

Reliability and stochastic synchronization in type I vs. type II neural oscillators

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Available online 9 November 2006

Abstract

Neural reliability and stochastic synchronization are remarkable features of real neurons with important consequences for neural computation. Both phenomena are general properties of any device with a resetting threshold, such as neurons. However, certain characteristics of the single neuron dynamics can notably improve neural reliability and stochastic synchronization. Here we show that neural resonators synchronize more reliably and more robustly than neural integrators. This suggests that neurons conveying sensory information in a spike-timing code are likely to be resonators, as supported by our recent studies on reliability and stochastic synchronization in the olfactory bulb.

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Keywords: Neuronal integrator; Neuronal resonator; Phase response curve; Phase oscillator; Synchrony

1. Introduction

Neurons respond to several repetitions of a rapidly fluctuating stimulus in a highly reproducible manner [1,7]. This property was referred to as neural reliability. The stochastic synchronization of an ensemble of neurons can be regarded as a generalization of this phenomenon: neurons receiving random and fast fluctuating signals that are spatially correlated will trigger correlated responses across the ensemble, which translates into synchronous action potentials [5,6,10]. The degree of synchronization depends on the reliability of the individual neurons in the ensemble and on the degree of spatial correlation of the inputs. Interestingly, stochastic synchronization occurs even when the neurons are not mutually connected [3,5].

Recently, we investigated the mechanisms for neural reliability and stochastic synchronization in experiments with acute brain slices of the olfactory bulb in rodents and also in computer simulations of simple neural models. We

concluded that both phenomena are universal properties of neurons, as devices with a resetting threshold [3,5]. Here we present further computational studies on phase-oscillator models of neurons revealing that type II neural oscillators (resonators) are more reliable and more susceptible to synchronize by stochastic inputs than are type I neural oscillators (integrators). We provide a heuristic explanation for this remarkable difference, which is based on the shape of the neuron's phase–response curve.

Neurons that fire regularly can be described as phase oscillators. To quantify the variability of the firing rate one can plot the distribution of interspike intervals. If the spikes are perfectly periodic, the interspike interval distribution will have zero width (zero standard deviation). In simulations and experimental data we have observed that the phase oscillator approximation and therefore, the estimation of the phase-response curve, is valid when the standard deviation of the interspike interval is at least up to 10% of the mean [2]. As a result, one can take advantage of the formalism of phase oscillators to study relevant properties of neural dynamics (see e.g. [4]). Consider two identical, not mutually connected neural oscillators driven by stochastic inputs ξ_i with zero mean (the mean of the

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input is actually considered in the term ω_0 because it is responsible for making the cell fire $\omega_0/(2\pi)$ spikes per second) and starting with different initial conditions:

$$\frac{d\varphi_i}{dt} = \omega_0 + Z(\varphi_i)\xi_i(t), \quad i = 1, 2, \quad (1)$$

where φ_i is the phase of the i th oscillator, ω_0 is the intrinsic angular frequency and $Z(\varphi)$ is the oscillator's phase response (or phase–resetting curve), which is an intrinsic dynamical property of the oscillator. The phase response tells us how much the phase of the oscillator is advanced ($Z(\varphi) > 0$) or delayed ($Z(\varphi) < 0$) when perturbing the oscillator at any phase φ of the intrinsic period with an infinitesimal positive pulse. $Z(\varphi)$ is strictly positive for integrators and partially positive and negative for resonators. The nomenclature integrator/resonator refers to the subthreshold dynamics of these neuronal types. Integrators behave as low-pass filters of the input current whereas resonators behave as band-pass filters, which accounts for subthreshold resonance. In addition, integrators can theoretically fire spikes at arbitrarily low frequencies (classical criterion of class-I excitability) whereas resonators start firing spikes at a finite frequency (classical criterion of class-II excitability). The biophysical mechanisms that make a neuron fall into one of these two categories (or none, like bursting neurons, whose dynamics cannot be fully described by a single parameter like the phase) are not unique, i.e. many different combinations of parameters in conductance models can lead to one type or the other. However, there are some “rules of thumb” to generate these dynamical features. For example, consider a neuron with an A-current (like in mitral cells), which tends to hyperpolarize the neuron. In this case, a positive pulse during the refractory period can accelerate the activation of this current, therefore delaying the next spike (negative part of $Z(\varphi)$, type II). If the pulse is delivered later on the cycle, it is likely to accelerate the inactivation of the A-current, therefore advancing the next spike (positive part of $Z(\varphi)$, type I). On the other hand, type I dynamics is characteristic of conductance models that are well described as leaky linear, quadratic or exponential integrate-and-fire models.

