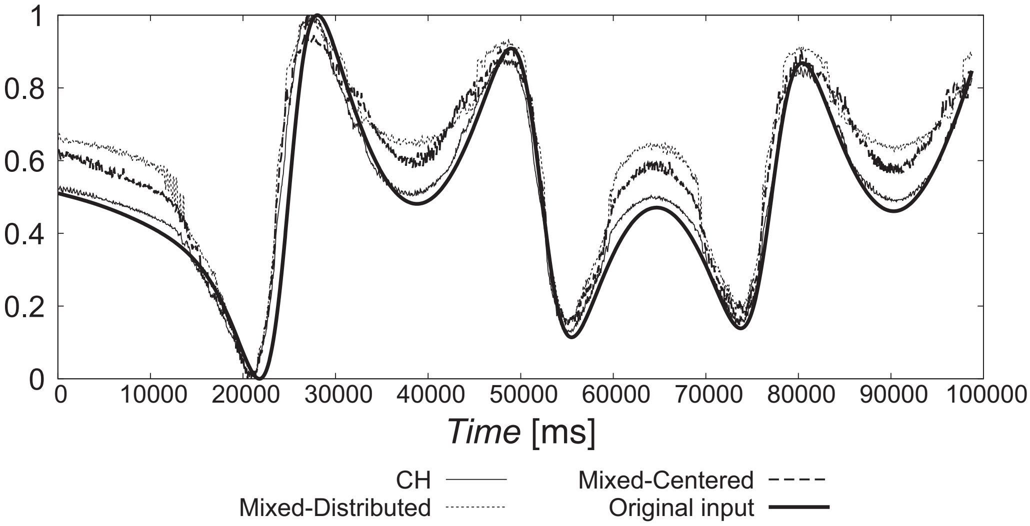


FIG. 8. Reconstructed common inputs using different types of neurons with a 500 ms time window (rescaled for comparison).

various neurons. Moreover, reconstruction accuracy mainly depends on the time window width and the firing patterns of neurons used; however, the number of firings per window is less influential. Even when we use various types of neurons simultaneously with a small number of neurons, we can reconstruct a common input as well. Thus, neither the existence of various types of neurons nor the use of a large number of neurons is a prerequisite for reconstructing a common input. If a constant input is applied to a nonchaotic neuron, the output firing rate is also constant. Thus, the common input reconstructed using the SRP method exhibits a constant common input that will be trivial. Similarly, if none of the neurons fire, the firing rate will constantly be indicated as zero. Even given this theoretical consideration, the SRP method accurately reconstructs the common input, yielding a constant common input. However, in the case of no spikes, we cannot discriminate between situations in which there are no common inputs and those in which the intensity of the common inputs is too weak to force the dynamics of the neurons. Hence, to apply the SRP method, we postulate that common inputs must possess a certain intensity to induce changes in the firing rates of dynamical systems.

C. Case III: Chaotic neurons

Chaotic neurons exhibit irregular firing patterns, yielding a wider and richer variety of firing intervals than those achieved by other types of neurons while receiving a common input. However, the SRP method focuses on the increase and decrease in firing rates within a period rather than on the detailed membrane dynamics of neurons. Therefore, we predict that this method would be capable of reconstructing a common input applied to chaotic neurons, although the $\mathcal{E}$ may increase.

In this section we use the Izhikevich model with a chaotic response to reconstruct a common input. While the Izhikevich model with a chaotic response is biologically unrealistic owing to its assumption of a large negative input, this model can phenomenologically reproduce the firing of a chaotic neuron. Thus, this model is useful for simulating the collective behavior of uncoupled chaotic neurons. We prepare 81 chaotic neuron models by changing the parameters $0.018 \leqslant a \leqslant 0.022$ and $0.198 \leqslant b \leqslant 0.202$ within a constant interval of 0.0005 based on the Izhikevich model with a chaotic response ($a = 0.2$, $b = 2$, $c = -56$, and $d = -16$). These models exhibit irregular firing patterns when they receive strong negative input. Thus, we rescale the common input generated by the Duffing equation to the range of $-99 \leqslant I_v(t) \leqslant -96$, in which the neural models exhibit irreg-

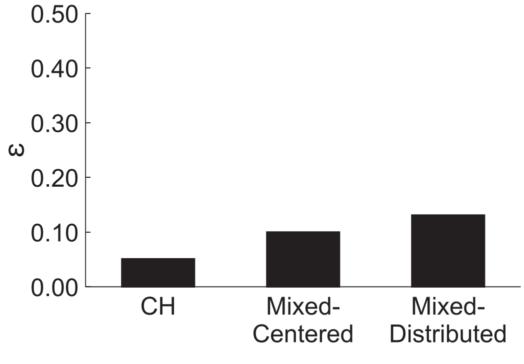


FIG. 9. RMSE $\mathcal{E}$ between the original common input and the reconstructed common inputs using various types of neurons.

