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

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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. In particular, we show that, under the same conditions, neural resonators are more reliable and more susceptible to synchronize by stochastic inputs than are neural integrators. This suggests that neurons conveying sensory information in a spike-timing code are likely to have evolved into resonators, as supported by our recent experimental studies on reliability and stochastic synchronization in the olfactory bulb.

1. Introduction

Neurons respond to several repetitions of a rapidly fluctuating stimulus in a highly reproducible manner [1,2]. This property has been 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 [3-5]. The degree of synchronization depends on the reliability of the neurons in the ensemble and on the degree of spatial correlation of the inputs. But interestingly, stochastic synchronization occurs even when the neurons are not mutually connected [5,6].

Recently we have 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 [5,6]. 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.

2. Results of simulations with phase models

Neurons that fire regularly can be described as phase oscillators. As a result, one can take advantage of the formalism of phase oscillators to study relevant properties of neural dynamics (see, e.g. [7]). Consider two identical, not mutually connected neural oscillators driven by stochastic inputs ξ_i and starting with different initial conditions:

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

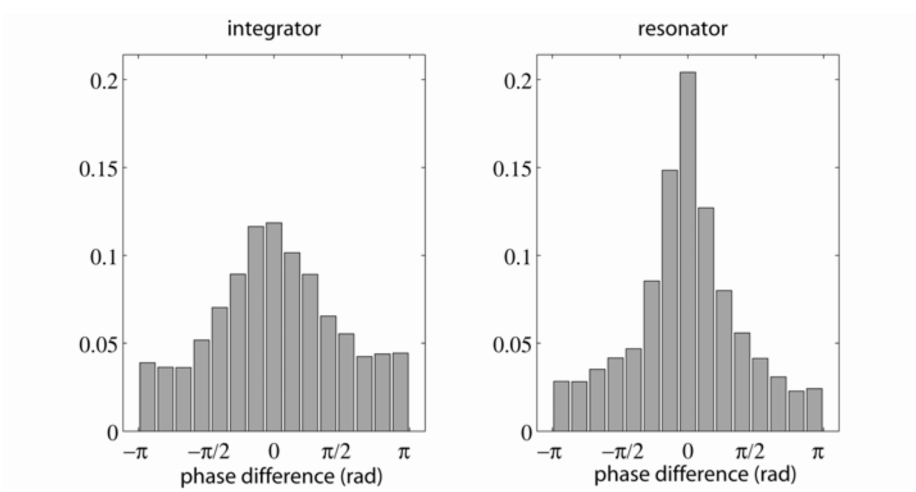
where φ_i is the phase of the i-th oscillator, ω_0 is the intrinsic angular frequency and $Z(\varphi)$ is the oscillator's phase response (or phase-resetting curve), which is an intrinsic dynamical property of the oscillator. The phase response tells us how much the phase of the oscillator is advanced ($Z(\varphi)>0$) 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. In the case of white noise inputs, it has been shown with stochastic calculus that the oscillators will synchronize regardless of the initial conditions and the neural phase response, provided that it is continuous [3]. 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, for the same stochastic input, type II neurons spend more time close to each 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.

3. Conclusions

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 are more reliable and more susceptible to synchronize by stochastic inputs than are integrators. Interestingly, in recent experimental studies on the olfactory system, we have shown that mitral cells behave as neural resonators [7], 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.

Fig.1: phase difference distribution of two neural oscillators: resonators spend more time close together than integrators.



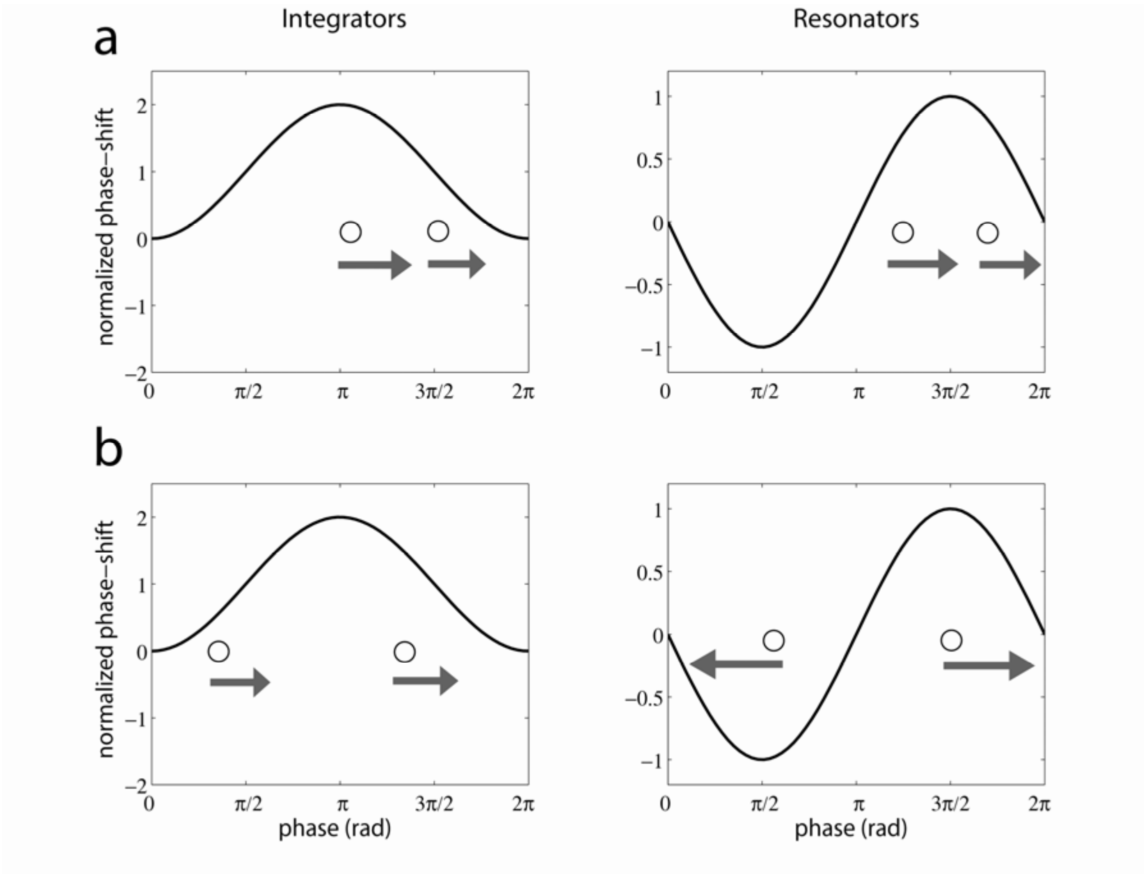


Figure 2: Phase changes of two neural oscillators driven by a correlated input fluctuation. Phase-response curves are plotted as black lines.

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