

Analysis of noise-induced phase synchronization in nervous systems: from algorithmic perspective

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Abstract

In many cases, a key step in neuronal information processing is phase synchronization of neurons (as oscillators). Substantial evidence suggests that an universal mechanism is behind the synchronization. Recently, stochastic equations were proposed to model the synchronization. However, it is unclear what force ultimately drives this universal mechanism. From algorithmic perspective, we analyze solutions of these stochastic equations. The result enhances the current analysis for the phase synchronization; importantly, it shows that noise is the ultimate driving force.

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1. Introduction

The brain is perhaps the most sophisticated information processor. Single neurons are able to resonate and oscillate at multiple frequencies. An emerging interdisciplinary field, “neuronal oscillations”, has attracted researchers from applied mathematics, biophysics, computational modeling, neuroscience, and psychophysics. We refer the reader to [1] for a comprehensive review. The following results mentioned therein are taken as the background of this note: (R1) In many cases, for a neuronal network to function well, phase synchronization of the oscillations of neurons in the network must be established. Such phase synchronization may be over several frequency bands. The mean frequencies of oscillator categories, from 0.05 to 500 Hz, form a

linear progression on a natural logarithmic scale with a constant ratio between neighboring frequencies, leading to the separation of frequency bands. (R2) The oscillatory properties of neurons and their behavioral correlates are largely preserved through mammalian evolution. This strongly suggests that there is a universal mechanism behind phase synchronization of neurons in mammalian brains. Although a great number of articles have been published (see [15] and references therein), search for model(s) of the underlying mechanism of phase synchronization of neuronal oscillations continues. Recently, considerable efforts have been made to study an important and yet almost entirely unsolved issue. How is noise exploited in biological information processing [12]?

Noise has long been thought as a negative factor in phase synchronization of neuronal oscillations. The first significant breakthrough was made by Teramae and

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Tanaka [13] and Nakao et al. [8]. Their work is based on the study pioneered by Pikovsky. See [10] for a comprehensive view. These studies profoundly changed our perception of noise in phase synchronization of oscillators. Pikovsky found that under variety of conditions, a common *weak* external noise can force *stable* phase synchronization among oscillators in many physical systems. This type of phenomena is now termed “noise-induced phase synchronization”. Since the middle of the 1990s, noise-induced phase synchronization has been documented in nervous systems, e.g., [7,11,14]. There were no satisfactory models to explain this type of phenomena until [13] and [8] showed that under a common weak external noise a population of identical and uncoupled neurons can be phase-synchronized in theory. A new experimental study by Galán et al. [3] strongly suggested that these theoretical models capture the underlying mechanism for phase synchronization of real olfactory bulb neurons. However, the force driving the mechanism for noise-induced phase synchronization was explained in different ways. In [13], only common external weak noise was considered. Nakao et al. [8] claimed that in addition to noise, external random impulses are the driving force behind the phase synchronization based on the following: It has been observed in experiments (e.g., [7,11,14]) that the same sequence of external impulses always produces the same oscillatory pattern of neurons, even under different type of common weak external noise. In [3] both external noise and random impulses were taken into account. Very recently, in [9] (June 2006) Nakao et al. showed that external fluctuation described by piece-wise-constant random function is the driving force; the authors also pointed out that continuous fluctuation matches the realistic condition in nervous systems, and they will prove it to be the driving force in future research. Therefore, it is unclear what force ultimately drives the mechanism for the phase synchronization. If, as previous studies suggested, there is a universal mechanism behind phase synchronization of neurons in mammalian brains, then there must be a force that ultimately drives the mechanism. The question is what is the driving force: common weak external noise or random impulses, or something else?

We will use a term “neuronal oscillator” to mean that a neuron is regarded as an oscillator. Three temporal traces of a neuronal oscillator are shown in Fig. 1 which are from our replication of the computer simulation in [3]. The proposed models in [13,8,9] were expressed by stochastic equations. We observe that the solution of such a stochastic equation is a stochastic process obtained by taking stochastic integration over the martin-

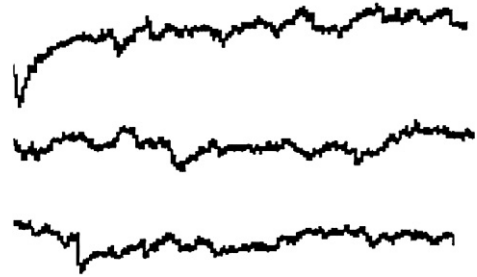


Fig. 1. Three temporal traces of oscillations of a neuron.