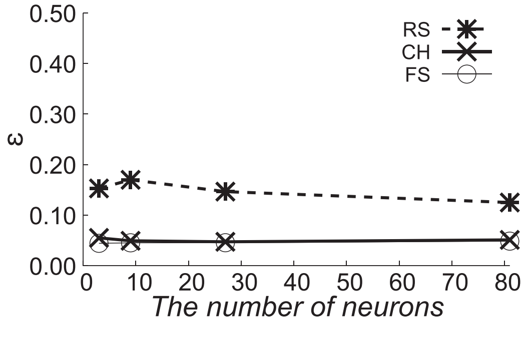
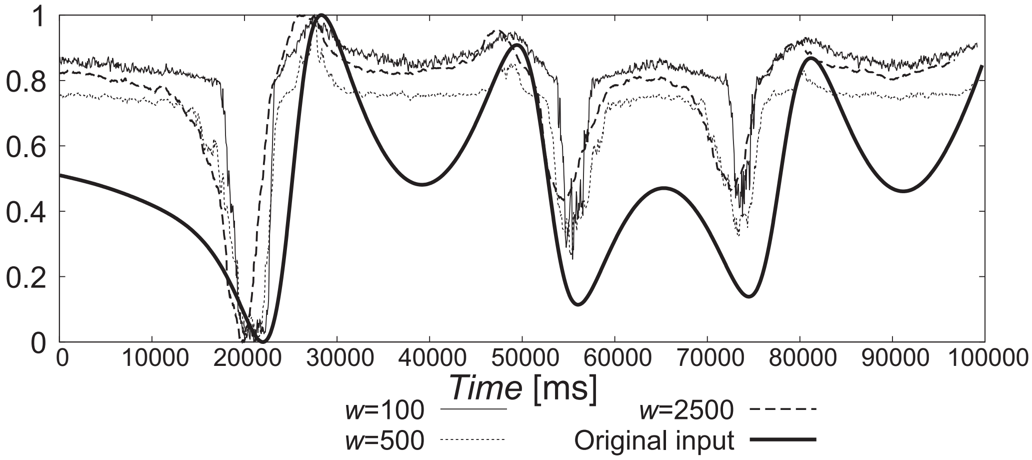
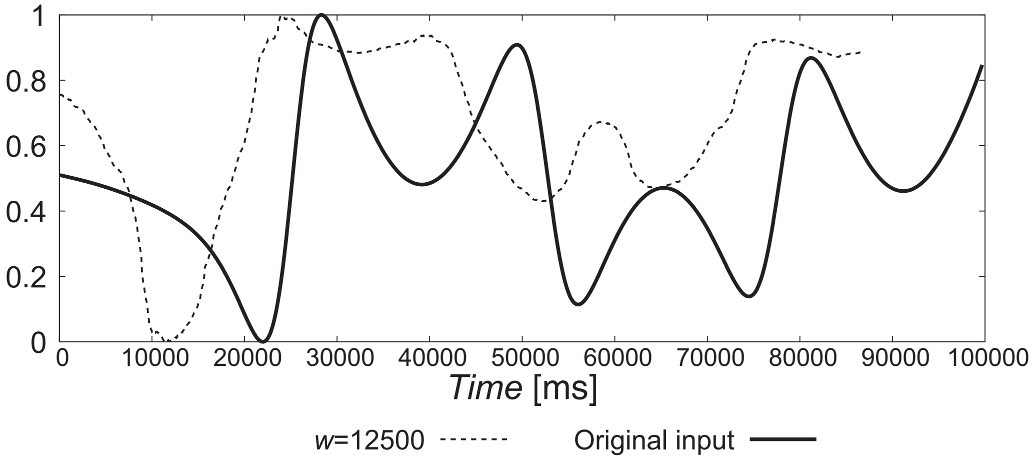


FIG. 10. RMSE $\mathcal{E}$ for each number of RS, CH, and FS neurons. The RMSEs $\mathcal{E}$ were calculated using 3^i ($i = 1, 2, 3,$ and 4).



