

Dependence of neural ergodicity on noise strength

Naoki Masuda^{†‡} and Kazuyuki Aihara^{‡§}

[†]Laboratory for Mathematical Neuroscience, RIKEN Brain Science Institute,

2-1 Hirosawa, Wako, Saitama 351-0198 Japan,

[‡]ERATO Aihara Complexity Modelling Project, JST,

45-18 Oyama, Shibuya-ku, Tokyo 151-0065 Japan

[§]Institute of Industrial Science, the University of Tokyo,

4-6-1 Komaba, Meguro-ku, Tokyo 153-8505 Japan,

Email: masuda@brain.riken.jp, aihara@sat.t.u-tokyo.ac.jp

Abstract—In electrophysiological experiments, we often record activities from one or just a few neurons with repetitive stimulus presentation to overcome noise in neural activities. If the collected data are relevant to brain functions, the spike statistics (e.g. time-dependent firing rates) based on average over trials must be equivalent to those based on average over a population of neurons. This is so-called the ergodicity problem. In this paper, using a model of excitatory neurons, we compare trial averages and population averages of firing rates. In particular, we show that dynamical noise should be either strong enough or weak enough for these two statistics to be consistent with each other.

1. Introduction

Neurons are far from perfect computational units, and they are perpetually subject to substantial background noise. Accordingly, spiking patterns from a specified neuron vary from trial to trial even when the neuron receives an identical stimulus under a stable condition [10]. In many experiments, a series of stimulus or task, as schematically shown in Fig. 1(a), is repetitively presented typically about 30 times or more. This is to overcome experimental noise and clarify the relation between firing patterns (e.g. increase in the firing rates at a certain moment) and animals' behavior, attention, memory function, cognition, and so on. In this context, the peri-stimulus time histogram (PSTH), or the time-dependent averaging of spike counts from many trials, is ubiquitously used to be interpreted as temporal profiles of firing rates of a *population* of relevant neurons (Fig. 1(b)). In other words, we implicitly identify cooperative activities of neurons such as synchronous and correlated firing [5, 14] with the corresponding trial-based features such as peaks in the PSTH obtained from a single neuron. This is the physiological ergodicity assumption [4, 11, 12].

The joint PSTH [2, 4, 14] also reveals task-dependent temporal modulations of neuronal cooper-

ativity, but in a similar sense as above, the quantities based on just two neurons are used to substitute those based on two groups of neurons. Let us mention that the ergodicity in this context has nothing to do with the standard definition of ergodicity in physics and mathematics, which indicates that the statistical ensemble average and the temporal average match each other. Although a better term could be coined for the physiological ergodicity examined in this work, here we stick to this term.

Only partial experimental and conceptual arguments exist in favor of the ergodicity of spike trains [11, 12]. The validity of ergodicity is also supported by the finding that neighboring neurons receiving common input sources [10] tend to belong to the same functional assembly [11].

Actually, these arguments are mostly concerned to homogeneous populations of neurons. However, even neighboring neurons may have different characteristics. Furthermore, how interaction between neurons via chemical and electrical synapses influences the ergodicity is not quite obvious. For example, in the presence of coupling, it can happen that a group of neurons fires synchronously, whereas the timing of synchronous firing differs in each trial. This type of synchrony, whose firing is not linked to external stimuli or other clocks, may be important in the formation of the synfire chain [1, 9]. Then, firing rates based on repeated recording of a single cell (trial firing rate) do not generally agree with population firing rates. Oscillatory and nonoscillatory synchronous firing, which is considered to be relevant to, for example, visual [5] and somatosensory [13] information processing, may accompany this type of inconsistency as well. On the other hand, ergodicity is also violated when population asynchrony and trial synchrony are simultaneously realized.

In [8], we have explored the conditions for the ergodicity to hold by neural network models, mostly consisting of leaky integrate-and-fire (LIF) neurons. Actually, the breakdown of ergodicity is shown to occur in some parameter configurations. In this work, we

concentrate on effects of the level of dynamical noise applied to neurons and examine in which cases ergodicity is sustained.