gale induced by the noise together with the sequences of random impulses or the fluctuations (if any). Viewing the three temporal traces in Fig. 1 as paths in a stochastic process, we can see that a given sequence of impulses as well as a given fluctuation constitutes the drift of paths. Thus, a question is: Can the martingale induced solely by a common weak external noise together with some mathematical properties induced by the physiological feature of neuronal oscillator ultimately yield phase synchronization, if consider one sequence of impulses or fluctuation at a time? A positive answer to this question promotes a new theoretical viewpoint: Noise, not anything else, is the fundamental factor in phase synchronization of neuronal oscillators. In Section 3, in a mathematical setting for analyzing computer simulation for the phase synchronization, we show that *as long as there is a common weak external noise, phase synchronization of n identical and uncoupled neuronal oscillators will occur for (i) a given sequence of impulses, or (ii) a given continuous fluctuation.* (Notice that (ii) is unsolved in [9].) This result indicates: Noise is the ultimate driving force behind the synchronization; while, a sequence of impulses or a fluctuation sets the phase value at which the synchronization emerges.

2. Stochastic equations

The models in [13,8] can be described by a stochastic equation system

$$\frac{dX_i(t)}{dt} = H_i(X_i(t)) + \delta I(t) + \xi_i(t), \quad i = 1, 2, \dots, n. \quad (1)$$

For each $1 \leq i \leq n$, H_i captures the intrinsic dynamics, i.e., the orbit of the i th neuronal oscillator without any external interferences. It is assumed that all n neuronal oscillators are identical and uncoupled. Thus, all H_i in (1) are the same. δ is constant to a given equation system of form (1), which takes values either 1 or 0. $I(t)$ represents a sequence of external random impulses, which is common to all the n neuronal oscillators. $\xi_i(t)$ are

used to capture the effect of noise. The physical explanation of (1) is as follows. At moment t , the sequence of impulses and the noise influence the orbit $H_i(X_i(t))$, which determines the direction $dX_i(t)/dt$ as the sum of $H_i(X_i(t))$, $\delta I(t)$ and $\xi_i(t)$. Therefore, (1) describes the process of phase synchronization of the n neuronal oscillators as a stochastic process (since at least the term $\xi_i(t)$ is random). In [13], in absence of $I(t)$ equivalent to $\delta = 0$, (1) was used as the model. In [8], (1) is used as the model with $\delta = 1$. Corresponding to (1), there is a phase evolving process. Let $\phi_i(t)$ be the phase function of the i th neuronal oscillator, i.e., $\phi_i(t)$ is the phase value of the orbit $H(X_i)$ at time t . Then (1) induces the following equation system

$$\frac{d\phi_i(t)}{dt} = G(\phi_i(t), \delta I(t), \xi_i(t)), \quad i = 1, 2, \dots, n, \quad (2)$$

where G is the same for all $1 \leq i \leq n$. In both [13] and [8], (2) was analyzed by the phase reduction method [6], that is, it was viewed as the description of a dynamic system, and the Lyapunov exponent was calculated to see if phase synchronization occurs.

We observe that if exists, the solution of (2) is a stochastic process. Because of the physiological feature of neuronal oscillator, this stochastic process has some inherent mathematical properties. Using these properties, we construct and analyze the stochastic process. For this reason, for the moment, we leave (2) in a symbolic setting. We will consider one (the i th) equation in (2) at a time, and with harmless notation abuse will call it (2).

3. Analysis

We first analyze the case where $I(t)$ in (2) is a given sequence of external impulses, and then extend the analysis to the case where $I(t)$ is a given continuous fluctuation.

3.1. The setting

A computer simulation algorithm runs within a finite time interval. We normalize the length of the time interval as 1. That is, we simulate the solution of (2) for $t \in [0, 1)$. Notice that under this normalization, the frequency bands of neuronal oscillator must change accordingly. However, based on (R1) (in Section 1), without loss of generality, we can assume that the frequency bands of neuronal oscillator are $2^{m'}$, $2^{m'+1}$, \dots , 2^m for fixed $m > m' > 0$. To observe the phase synchronization, we can run the algorithm for several rounds. In each round the algorithm is running over time instances $\frac{k}{N}$, $k = 0, 1, \dots, N - 1$, $N \gg 2^m$. Notice that since the

time interval is normalized as 1 and m is fixed, we may need to run the algorithm over time instances $\frac{k}{N}$ for unlimitedly large N , which requires a computer with unlimited computational power. This is fine with our theoretical analysis.

