Reliability of temporal coding on pulse-coupled networks of oscillators

Jun-nosuke Teramae and Tomoki Fukai
Laboratory for Neural Circuit Theory, RIKEN Brain Science Institute, Saitama, Japan

We study the reliability of spike output in a general class of pulse-coupled oscillators receiving a fluctuating input. Showing that this problem is equivalent to noise-induced synchronization between identical networks of oscillators, we employ the phase reduction method to analytically derive the average Lyapunov exponent of the synchronized state. We show that a transition occurs between reliable and unreliable responses at a critical coupling strength, which is determined through the competition between the external input and recurrent input. To our surprise, the critical value does not depend on intrinsic properties of oscillators.

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Noise-induced synchronization appears in a variety of phenomena including lasers [1], chemical reactions [2], gene networks [3] and neuronal systems [4, 5]. In these systems, periodic or chaotic oscillators driven by a common fluctuating input synchronize with each other due to the nonlinearity of oscillators and the stochastic nature of the input [6]. The phase reduction [7] and the Lyapunov analysis proved that two or more identical oscillators receiving a common fluctuating input are always in-phase synchronized regardless of their intrinsic properties and initial phases [8, 9]. We can interpret such oscillators as a single oscillator receiving the same input repeatedly, but with different initial phases, i.e. many trials of an input application. Therefore, the in-phase synchronization of input-driven oscillators implies, in a single oscillator, the reproducibility of the responses to a repeated input, or response reliability, which is particularly important for processing external signals. Reliable responses to a fluctuating input are actually measured from single cortical neurons [4]. However, neurons and other oscillators in the real world work collectively in their networks rather than individually. To study whether a network of oscillators still has response reliability, we develop a theory of noise-induced synchronization between networks of oscillators rather than between single oscillators. We find a transition from reliable to unreliable responses at a critical coupling strength. Deriving average Lyapunov exponent analytically, we reveal that the critical value is determined through the competition between variance of the external input and of internal recurrent inputs regardless of details of oscillators. Around the transition point where magnitude of the average Lyapunov exponent is small, information of initial states can stay in the network for a long time. We discuss a possible role of the long time scale in role-sharing between rate and temporal coding on neuronal computation in the brain.

A network of pulse-coupled $N$ limit-cycle oscillators receiving fluctuating inputs are described as:

$$\frac{dX_i}{dt} = F(X_i) + \xi_i(t) + \sum_{j=1}^{N} g_{ij} \delta(t - t^{spike}_j) \hat{\gamma},$$

where $i = 1, \ldots, N$ and $\dot{X} = F(X)$ has a stable limit-cycle solution $X_0(t)$. A unit vector $\hat{\gamma}$ indicates the direction of interactions in the multidimensional space spanned by $X$. We assume, with neuronal oscillators in mind, coupling matrix $g_{ij}$ is a sparse random matrix with connection probability $p$, and each nonzero component of $g_{ij}$ is either $g$ or $-g$ if $j$ refers to an excitatory or an inhibitory cell, respectively. The network consists of $N_E$ excitatory neurons and $N_I = N - N_E$ inhibitory neurons. Fluctuating external inputs $\xi_i$ represent independent white Gaussian processes with strength $\langle \xi_i(t) \xi_j(s) \rangle = 2\sigma^2 \delta_{ij} \delta(t - s)$, and $t^{spike}_j$ represents spike times of the $j$th neuron. We use $g$ as a control parameter of the network and require, for simplicity, that $g_I$ is in proportional to $g$ and satisfies the balance condition $g N_E + (-g_I) N_I = 0$, whereas results of the paper are independent of the restriction. When $g = 0$, response of oscillators are always reliable, i.e. the spike sequence of each oscillator converges into the same sequence in different trials. Figure 1a and 1b demonstrates the reliable responses obtained from numerical calculations of quadratic integrate-and-fire (QIF) neurons, $F(X) = X^2 + I$, with variable resetting $X(t^{spike}) = \infty \rightarrow X(t^{spike} + 0) = -\infty$ [12]. Whereas two trials start from different initial states, raster plots of them converge into same sequences, i.e. same spike times. We then introduce finite couplings $g > 0$ to the network of oscillators and calculate firing responses in a similar way to Fig. 1b. When coupling strength is small, the population is still reliable, spike sequences of different trials converge into the same one (Fig. 1c). However, the reliability is lost from the population when coupling strength is sufficiently large (Fig. 1d). Spike sequences of two trials never converge into the same one while we apply the same input to trials. In terms of synchronization, the result means that fluctuating inputs induce phase synchronization to two identical networks of oscillators only when coupling strength of the

*Electronic address: teramae@brain.riken.jp*
network is sufficiently weak.