2. Results of simulations with phase models

In the case of white-noise inputs that are identical for all neural oscillators ($\xi_i = \xi$), it has been shown with stochastic calculus that the oscillators in Eq. (1) will synchronize regardless of the initial conditions and the neural phase response, provided that it is continuous [10]. But interestingly, in the more general and common case when the stochastic inputs are not identical but just correlated, remarkable differences in the distribution of the phase difference, $\Delta\varphi = \varphi_2 - \varphi_1$, emerge. As shown in Fig. 1, where two type I and two type II neurons start with the same initial conditions and receive the same correlated inputs, type II neurons spend more time close to each

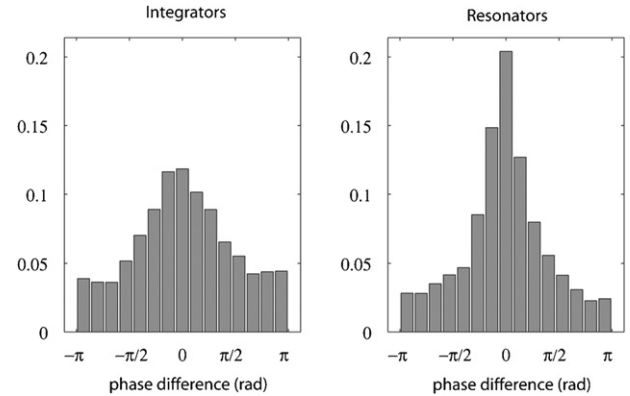


Fig. 1. Phase-difference distribution for two neural oscillators (left, type I or integrators; right, type II or resonators). Resonators spend more time close together than integrators, as indicated by the larger peak at zero phase difference.

other, as indicated by the higher peak at $\Delta\varphi = 0$. Unfortunately, the stochastic calculus becomes intractable in the case of not perfectly correlated inputs, so an analytic treatment of this problem is not possible. However, the reason for this difference is intuitively comprehensible, as explained below.

Consider two neural oscillators with similar phases at a given point in time (Fig. 2a). If they receive a correlated fluctuation, they will remain close to each other in both, the resonator and the integrator case. Consider now two neural oscillators at opposite extremes of the intrinsic period (Fig. 2b). In this case, if they receive a correlated fluctuation, the phase difference of the integrators and of the resonators will evolve differently: whereas both integrators will move in the same direction, and therefore without remarkably changing their phase difference, both resonators will move in opposite directions. However, because the phase is periodic (with period 2π) moving in opposite directions actually means coming closer to each other. Thus, correlated fluctuations will tend to diminish the phase difference between resonators no matter what their current phase is.

The explanation for the phenomenon just described is not only valid for the simple phase responses plotted in Fig. 2 but also for phase responses obtained from conductance models (see Fig. 3a), like a variation of the Morris–Lecar model described in [8], which in turn closely resemble those obtained in experiments [2]. Our argument on stochastic synchronization for system (1) with two oscillators holds true for the case of a large population of N non-connected neurons driven by correlated noise. To study this case for an arbitrary $Z(\varphi)$, we introduce the order parameter $\psi(t)$,

$$\psi(t) = \left| \frac{1}{N} \sum_{n=1}^N \exp(i\varphi_n(t)) \right|^2.$$

Clearly, $\psi(t)$ is bounded between 0 (homogenous distribution of oscillators between 0 and 2π) and 1 (perfect