Unlike in [3] and [8], we take different noise resources into consideration. We run the algorithm for multiple groups of rounds. For a group, an arbitrarily chosen sequence of impulses from $I(t)$ is used, and in each round (in the group) different noise resource equivalent to different $\xi_i(t)$ is used. Notice that the occurrences of the phase synchronization under arbitrarily chosen sequences of impulses with different noise resources imply the same occurrences under random sequences of impulses with a fixed noise resource (which was adopted for simulation in [3] and [8]). In what follows, we consider one sequence arbitrarily chosen from $I(t)$ at a time, and simply denote it by $I(t)$.

Two properties listed below were used in [13] and [8], as well as in [3] which concluded that (1) captures the underlying mechanism for phase synchronization of real olfactory bulb neurons.

(P1) Existence and uniqueness of solution.

(1) (and consequently, (2)) has a unique solution which describes a limit-cycle oscillator (i.e., its frequency is limited). Moreover, if there are no external interference, the orbit of the i th neuronal oscillator described by H_i in (1) is a two-dimensional analytic curve. In this case, the orbit typically is a sine wave (see [5]).

(P2) Regularity of impulse.

The frequency of the occurrences of the impulses is not higher than 2^m , the highest frequency of a neuronal oscillator. Moreover, an impulse at most causes a fixed number of disruptions on the orbit of a neuronal oscillator. That is, at the moment when a disruption emerges, a jump in the orbit may occur; however, after this moment the orbit is still a two-dimensional curve with continuous derivative. We note that external impulse was not considered in [13].

Since (2) has a unique solution (by (P1)), we can fix a sequence \mathcal{N} of integers $N \uparrow \infty$ and then consider the path-by-path definition of the solution along time instances $\frac{k}{N}$, $k = 0, 1, \dots, N - 1$, for $N \in \mathcal{N}$. Given (2), we construct \mathcal{N} as follows. Recall that the highest frequency of a neuronal oscillator is limited to 2^m for a fixed $m > 0$. That is, the shortest period τ of a neuronal oscillator has a fixed lower bound. By the second part of (P1) within the period τ , without any external influ-

ences, the phase evolving process of the i th neuronal oscillator is deterministic described by an analytic function. For a given sequence of external impulses, by (P2) within the period τ there are at most a fixed number of jumps on the analytic function can be caused by an impulse. Therefore, given a sequence of impulses, there is a constant $N_0 > \frac{1}{\tau} > 0$ such that within each interval $[\frac{k-1}{N_0}, \frac{k}{N_0}]$, $1 \leq k \leq N_0$, if we count only the influence of impulse but not noise, then the phase evolving process of the i th neuronal oscillator is deterministic described by a function $\tilde{h}_i(t)$ with continuous derivative.

We define $\mathcal{N} \stackrel{\text{def}}{=} \{2^j N_0: j = 1, 2, \dots\}$. We do not specify a simulation algorithm, since for a given type of neuronal oscillator (2) can be explicitly expressed (see [5]). All we need to do is checking $\phi_i(t)$, the phase value, at $t = \frac{k}{N}$, $k = 0, 1, \dots, N-1$. With care we will let $\phi_i(t)$ continuously accumulate over time. This is fine, since for phase synchronization we need only to show that all $\phi_i(t)$ ($1 \leq i \leq n$) will be locked at the same value at the same time.