Regarding the fluctuating signals and recurrent connections as perturbations to the deterministic oscillators, we apply the standard phase reduction method to Eq. (1) and obtain stochastic equations of phases $\phi_i$ as,

$$\frac{d\phi_i}{dt} = \omega + Z(\phi_i) \left( \xi_i(t) + \sum_{j=1}^{N} \sum_{\text{spike}} g_{ij} \delta(t - t_{j}^{\text{spike}}) \right),$$

where $\omega$ is an intrinsic frequency of the unperturbed oscillators. Phase sensitivity function or phase response function is defined uniquely from $X_0(\phi)$ as $Z(\phi) = \text{grad}_{X} X_0(\phi)$ [2]. To simplify notations, we assumed without loss of generality that $\hat{\mathbf{g}}$ is in parallel with $\xi$ and replaced vector variables $Z(\phi) \hat{\mathbf{g}}$ and $Z(\phi) \xi$ to scalar variables $Z(\phi)$ and $Z(\phi) \xi$ in Eq. (2). For the QIF model, for instance, $\omega = 1 - \frac{1}{2}, Z(\phi) = \omega (1 + \cos(\phi))$. Note that discontinuous variable resetting $X(t_{j}^{\text{spike}}) = \infty \to X(t_{j}^{\text{spike}} + 0) = -\infty$ is now reduced to continuous dynamics over a spike threshold $\phi = \pi$ because derivation of $F$ is continuous between $X = \infty$ and $X = -\infty$, $F'(\infty) = F'(-\infty)$. To avoid unrealistic cases where an oscillator sends numerous spikes within a short interval of time when its fluctuating phase crosses the firing threshold, $Z(\phi)$ should be vanish around the threshold. Realistic neuron models including the QIF model satisfy the condition. Reliability of the firing responses is equivalent to that of phase dynamics because phase deviation is proportional to deviation of firing time. Phases of two trials, $\tilde{\phi}_i$ and $\tilde{\phi}_i$, evolve satisfying Eq. (2) from different initial phases, $\xi_i$, in the same network, $g_{ij}$. Since phase synchronized state, $\phi_i = \tilde{\phi}_i$, is an obvious solution of these two equations, linear stability around the solution determines the response reliability.

To evaluate the stability we linearize Eq. (2) in terms of small phase differences, $\psi_i = \tilde{\phi}_i - \phi_i$, and calculate average Lyapunov exponent [13] over all oscillators in the network.

Coupling terms are linearized as follows. Consider increment of $\psi_i$, when $j$th cell fires. We can take firing time of $\tilde{\phi}_j$ is $t = 0$, firing time of $\phi_j$ is therefore $t = dT = \psi_j/\omega$. We can assume $dT > 0$ without loss of generality. At $t = 0$, $\phi_i$ receives a spike from $\tilde{\phi}_j$,

$$\begin{align*}
\tilde{\phi}_i(0^+) &= \tilde{\phi}_i(0) + g_{ij} Z(\tilde{\phi}_i(0)) , \\
\phi_i(0^+) &= \phi_i(0) .
\end{align*}$$

(3)

Phases evolve as follows from $t = 0^+ \to dT$, because $dT$ is a short interval,

$$\begin{align*}
\tilde{\phi}_i(dT) &= \tilde{\phi}_i(0^+) + \left( \omega + \sigma^2 Z'(\tilde{\phi}_i(0^+)) \right) dT \\
&\quad + Z(\tilde{\phi}_i(0^+)) dW \\
\phi_i(dT) &= \phi_i(0^+) + \left( \omega + \sigma^2 Z'(\phi_i(0^+)) \right) dT \\
&\quad + Z(\phi_i(0^+)) dW .
\end{align*}$$