(a)



(b)

FIG. 11. Original common input and reconstructed common inputs using uncoupled chaotic neurons (rescaled for comparison). Reconstructed common inputs used (a) a 100–2500 ms time window and (b) a 12 500 ms time window.

ular firings [17]. We then reconstruct the common input using the firing rates of the 81 chaotic neuron models.

Figure 11 shows the original and reconstructed common inputs for the chaotic neurons. These results demonstrate that we are able to obtain the time series even when we use an assembly of chaotic neurons. As predicted, the $\mathcal{E}$ is larger (Fig. 12), which is three to four times as large as the $\mathcal{E}$ obtained when we use the other types of neurons. However, the timings of peak amplitudes are precisely detected when we use the 100–2500 ms time window (Fig. 11).

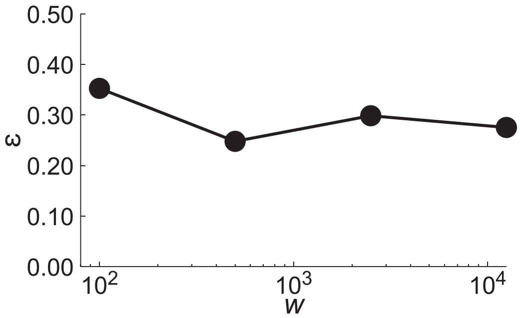


FIG. 12. Influences of window width w on RMSE $\mathcal{E}$ for neurons with chaotic responses: $w = 100 \times 5^i$ ($i = 0, 1, 2,$ and 3).

In these cases, regarding the other time points, the amplitude of the reconstructed common input deviates from that of the original common input. Nonetheless, we find that the trends, that is, the increase or decrease in the amplitude of the reconstructed common inputs, correspond to the original common input. These results suggest that the SRP method is capable of reconstructing the variabilities of the common input using neurons with chaotic responses, although the exact amplitude cannot be reconstructed. For $w = 12\,500$ ms, however, the time location of the first peak shifts forward by approximately 10 000 ms compared with the original input, which is similar to the results obtained from CH neurons [Fig. 4(b)]. This may be due to the fact that the time window is wider than the fluctuations in the common input.

Figure 13 shows the SRPs in the case of chaotic neurons with the 100–12 500 ms time window. The resulting SRPs possess the features of the RP of the common input. For

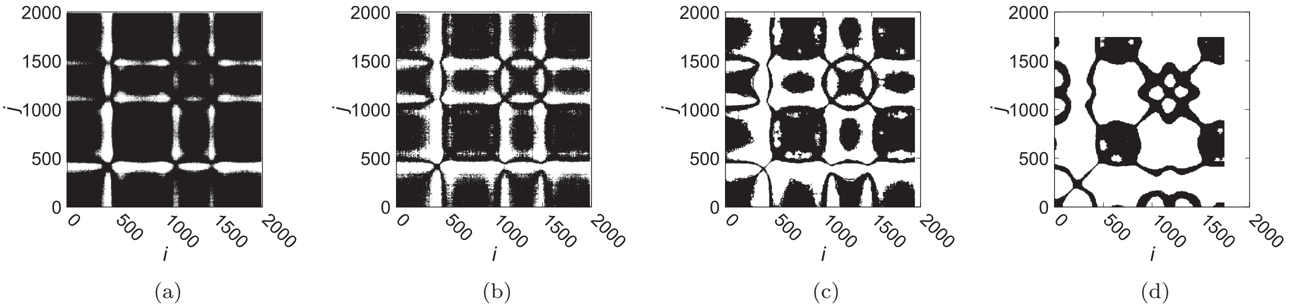


FIG. 13. Variation of SRPs for chaotic neurons in the case of changing the width of the window w: (a) $w = 100$, (b) $w = 500$, (c) $w = 2500$, and (d) $w = 12\,500$.

$w = 12\,500$, similar to the SRP calculated using CH neurons, the main islands in the SRP disappear. These results suggest that the variations in the neuron's chaotic responses in the firing intervals are larger than those provided by the common input; the firing rates cannot be determined only by the amplitude of the common input because it increases and decreases irregularly when compared to nonchaotic neurons.