3.2. Construction of the process

We will apply some basics of stochastic integration. An insightful introduction to the theory can be found in [2]. We formulate a weak noise by the continuous martingale \mathcal{M}_t induced by it. For example, for the Gaussian white noise, \mathcal{M}_t is characterized by the Brownian motion. Consider a continuous martingale \mathcal{M}_t , $t \in [0, 1]$, such that for any $0 \leq t_0 < \dots < t_{k-1} < t_k < \dots < t_N \leq 1$,

$$\mathcal{M}_{t_k} - \mathcal{M}_{t_{k-1}}, k = 1, \dots, N, \text{ are independent.} \quad (3)$$

(3) characterizes the probabilistic behavior of a noise. Furthermore, there are constant b , $\lambda > 0$ such that for each $1 \leq k \leq N$

$$\mathcal{M}_{t_k} - \mathcal{M}_{t_{k-1}} \text{ has zero mean and support in } (t_k - t_{k-1})^{(1+\lambda)/2} [-\frac{b}{2}, \frac{b}{2}]. \quad (4)$$

For the Gaussian white noise, $\mathcal{M}_{t_k} - \mathcal{M}_{t_{k-1}}$ has the Gaussian distribution with zero mean and variance $t_k - t_{k-1}$. (4) expresses the weakness of a noise by truncating the Gaussian distribution with $b(t_k - t_{k-1})^{(1+\lambda)/2}$. The choice of b is from that the intensity of a noise in a nervous system is always bounded; and λ is used to formulate how a noise is weaker than the Gaussian white for which the truncation should be by $b(t_k - t_{k-1})^{1/2}$, if any. The weakness of a noise was formulated only in [13] by a Gaussian random variable with zero mean and a small variance $\ll 1$ (without further quantification). Here, λ that formulates the weakness will play a critical role later (see Theorem 2).

Let $N \in \mathcal{N}$ and consider an interval $[\frac{k-1}{N}, \frac{k}{N}]$, $1 \leq k \leq N$. According to [6], there is a function $\mathbf{Z}^{(N,k)}$ such that the phase evolving (stochastic) process of the i th neuronal oscillator within the interval can be expressed by stochastic integration as follows:

$$\tilde{h}_i \left(\frac{k-1}{N} \right) + \int_{[(k-1)/N, k/N]} \mathbf{Z}^{(N,k)}(\tilde{h}_i(t)) d\mathcal{M}_t. \quad (5)$$

Kuramoto proved the existence of $\mathbf{Z}^{(N,k)}$ and formulated it [6] (which was a significant contribution to the study of chemical oscillator). As in [13] (see Eq. (2) and the discussion therein), we only use the existence, and assume that for all $N \in \mathcal{N}$ and all $1 \leq k \leq N$, $\mathbf{Z}^{(N,k)}$ has continuous derivative, and is uniformly bounded, i.e., for a constant $c > 0$

$$|\mathbf{Z}^{(N,k)}(\cdot)| \leq c \text{ for all } N \in \mathcal{N} \text{ and for all } 1 \leq k \leq N. \quad (6)$$

That is, if we partition $[0, 1]$ into subintervals $[\frac{k-1}{N}, \frac{k}{N}]$, $1 \leq k \leq N$ and $N \in \mathcal{N}$, then within each subinterval the phase evolving (stochastic) process of a neuronal oscillator is stochastic integration on a smooth and bounded function. To this extent, (6) summarizes the mathematical properties induced by the physiological properties of a neuronal oscillator.

$\mathbf{Z}^{(N,k)}$ may vary from one pair (N, k) to another. To construct the solution of (2) we need to extend (5) to the entire time interval $[0, 1]$. For each $N \in \mathcal{N}$ we define a random variable for every $1 \leq k \leq N$

$$z_k^{(N)}(i) \stackrel{\text{def}}{=} \lim_{\alpha \uparrow \infty} \sum_{l=0}^{2^\alpha - 1} \mathbf{Z}^{(N,k)} \left(\tilde{h}_i \left(\frac{k-1}{N} + \frac{l}{2^\alpha N} \right) \right) \times (\mathcal{M}_{(k-1)/N + (l+1)/2^\alpha N} - \mathcal{M}_{(k-1)/N + l/2^\alpha N}).$$

By (3), (4) and the definitions of \tilde{h}_i and $\mathbf{Z}^{(N,k)}$, the right side of the equation above converges strongly. This with (3) yields

$$z_k^{(N)}(i) \text{ are independent and } |z_k^{(N)}(i)| \leq bc/N^{(1+\lambda)/2}, \text{ for all } N \in \mathcal{N}, \quad (7)$$