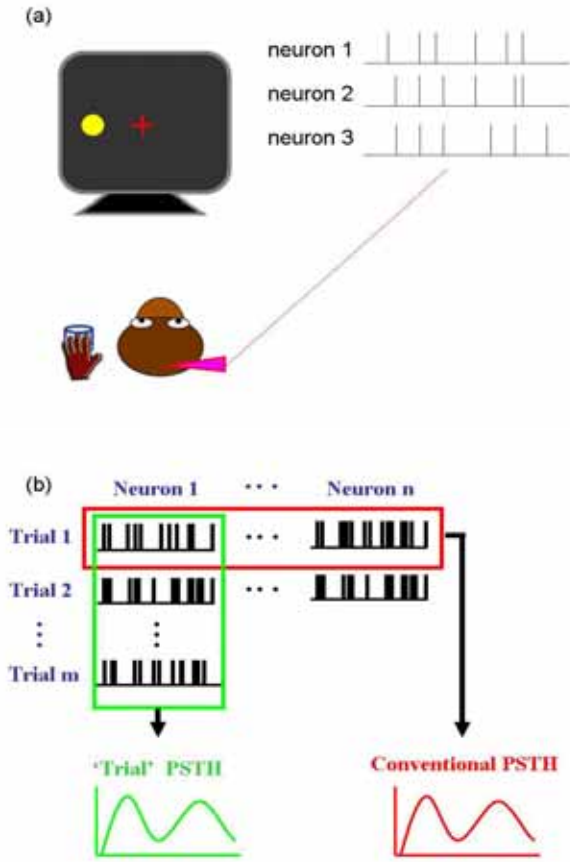


Figure 1: (a) Schematic picture of multiunit recording from the brain of a monkey engaged in a repeated task. (b) The problem of ergodicity of spike trains. Single-trial spike trains from multiunit recording and single-unit spike trains from repeated trials are compared.

2. Model and Results

We numerically simulate 100 pulse-coupled LIF neurons, whose architecture is schematically shown in Fig. 2. They are among the simplest models of spiking neurons and fire either synchronously or asynchronously depending on the noise intensity [3, 6, 15] or the values of other model parameters [1, 3, 7]. We apply dynamical noise independent for different neurons and inspect the ergodicity in terms of the degree of synchrony. We set the membrane potential leak rate $\gamma = 0.04 \text{ ms}^{-1}$ and use different noise level D' . Actually, D' is the standard deviation of the Gaussian noise

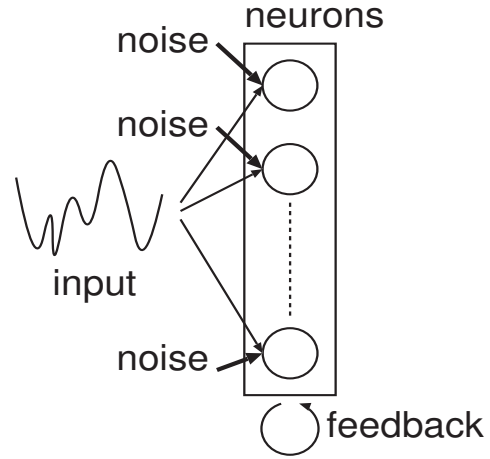


Figure 2: Architecture of the pulse-coupled network of LIF neurons.

applied independently to each neuron every $dt = 0.025$ ms. A neuron sends feedback spikes with amplitude $\epsilon = 0.008$ and synaptic delay 0.8 ms to 30 randomly chosen neurons. The time course of the synaptic current is represented by the delta function for simplicity. As the deterministic part of an external input, we use

$$I_{ext}(t) = A (4.9 \cdot 10^{-2} + 5.6 \cdot 10^{-3} \sin(2\pi t/T_{ext})) \quad (1)$$

with $A = 0.92$ and $T_{ext} = 14$ ms. For illustration, time courses of population firing rates and ones of trial-averaged firing rates are shown in Figs. 3(a) and 3(b) for $D' = 0.002$ and $D' = 0.004$, respectively. Naturally, smaller dynamical noise (Fig. 3(a)) results in more synchrony across both different neurons and different trials. In Fig. 3(b), both the population activity and the trial-averaged activity are asynchronous because of large noise. In either case, the network is in the ergodic situation as far as we are concerned only to the profile of firing rates. Particularly in the latter case, firing rates averaged over the neurons or the trials asynchronously reproduce a relatively precise temporal waveform of $I_{ext}(t)$ [6, 7, 15], enabling efficient rate coding.