V. DISCUSSION

When we use the SRP method, we are able to reconstruct the common input applied to three cases: (i) uncoupled neurons with small differences, (ii) three different assemblies of neurons comprising three types of neurons, and (iii) chaotic neurons. In the first case, the reconstructed common input becomes more accurate when we use CH and FS neurons with a 100–2500 ms time window. These neurons exhibit higher firing rates, thus suggesting that the accuracy of the reconstruction method depends on the number of firings occurring within the time window. All three types of neurons (RS, FS, and CH) fire frequently to reconstruct the common input. We conclude that relatively narrow time windows are necessary and that the aimed common input must possess a certain intensity to induce changes in the firing rates.

In the second case, the reconstruction accuracy depends on the types and number of neurons used. By changing the number of neurons, that is, 3^i ($i = 1$, 2, 3, and 4), the number of neurons is less influential in the reconstruction accuracy. Therefore, the key condition is the shared information about states in the state space that is represented as an SRP, and we are able to reconstruct the unknown common input using the firing rates obtained from only a few neurons when the firing rates possess information from the original common input. These results indicate that the accuracy is not directly proportional to the number of neurons used in the SRP method and that a wide range of model parameters is not necessary for high accuracy; the accuracy is at a similar level when we use three different mixtures of the three types of neurons.

Regarding the third case, the SRP method is also capable of reconstructing a common input time series using the firing rates of neurons with chaotic responses. In particular, the timing of the peaks in the reconstructed common input corresponds to that of the original common input when we use the 100–2500 ms time window. Therefore, we are able to predict the peaks of an unknown common input based on the reconstructed common input even when using chaotic neurons, as long as we use a narrower time window compared to the fluctuations of the common input. Moreover, this result suggests that we can predict the approximate trends of the common input, although we cannot determine the exact amplitude of the original common input owing to large errors. A previous study [17] reported that RPs that use the firing intervals of chaotic neurons cannot represent the information of a common input. By contrast, the SRP method focuses on the increase and decrease in firing rates rather than on detailed firing patterns and timings. We are able to retain the time resolutions when we use overlapping time windows with small intervals, for example, $w = 500$ and $s = 50$. In summary, despite the irregular firing patterns of chaotic neurons, the SRP method accurately predicted the timing of the peak amplitudes and the approximate trends of the original common input.

The results may also be applicable to studies regarding whole-brain communication among neurons because our results indicate that we could reconstruct a common input by using a set of different types of neurons. The hypothesis that a common input applied across several brain areas transmits information utilizing rate coding is consistent with our results. Each neuron exhibits increased firing when receiving a stronger common input, although the baseline firing numbers varies depending on neuron characteristics. Small differences in the firing times caused by the model parameters are crucial for reconstructing a common input. These differences among neurons cancel out the specific dynamics between neurons; thus, only common features remain. One theoretical prediction is that governance by a common input in the brain does not require one-to-one correspondence between firings of local neurons. Rather, collective firing features among neurons are a key factor. More precisely, it may be necessary for neurons to transit collectively into similar firing-rate states by receiving a common input. In this study, such collective transitions are quantified as the common features depicted in the SRP, that is, the quantified neighboring states in the state space. The assumption that neurons in the brain possess this mechanism may be unrealistic. However, the results of this study support our hypothesis that different types of neurons retain information on commonly applied inputs in firing rates. This information can serve as the basis for rate coding.

Enhancement of the working memory by common external electrical inputs in certain brain areas [2] suggests that widely distributed neurons can function consistently without interfering with each other. If different types of neurons retain commonly applied inputs, brain activities such as theta-band waves [5] across different brain areas may contribute to whole-brain coordination. Therefore, our findings would provide a perspective that connects different scales of brain phenomena: (i) on a microscopic level, firing patterns of single cells that receive common inputs, which are measured as local field potential, and (2) on mesoscopic and macroscopic levels, more global brain activities, which are measured as an electroencephalogram. Thus, it will be an important future perspective to study how higher-order cognition [2] emerges from the firing patterns of neurons.

VI. CONCLUSION

In this study we investigated the reconstruction of locally applied and more widely applied common inputs using the output firing rates of uncoupled neurons. We demonstrated that the SRP method could reconstruct a common input, even when using chaotic neurons, although the accuracy was lower than when other neuron types were used. When we select an adequate time window for firing-rate calculations, the method developed in this study can robustly reconstruct a common input applied to systems that yield a variety of point processes. Moreover, even combinations of different types of systems, which had differences in firing rates of a magnitude of four to seven times (15–20 spikes/s for RS and 80–138 spikes/s for FS neurons), were also beneficial for reconstruction.