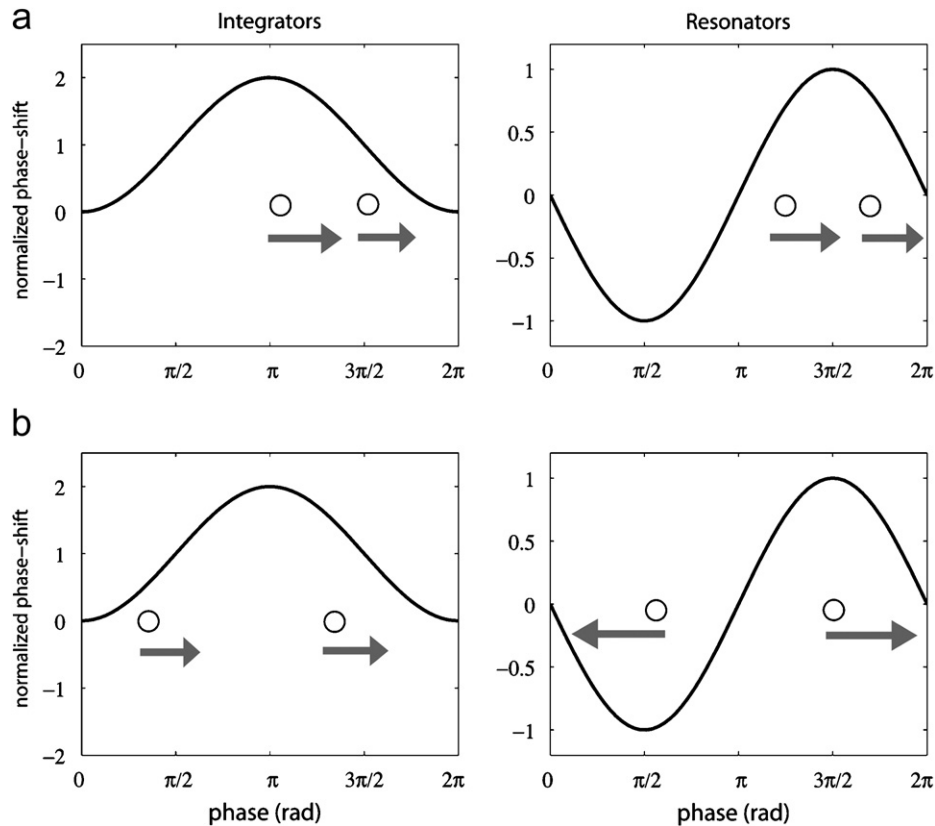


Fig. 2. Phase changes of two neural oscillators driven by a correlated input fluctuation. Phase-response curves are plotted as black lines. Circles represent the state of two oscillators in each case and the arrows indicate the change in phase predicted by the phase-response curve when they receive a correlated fluctuation. (a) Phase changes expected when both oscillators are on similar phases of the oscillation period. (b) Phase changes expected when the oscillators are far apart on the cycle.

synchronization of all oscillators). Then, one can quantify the degree of synchrony over a large time interval as the temporal average of $\psi(t)$, which can be plotted against the mean cross-correlation of the inputs, i.e. the mean of the cross-correlations, $\langle \xi_i(t)\xi_j(t) \rangle$, with $i = 1, 2, \dots, N$, $j = 1, 2, \dots, N$ and $i < j$. These cross-correlations between the inputs have been generated with the method presented by the authors in [5]. As expected, population synchrony increases with increasing input cross-correlation (Fig. 3b). In addition, the populations of type II neurons are clearly more synchronized than the populations of type I neurons over a wide range of input correlation. Interestingly, the type II phase response of Fig. 2, is consistently more efficient than the type II phase response of the realistic conductance model. This is to be expected, since according to our explanation, stochastic synchronization must be more efficient when the positive and negative area of the phase response $Z(\varphi)$ cancel each other. Finer details of the shape of $Z(\varphi)$ contribute to reliability and stochastic synchronization in a lesser degree as seen in Fig. 3.