Is there any intermediate scheme in which the ergodicity breaks down? Presumably, trial asynchrony emerges with a smaller noise strength than population asynchrony does. This is because population synchrony is more easily realized owing to the feedback coupling. On the other hand, there is no coupling between different runs of experiments, except a smaller synchronizing tendency due to the repeated use of an identical stimulus and homogeneity of a neuron across trials.

To be more quantitative, we compare the degree of synchrony calculated from traces of population firing

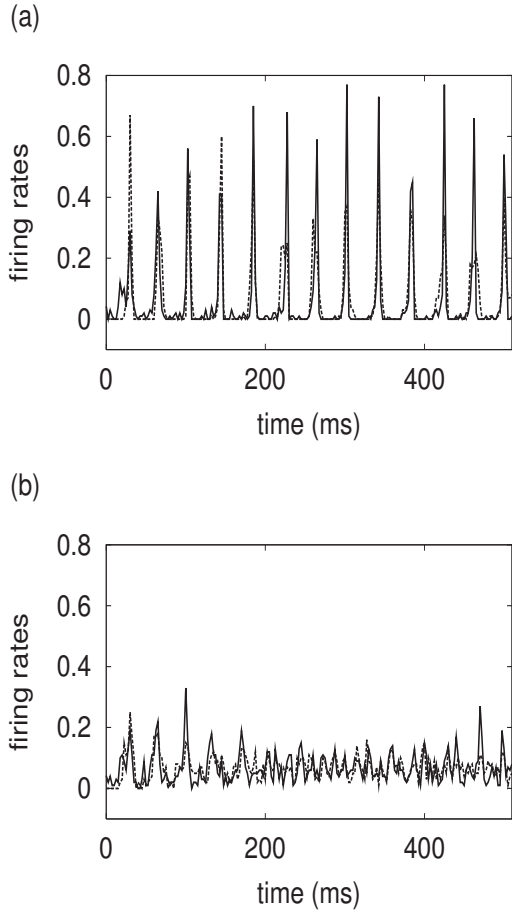


Figure 3: Example traces of population firing rates (solid lines) and trial firing rates (dotted lines) of 100 pulse-coupled LIF neurons. (a) $D' = 0.002$ and (b) $D' = 0.004$. The statistics are based on 100 trials with an identical stimulus and identical initial conditions.

rates and trial firing rates for various noise levels. The degree of synchrony is measured by the standard deviation of firing rates normalized by the temporal average of the firing rates. With the model parameters same as those used in Fig. 3, the results are shown in Fig. 4(a) together with the difference between the degree of population synchrony and that of trial synchrony (Fig. 4(b)). As expected, both degrees of synchrony are large for small values of D' , and just a small discrepancy is found. The discrepancy is also small for a large noise level D' . In this case, the coupling effect is smeared out by the noise, and both firing rates indicate asynchrony. However, in the middle range of D' (around $D' \cong 0.002$), population synchrony is more persistent, whereas trial synchrony is more readily lost. As mentioned, this is because there is no coupling between spike trains from different trials. On the other

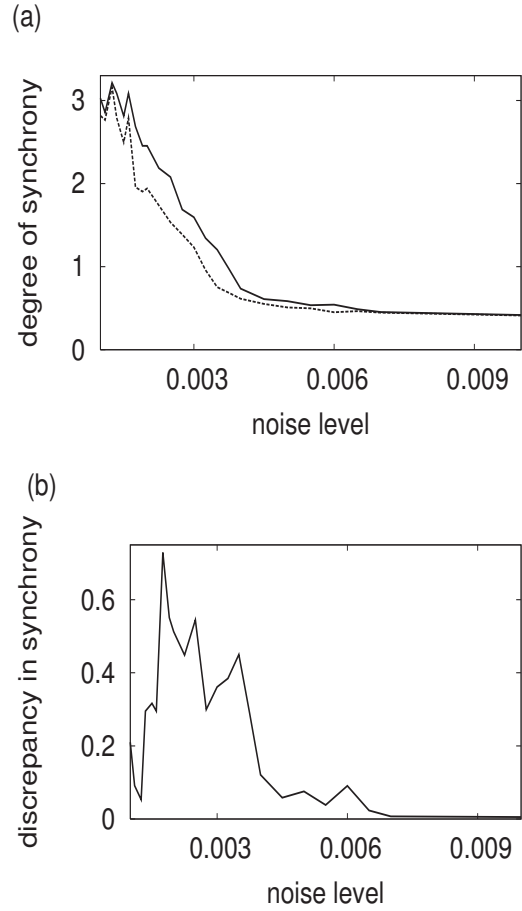


Figure 4: (a) Degrees of population synchrony (solid line) and trial synchrony (dotted line) as functions of the noise level D' . (b) The difference between two synchrony levels. We use 100 pulse-coupled LIF neurons with the same parameter values as those used in Fig. 3.

hand, a population of neurons are interconnected to resist to desynchronizing factors [3, 6]. The ergodicity is violated in this intermediate scheme, which is a warning for the interpretation of experimental data.