Neurons in the brain are generally subjected to dynamical noise and membrane dynamics. Thus, it is an important future issue to systematically investigate the effects of dynamical noise on the reconstruction accuracy of the SRP method.

This reconstruction ability facilitates further application of the SRP method. In addition to neuron-related applications, this method may be applicable to a variety of systems that yield a point process. Therefore, this method may contribute to the reconstruction of a common input applied to multiple nonlinear, possibly chaotic, dynamical systems, as well as to the assembly of the simple mathematical models considered in this study. We expect that in the future, the SRP method will be widely applicable to the fields of biology, engineering, and cognitive science [19].

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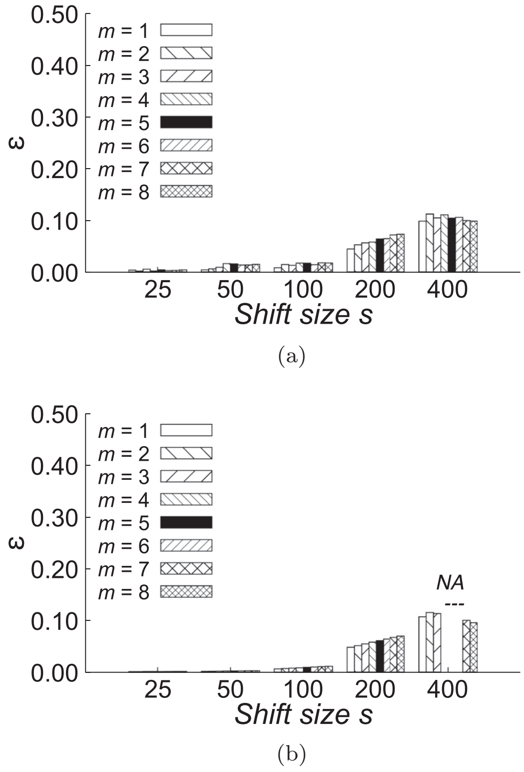
APPENDIX A: INFLUENCE OF DIMENSION *m* AND SHIFT SIZE *s* ON RECONSTRUCTION ACCURACY FOR RS AND FS NEURONS

To examine the parameter dependence, we first calculated $\mathcal{E}$ by changing the shift size s to obtain firing rates and dimension m to transform the time series into states in a state space (refer to the main text, Sec. III D) using the RS (RS$^{(1)}$–RS$^{(81)}$) and FS (FS$^{(1)}$–FS$^{(81)}$) neurons. In this examination, we used $\tau = 1$ and $w = 500$ ms. As shown in Figs. 14(a) and 14(b), $\mathcal{E}$ between the original and reconstructed common inputs became larger when we used a shift size of more than 100 ms. Contrary to this trend, $\mathcal{E}$ were almost constant regardless of the dimensions in each shift size. These trends were also found when we used CH neurons (CH$^{(1)}$–CH$^{(81)}$), as shown in the main text (Fig. 2).



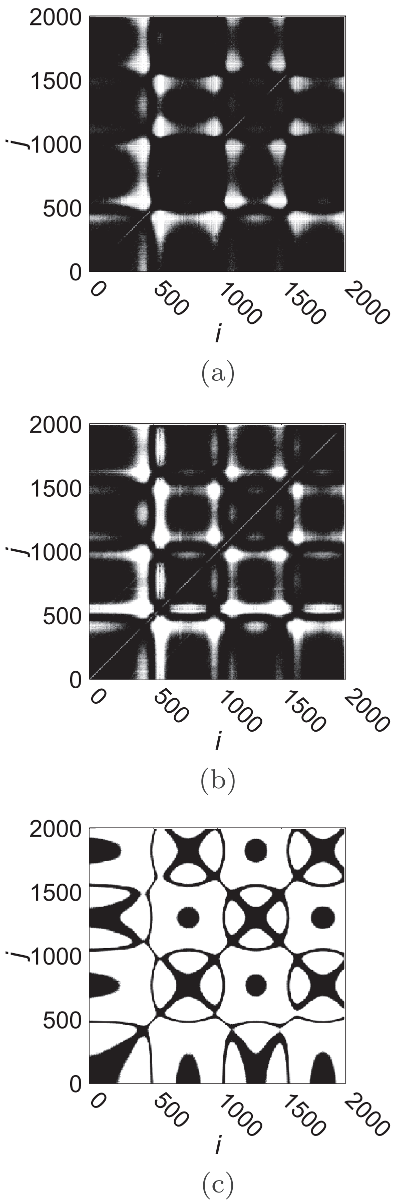
(a)

(b)

FIG. 14. Influence of embedding dimension m and shift size s on RMSE $\mathcal{E}$ for (a) RS and (b) FS neurons. Regarding the results of FS neurons, NA indicates that data are not available because common inputs were not reconstructed when $m = 4, 5, 6$. For these parameters, the primary lines disappeared in the SRPs for reconstruction.

