Changes in firing variability depend on network resilience

Kazuhiro Sakamoto (P)1, Yuichi Katori2, Kazuyuki Aihara2 and Hajime Mushiake3,4

1 Research Institute of Electrical Communication, Tohoku University
2 Institute of Industrial Science, University of Tokyo
3 Department of Physiology, Tohoku University School of Medicine
4 CREST
E-mail: sakamoto@riec.tohoku.ac.jp

Abstract—In general, increase in the fluctuations in dynamical systems serves as symptoms of state transitions. However, whether increases in the variability of firing in neural systems are caused by losses in stability before transitions remains poorly understood. We demonstrated that firing variability monotonically increases as a function of the degree of instability in attractor neural networks by measuring the resilience of such systems.

Keywords—Attractor Neural Network, Firing Variability, Resilience

1. Introduction

Generic symptoms indicating whether a critical point for transition is approaching exist in many complex dynamical systems characterized by state transitions [1–3]. Increases in the fluctuations of available measures, the so-called critical fluctuations, is one of these generic symptoms of dynamical systems’ losing stability immediately before transitions and becoming sensitive to small perturbations [4]. However, whether the loss of stability in neural systems causes increases in the firing variability remains unclear. To answer this question, we examined the relationship between firing variability and the stability of attractor neural networks.

2. Methods

2.1. Attractor neural network model

We used mutually connected neural populations, shown in Figure 1a, and defined the dynamics of a population as follows:

\[ \tau \dot{x}_i = -x_i + S_i(x_i + \text{noise}). \tag{1} \]

Here, we considered mutually connected two populations. Thus, \( i \) is 1, 2. \( S \) is a Naka–Rushton i/o function [5]

\[ S_i(x_i) = \begin{cases} 1 & \text{for } r \frac{B_i + w_{i,x_i}}{B_i + B(x_i)} > 1 \\ r \frac{B_i + w_{i,x_i}}{B_i + B(x_i)} & \text{for } B_i + w_{i,x_i} > 0 \\ 0 & \text{for } B_i + w_{i,x_i} < 0 \end{cases} \tag{2} \]

\( r, B_i, \theta_{ij} \) and \( \theta_{oi} \) define the maximum effect of input, the bias, and the value of \( x_i \) at which \( S_i(x_i) \) reaches the half of the maximum, respectively. \( w_{oi} \) is the connectivity from population \( x_i \) to \( x_j \): 1.0 for excitatory connectivity; -1.0 for inhibitory one. Small amounts of Gaussian noise (\( \sigma = 1/40 \)) were added to the i/o functions at each time step. However, we used parameters to obtain almost “linear” functions to avoid the effects of asymmetry around attractors and other phenomena; \( \tau \) is the time constant (20 ms). The firing of each neuron in a population depends on population-level activity. We used a phase model so that the population-level activity would be directly reflected in the firing rate. The neuron in population \( x_i \) emits a spike when the phase \( \phi_i \) reaches \( 2\pi n \), as shown in Figure 1b.

In other words, the population-level activity defines the phase velocity of each neuron.

\[ r \dot{\phi}_i = 2\pi \tau \]

\[ (3) \]

2.2. Index of the stability of attractors

The stability of a steady state of a dynamical system is usually discussed in terms of the eigenvalues of the linear approximation of the small deviation from the steady state in equation (1). We used resilience as an index of the stability of attractors and defined this construct as follows:

\[ g = \prod_{i=1}^{n} (-\lambda_i). \tag{4} \]

\( \lambda_i \) is the \( i \)th eigenvalue. The \( n \) dimensional coordinates \( x_i \) \((i = 1…n)\) with which the activity of the \( i \)th population is represented can be transformed into the other coordinates, \( x'_j \) \((j = 1…n)\), each of which is defined as the direction of an eigenvector. By using these new coordinates, potential can be defined as follows (see Fig.1c):

\[ U = \frac{1}{2} \sum_{j=1}^{n} (-\lambda_j x'_j). \tag{5} \]

Then, the volume of the hyperellipsoid surrounded by the equipotential surface of \( U = U_0 \) is as follows:

\[ 2U_0 \frac{\pi^{n/2}}{\Gamma(n/2 + 1)} g. \tag{6} \]

\( \Gamma \) is a gamma function. Thus, as \( g \) increases, the volume of the hyperellipsoid decreases (Fig.1d). That is, the larger \( g \) is, the steeper the potential becomes. In the case of \( n = 2 \), if we take the attractor network to be analogous with a spring pendulum, the resilience corresponds to the stiffness of the spring.

2.3. Index of firing variability

To evaluate firing variability, we analyzed the variability in the interspike intervals (ISI). We used a metric known as \( L/R \) [6] and defined as follows:

\[ L/R(i) = \left( 1 - \frac{4\text{ISI}_{i,i} \text{ISI}_{i}}{\text{ISI}^2_{i,i} + \text{ISI}^2_{i}} \right) + \frac{4R}{\text{ISI}^2_{i,i} + \text{ISI}_{i}}. \tag{7} \]
This excludes the effects of firing rate. The constant, $R$, compensates for the effect of the refractoriness of a previous spike.

3. Results

Figure 1b shows an example of a neuron firing in a network with two populations characterized by mutual excitation ($g = 0.75$) (Fig. 1a). In this case, the firing variability was 0.26.

The firing variability of a neuron in two-population networks is plotted in Figure 1e and g. In these cases, the i/o functions were excitatory. Note that the firing variability increased systematically across networks as resilience decreased. These systematic changes would not be derived from the nature of the individual i/o function of $x_1$ because its i/o function was not altered.

Figure 1g and h show examples of the relationship between resilience and firing variability in three-population models. These models also exhibited increased firing variability as a function of decreases in the value of $g$, which is consistent with two-population models.

4. Conclusion

In this paper, we demonstrated that firing variability can increase as attractors of simple neuronal networks lose their stability. In general, it is known that the measures of dynamical systems fluctuate increasingly as their states lose their stability before state transitions. Our results suggest that firing variability can serve as an index for the stability of the dynamical state of underlying neural networks. The argument in this paper is thought to be applicable to networks consisting of the conductance model, since a neuron of the leaky integrate-and-fire model exhibits high firing variability when the input includes large fluctuations (data not shown).

References


Figure 1. Stability of the network and its firing variability. a, An example of null clines of mutually connected neural populations (mutual excitation). b, A spike train emitted by a neuron in the population $x_1$. c, d, Images of the relationship between the potential and resilience. e-h, the relationship between resilience and firing variability in different network patterns.