where b and c are defined in (3) and (6), respectively. Using $z_k^{(N)}(i)$ we construct the solution of (2). Take a large $N \in \mathcal{N}$. When $k = 1$, in $[0, \frac{1}{N})$ we have $z_1^{(N)}(i) \approx \tilde{h}_i(0)(\mathcal{M}_{1/N} - \mathcal{M}_0)$ (since N is large), meaning that the initial phase value for the i th neuronal oscillator is randomly chosen by the noise. Here, without loss of generality, we assume that all impulses occur later than time $t = \frac{1}{N}$. Consider $[\frac{k-1}{N}, \frac{k}{N}]$, $k > 1$. There may be jumps in paths from time $\frac{k-1}{N-0}$ to $\frac{k-1}{N+0}$. However, since the sequence of impulses is given, the changes in paths

are deterministic. Furthermore, since $N \in \mathcal{N}$, by definition all the changes are taken into account. Hence, we can simply use $y_k^{(N)}(i) \stackrel{\text{def}}{=} \sum_{s=1}^k z_s^{(N)}(i)$ to accumulate all the changes caused by impulses and noise up to time $\frac{k}{N-0}$. Let $Y_i^{(N)} \stackrel{\text{def}}{=} \{y_k^{(N)}(i): k = 1, 2, \dots, N\}$. Recall that (2) has a unique solution. Thus, $Y_i^{(N)}$ can be viewed as the result by looking at the solution of (2) at time instances $0, \frac{1}{N}, \dots, \frac{N-1}{N}$.

It is not hard to see that all arguments made thus far in this section are applicable to the case when $I(t)$ is a continuous or discontinuous fluctuation as long as that the fluctuation is not too irregular so that it fits the setting described in Section 3.1. Hence, we arrive at the following:

Lemma 1. *Let $I(t)$ be a given sequence of impulses, or a given continuous or discontinuous fluctuation. Suppose that in either case $I(t)$ fits the setting as described in Section 3.1. Assume that the noise is weak as characterized in (4). Then, the unique solution of (2) is the strong limit of $Y_i^{(N)}$ as $N \uparrow \infty$. In particular, the random variable $y_N^{(N)}(i)$ has the distribution for the phase value ϕ_i at time $t = \frac{N-1}{N}$, $i = 1, 2, \dots, n$.*

Recall that we consider n identical and uncoupled neuronal oscillators, and $I(t)$ (a sequence of impulses or a fluctuation) is common to all the oscillators, which implies that G in (2) is the same for all $1 \leq i \leq n$. This means that the n oscillators have the same phase evolving (stochastic) process. Define $\theta^* \stackrel{\text{def}}{=} E[y_N^{(N)}(i)]$. If as N getting large, all $y_N^{(N)}(i)$ highly concentrate on θ^* , then by Lemma 1 all the n equations in (2) have their phase value ϕ_i highly concentrate on θ^* at time $t = \frac{N-1}{N}$. That is, the phase value of the n neuronal oscillators will then be almost surely locked at θ^* . We have

Theorem 2. *For all $\varepsilon > 0$*

$$\Pr \left\{ \max_{1 \leq i \leq n} |y_N^{(N)}(i) - \theta^*| \leq \varepsilon \right\} > 1 - 2n \cdot \exp \left(-\frac{2\varepsilon^2 N^\lambda}{b^2 c^2} \right). \quad (8)$$

Proof. Fix i , $1 \leq i \leq n$. With (7) we apply the Hoeffding inequality [4] to $y_N^{(N)}(i) = \sum_{s=1}^N z_s^{(N)}(i)$, having

$$\Pr \{ |y_N^{(N)}(i) - E[y_N^{(N)}(i)]| \leq \varepsilon \} > 1 - 2 \exp \left(-\frac{2\varepsilon^2 N^\lambda}{b^2 c^2} \right).$$

The theorem follows from this. \square

To see that the synchronization is stable, we let $\varepsilon = N^{-\lambda/3}$ in (8) to have

$$\Pr \left\{ \max_{1 \leq i \leq n} |y_N^{(N)}(i) - \theta^*| \leq \frac{1}{N^{\lambda/3}} \right\} > 1 - 2n \cdot \exp \left(-\frac{2N^{\lambda/3}}{b^2 c^2} \right).$$

For the same oscillator and noise, θ^* is determined by $I(t)$; and to this extent, $I(t)$ sets the phase value at which the synchronization emerges. The independence induced by a noise expressed in (3) is the key to proving the result, which indicates that noise is the ultimate driving force in the following sense: *A common weak noise engineers a martingale as a random field to let phase synchronization of neuronal oscillators occur.*

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