(4)

where $dW = \xi_i dT$. In order to evaluate phase responses $Z(\phi)$ at precise timings just before spike inputs, we translated Eq. (2) to equivalent Ito integrals in Eq. (3) [14]. Third terms of Eq. (3) result from the translation. Finally, at $t = dT$, $\phi_i$ receives a spike from $\tilde{\phi}_j$,

$$\begin{align*}
\tilde{\phi}_i(dT^+) &= \tilde{\phi}_i(dT) \\
\phi_i(dT^+) &= \phi_i(dT) + g_{ij} Z(\phi_i(dT)) .
\end{align*}$$

(5)

We can linearize from Eq. (3) to (5) in terms of $\psi$ with an attention that $dW$ is the order of $dT^{3/2}$ and then the order of $\psi_i^{1/2}$. Taking all connections into account and neglecting terms higher than the order of $g^2$, we obtain linearized equation of $\psi$ as

$$\begin{align*}
\frac{d\psi_i}{dt} &= \left( \sigma^2 (Z'(\phi_i) Z(\phi_i))' + Z'(\phi_i) \xi_i \right) \psi_i \\
&\quad + \sum_{j=1}^{N} \sum_{\text{spike}} g_{ij} Z'(\phi_i) \delta(t - t_{j}^\text{spike}) (\psi_i - \psi_j) .
\end{align*}$$

(6)

By introducing new variables $y_i = (\log \psi_i^2)/2$, Eq. (6) is further rewritten as

$$\begin{align*}
\frac{dy_i}{dt} &= \sigma^2 (Z'(\phi_i) Z(\phi_i))' + Z'(\phi_i) \xi_i - \sigma^2 Z'(\phi_i)^2 \\
&\quad + \sum_{j=1}^{N} \sum_{\text{spike}} \delta(t - t_{j}^\text{spike}) \log \left| 1 + g_{ij} Z'(\phi_i) \left( 1 - \frac{\psi_j}{\psi_i} \right) \right| .
\end{align*}$$

(7)

Since the Lyapunov exponent $\lambda_i$ is defined as $\lim_{T \to \infty} (y_i(T) - y_i(0))/T$, the long time average of the Eq. (7) coincides with $\lambda_i$. We assume that the network is in asynchronous steady firing state due to fluctuating inputs and replace spike times of cells by independent
Poisson processes with firing rate $r$ \cite{15}. Then averaging of Eq. \eqref{eq:7} over the Poisson processes and over all oscillators in the network gives

$$
\frac{dy_i}{dt} = \langle Z'^2 \rangle \left(-\sigma^2 + Nr \frac{(g^2)}{2} \left(1 + \frac{\psi_i^2}{\psi_j^2}\right)\right), \tag{8}
$$

where $\langle Z'^2 \rangle = (2\pi)^{-1} \int_0^{2\pi} Z'(\phi)^2 d\phi$. Here we used the assumption of weak inputs and weak interactions and reduced distributions of phases to uniform distributions in $[0, 2\pi]$. Unfortunately, Eq. \eqref{eq:8} is not a closed form of $y_i$. However, when variance of $\psi^2$ is small, or $\langle \psi^4 \rangle \simeq \langle \psi^2 \rangle^2$, the last term of Eq. \eqref{eq:8} is approximated as $\langle \psi_i^2/\psi_j^2 \rangle = 1$ and we finally obtain the following main formula of the average Lyapunov exponent:

$$
\lambda = \langle Z'^2 \rangle \left(-\sigma^2 + Nr(g^2)\right). \tag{9}
$$

Note that when variance of $\psi^2$ is not small, Eq. \eqref{eq:9} gives the lower bound of $\lambda$ because $\langle \psi_i^2/\psi_j^2 \rangle \geq 1$ in generally.

To confirm the above analysis, we calculate averaged dynamics of $y_i = \langle \log \psi_i^2 \rangle / 2$ numerically for networks of QIF oscillators. Due to fluctuating inputs and recurrent interactions, $y_i$ themselves do not evolve monotonically. However, population averages of $y_i$ decrease or increase almost linearly depending on coupling strengths $g$ as predicted by Eq. \eqref{eq:9}.