3. Conclusions and discussion

Neural reliability and stochastic synchronization are remarkable features of real neurons with relevant consequences

for neural computation: Whereas neural reliability is crucial for the high fidelity of sensory processing, stochastic synchronization may provide a general mechanism for binding neural representations of stimuli even across sensory modalities, and therefore for routing information in the brain. Here we have shown that neural resonators (type II neurons) are more reliable and more susceptible to synchronize by stochastic inputs than integrators (type I neurons). Interestingly, in recent experimental studies on the olfactory system, we have shown that mitral cells behave as neural resonators [2], which suggests that they have evolved to optimize sensory reliability and to quickly synchronize through spatially correlated barrages of inhibitory inputs from granule cells. The later mechanism may explain the emergence of oscillations in this neural network in the beta and gamma frequency bands. Finally, a recently published experimental study on neuronal excitability in the layer 2/3 of the somatosensory cortex of rats has shown that regular-spiking pyramidal neurons are type I whereas fast-spiking inhibitory interneurons are type II [9]. In their paper, the authors report a remarkably higher reliability of the responses to fluctuating inputs in fast-spiking cells than in regular-spiking cells, which is in perfect agreement with the results we have presented here.

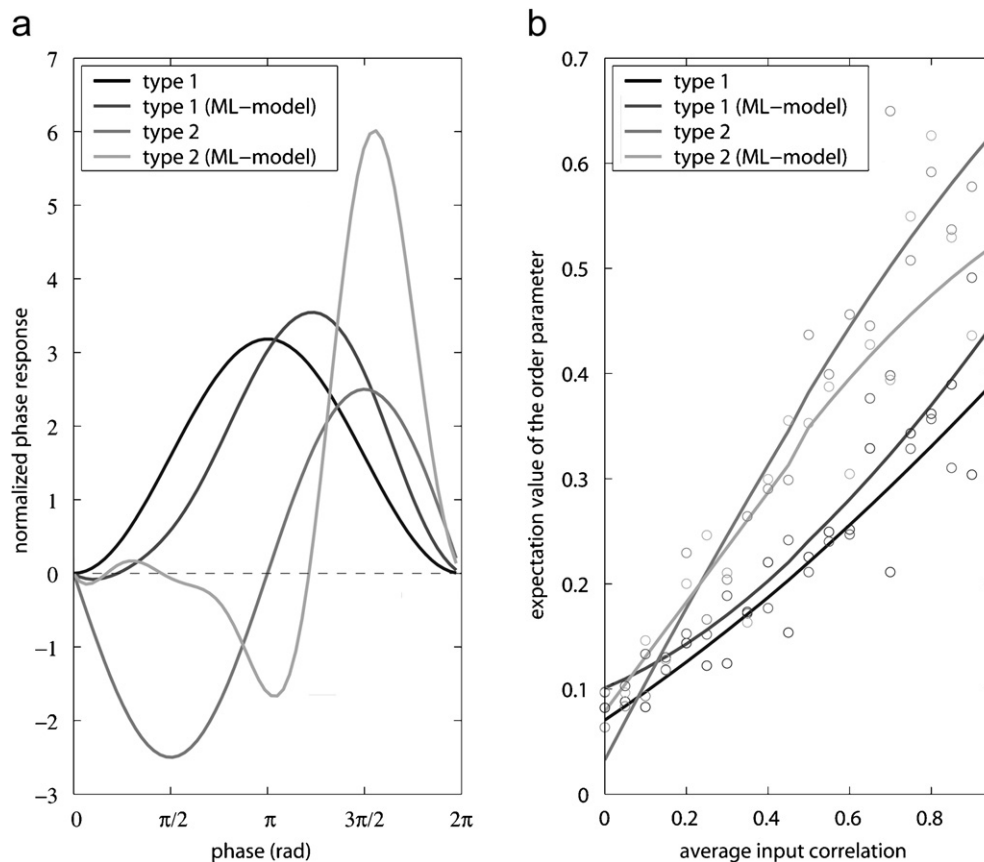


Fig. 3. (a) Phase responses $Z(\phi)$ displayed in Fig. 2 and also from a modified Morris-Lecar (ML) model of type I and type II. The curves were normalized so that the integral of their absolute value is the same for all the curves. (b) Temporal average of the order parameter ψ as a function of the mean cross-correlation of the inputs to the ($N = 40$) oscillators. Clearly, populations of type II oscillators (resonators) are more synchronized than the populations of type I oscillators (integrators) over a wide range of input correlations (circles: results of the simulations in each case; lines: smoothed version of these results with a Savitzky–Golay filter of order 2).

Acknowledgements

This work has been supported by NIDCD DC005798 and NSF MS0513500.

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