3. Conclusions

We have examined how dynamical independent noise affects the degree of ergodicity. The grade of population synchrony and that of trial synchrony deviate from each other for the intermediate noise strength. Of course, there are many other factors that influence the ergodicity [8], and how these factors and the noise interact is far from trivial. To work with more realistic neural networks and experimental data is our future problem.

Acknowledgments

We thank Y. Igarashi, S. Omae, R. Kimura, S. Koyama, M. Sato, Y. Tsubo, H. Nakamura, and H. Yamada, who were the members of the ergodicity workgroup in 2003 Neuroinformatics Summer School (JNNS), for fruitful discussion and the assistance in generating Fig. 1.

References

- [1] M. Abeles, *Corticonics*, Cambridge University Press, Cambridge, 1991.
- [2] A. M. H. J. Aertsen, G. L. Gerstein, M. K. Habib and G. Palm, “Dynamics of neuronal firing correlation: modulation of “effective connectivity”,” *J. Neurophysiol.*, vol.61(5), pp.900–917, 1989.
- [3] N. Brunel, “Dynamics of sparsely connected networks of excitatory and inhibitory spiking neurons,” *J. Comput. Neurosci.*, vol.8, pp.183–208, 2000.
- [4] G. L. Gerstein, P. Bedenbaugh and A. M. H. J. Aertsen, “Neuronal Assemblies,” *IEEE Trans. Biomedical Engineering*, vol.36(1), pp.4–14, 1989.
- [5] C. M. Gray, P. König, A. K. Engel, W. Singer, “Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties,” *Nature*, vol.338, pp.334–337, 1989.
- [6] N. Masuda and K. Aihara, “Bridging rate coding and temporal spike coding by effect of noise,” *Phys. Rev. Lett.*, vol.88(24), 248101, 2002.
- [7] N. Masuda and K. Aihara, “Duality of rate coding and temporal spike coding in multilayered feedforward networks,” *Neural Comput.*, vol.15, pp.103–125, 2003.
- [8] N. Masuda and K. Aihara, “Ergodicity of spike trains: when does trial averaging make sense?,” *Neural Comput.*, vol.15, pp.1341–1372, 2003.
- [9] A. D. Reyes, “Synchrony-dependent propagation of firing rate in iteratively constructed networks *in vitro*,” *Nature Neurosci.*, vol.6(6), pp.593–599, 2003.
- [10] M. N. Shadlen and W. T. Newsome, “The variable discharge of cortical neurons: implications for connectivity, computation, and information coding,” *J. Neurosci.*, vol.18(10), pp.3870–3896, 1998.
- [11] G. L. Shaw, E. Harth and A. B. Scheibel, “Cooperativity in brain function: assemblies of approximately 30 neurons,” *Exp. Neurol.*, vol.77, pp.324–358, 1982.
- [12] G. L. Shaw and D. J. Silverman, “Simulations of the trion model and the search for the code of higher cortical processing,” In *Computer simulation in brain science*, Ed. Cotterill, R., M., J., pp.189–209, Cambridge University Press, Cambridge, 1988.
- [13] P. N. Steinmetz, A. Roy, P. J. Fitzgerald, S. S. Hsiao, K. O. Johnson and E. Niebur, “Attention modulates synchronized neuronal firing in primate somatosensory cortex,” *Nature*, vol.404, pp.187–190, 2000.
- [14] E. Vaadia, L. Haalman, M. Abeles, H. Bergman, Y. Prut, H. Slovin and A. Aertsen, “Dynamics of neuronal interactions in monkey cortex in relation to behavioural events,” *Nature*, vol.373, pp.515–518, 1995.
- [15] M. C. W. van Rossum, G. G. Turrigiano and S. B. Nelson, “Fast propagation of firing rates through layered networks of noisy neurons,” *J. Neurosci.*, vol.22(5), pp.1956–1966, 2002.