Our expression of the Lyapunov exponent, Eq. \eqref{eq:9}, tells us two important facts of the reliability transition. First, the transition stems from a competition between two variances, variance of input signals $\sigma^2$ and variance of recurrent inputs $Nr(g^2)$. Whereas the first contribution to the exponent is negative, the second is always positive. Therefore, the network lost their reliability when the second exceeds the first. Second, the factor of $\langle Z'^2 \rangle$ which reflects intrinsic properties of oscillators is multiplied equivalently to these two factors $\sigma^2$ and $Nr(g^2)$ in Eq. \eqref{eq:9}. Therefore, the critical coupling strength $g_c$, given as the solution of $\lambda = 0$, is universal in the sense that $g_c$ is independent of details of oscillators. For the network structure we used in Fig. 1 the critical value is given as $g_c = \sigma \sqrt{(Npr)^{-1} N_f/E}$ regardless of oscillators on the network. If we use another natural normalization of coupling strengths as $g \rightarrow g/\sqrt{Np}$ \cite{11}, we can eliminate $N$ from the critical strength, $g_c = \sigma \sqrt{r^{-1} N_f/E}$.

In the vicinity of the critical coupling strength $g = g_c$ where $|\lambda| \ll 1$, information on the initial states of oscillators may disappear quite slowly after the onset of input. This slow transient behavior might have the following implications for computations by cortical networks. The output of the computation is not simply determined by the current input, but is also modulated by the brain’s internal state and/or input histories \cite{16, 17}. In our model, the membrane time constant sets the short time scale that enables the network to respond quickly to an external input with firing rate of population dynamics \cite{11, 18}. By contrast, the critical dynamics of temporal spike sequences may set a much longer time scale to ensure the response diversity reflecting the initial state or input histories. This implies that neuronal populations may simultaneously achieve two different time scales by parallel use of rate code and temporal code. Further studies are required for clarifying this possibility.

So far, we have restricted our study to super-threshold neurons which continue to fire without external inputs. Numerical simulations of sub-threshold QIF model with $I < 0$, however, suggest that similar transition also occurs in a network of sub-threshold neuron models (figure\textsuperscript{3}). It remains unknown whether this transition may appear in a broad class of sub-threshold neuron models because the phase reduction method is not applicable to sub-threshold neuron models. A unified treatment of

\textbf{FIG. 2:} Time evolutions of logarithm of phase differences $y_i$ of randomly chosen 5 oscillators (gray lines). Sudden tentative jumps to large values on these lines are because of differences of spike times between two trials (see Eq. \eqref{eq:3} and \eqref{eq:5}). Thick black curves are averages of $y_i$ over all oscillators in the network. Slopes of these curves agree well with the analytical results of Eq. \eqref{eq:9} shown by slopes of thin black lines. The values of parameters are the same as in Fig. \textbf{4} except that $\sigma = 0.2$, and $g = 0.01$ (a), 0.05 (b) and 0.1 (c).
super- and sub-threshold neuron models is awaited. We have assumed that couplings among oscillators are delta-functions. To remove a doubt that our results might be pathological phenomena come from singularity of delta-functions, we calculated reliability of coupled oscillators numerically using an alpha-function, $\alpha(t) = \alpha^2 t \exp(-\alpha t)$, instead of $\delta(t)$. Again, we could see similar transition from reliable to unreliable responses (results not shown).

Linear integrate-and-fire model is the most useful description of firing neurons. This model, however, behave unrealistically about response reliability even when $g = 0$ because of its anomalous variable resetting. Here, we use quadratic integrate-and-fire model to avoid the problem. Coupled oscillators may synchronize with each other if $g$ is sufficiently large, whereas we have only concentrated on the asynchronous steady state. Synchronization may affect average Lyapunov exponent and may change the transition significantly because we must use correlated stochastic processes instead of independent Poisson processes when we average Eq. (8) to obtain $\lambda$.

In conclusion, coupled reliable elements are not necessarily reliable any more. Spike responses of coupled oscillators to fluctuating inputs show transition from reliable responses to unreliable responses. In terms of noise-induced synchronization, common noises fail to induce phase synchronization to networks of strongly coupled oscillators whereas same inputs always induce synchronization to single oscillators. Underlying mechanism of the transition is competition between a variance of external signals and a variance of internal recurrent inputs. Critical coupling strength derived analytically is independent of details of oscillators because phase response functions appear equivalently in these competing factors.

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