Unifying Strong and Weak Pyramidal-Interneuronal-Gamma (PING) Rhythms with a fully solvable model of phase oscillators

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The interplay between excitation and inhibition is a prominent mechanism of generation of neuronal oscillations. This mechanism of rhythmogenesis, usually called excitatory-inhibitory (E-I) feedback loop, or Pyramidal-Interneuronal-Gamma (PING) rhythm, is robustly observed in mathematical models consisting of large populations of interacting E and I spiking neurons. According to these models, each oscillatory cycle is initiated by an excitatory boost of activity, which triggers an inhibitory increase of activity, halting excitatory cells. Once inhibition has worn off, excitation can increase again, and a new cycle begins. In addition, the PING mechanism manifests itself into two distinct dynamical regimes, which are often referred to as "strong" and "weak" PING. In strong PING, both excitatory and inhibitory cells fire regularly with a firing rate that coincides with that of the population frequency. In contrast, in the weak PING regime excitatory neurons fire sparsely, with a firing rate much lower than the frequency of the global oscillations. Recently, it has been shown that a two-population Kuramoto model (KM) accounts for the main features of the strong PING regime, and hence ---due to the analytical tractability of the KM--- this allows for a thorough understanding of strong PING rhythms as a remarkable example of collective synchronization of large ensembles of self-sustained oscillators. In contrast, a description of weak PING in terms of reduced, analytically tractable, phase oscillator models is lagging, as well as a simple and unified explanation of weak and strong PING rhythms. Here we show that an extension of the E-I Kuramoto model, which takes into account intrinsic properties of the E and I neurons (i.e. their phase resetting curves) fully accounts for both weak and strong PING regimes. Indeed, besides the standard fully synchronous states analogous to strong PING oscillations, the model displays a novel class of quasiperiodic partially synchronized states, where E cells fire sparsely, at a lower frequency than I cells. Remarkably, such partially synchronous states arise in parameter regimes that are in agreement with the weak oscillations found in numerical simulations of biophysically realistic (Hodgkin-Huxley-like) models. Moreover, the mathematical analysis of the extended E-I Kuramoto model, allows us to identify the balance between excitation and inhibition as a key factor controlling the emergence of either strong or weak PING rhythms. Our results represent the first complete understanding of the emergence of PING rhythms in terms of simple, exactly solvable phase oscillator models. In addition, this novel mathematical framework provides a mechanistic explanation for the dichotomy between strong and weak PING rhythms.