APPENDIX B: RECURRENCE PLOTS USING A NARROWER TIME WINDOW

For CH neurons, the $\mathcal{E}$ was larger when we used a narrow ($w = 100$) time window compared to using a wider time window ($w = 500$). Nonetheless, for the FS neurons, the $\mathcal{E}$ was the smallest under the condition that $w = 100$. To explore the cause of this difference, we compared the SRPs of the RS, CH, and FS neurons when using $w = 100$ (Fig. 15). The SRP of the FS neurons was very similar to that of the original common input. However, in other two PRs, most pixels were filled with black. Hence, the lower $\mathcal{E}$ for CH neurons would be due to the small variations among the states corresponding to each pixel. The time window would be too narrow to obtain sufficient information on firing.



(a)

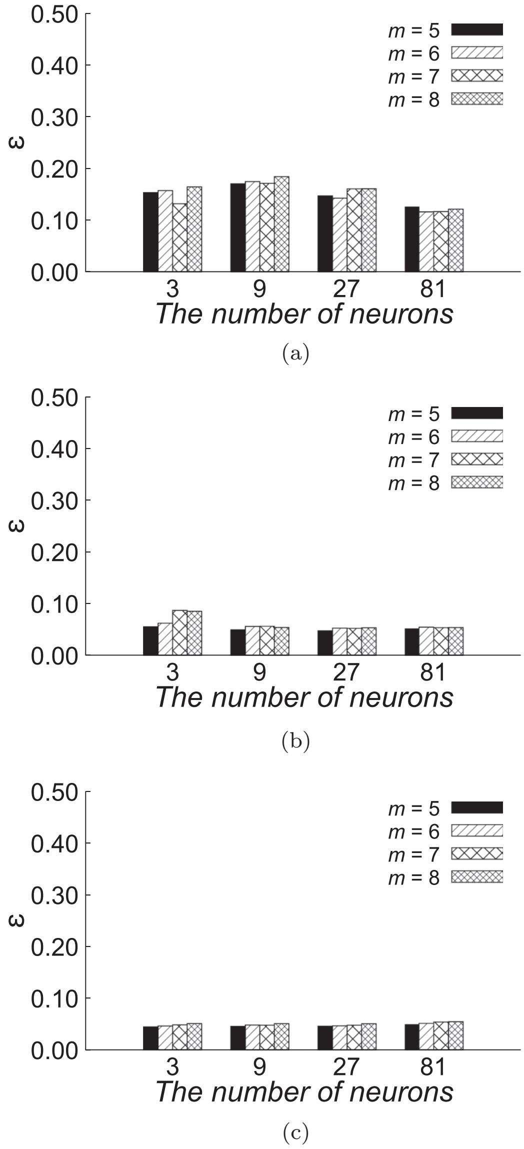
(b)

(c)

FIG. 15. Variations of SRPs for (a) RS, (b) CH, and (c) FS neurons using windows of $w = 100$.

APPENDIX C: DEPENDENCE OF DIMENSION AND THE NUMBER OF NEURONS ON RECONSTRUCTION ACCURACY

In the main text we also examined reconstruction accuracy by modulating the number of neurons. Although the results demonstrated that we can reconstruct a common input using few neurons, the reconstruction accuracy may depend on the dimensions as well.



(a)

(b)

(c)

FIG. 16. RMSE $\mathcal{E}$ for each number of neurons and dimension with using (a) RS, (b) CH, and (c) FS neurons.

We then calculated $\mathcal{E}$ by modulating the number of RS, CH, and FS neurons. In this examination, we used $\tau = 1$ and $w = 500$. As shown in Fig. 16, the RMSE $\mathcal{E}$ were improved when we used a large number of neurons. The improvement was larger when RS neurons were used than when CH and FS neurons were used. These results suggest that the reconstruction accuracy depends on the firing patterns rather than the dimensions or the number of neurons used. The results shown in Fig. 10 in the main text were supported as well when sufficiently higher dimensions ($m \geqslant 5$) are used.

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