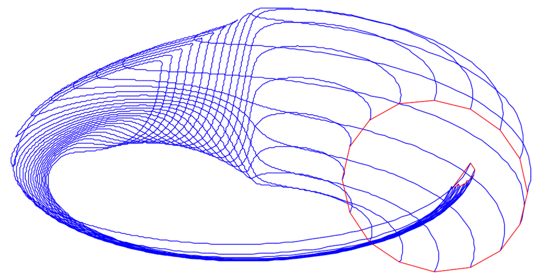

GAMMA (γ) RHYTHMS UNDER PERIODIC FORCING

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QUESTIONS

ING (interneuronal network gamma) and **PING** (pyramidal-interneuronal network gamma) are well-established theories of the mechanistic generation of γ-rhythms ($\approx$ 35-100 Hz). (2) However, the capacity of these mechanisms to dynamically respond to external inputs and phase-lock with upstream rhythms has not been studied.

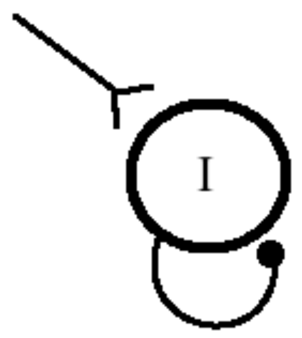
We pose the questions:

- **What range of dynamics is possible for these models under periodic forcing?**
- **How do the properties of these models compare to those of other commonly studied forced oscillators?**
- **Are these mechanisms well-suited to rapidly establish reliable phase-locked relationships with upstream γ-rhythms?**

We address these questions by mathematically analyzing simple **ING** and **PING** models and comparing them to **phase oscillators** and **relaxation oscillators**.

GAMMA-GENERATING MECHANISMS

ING is modeled as a synchronous population of inhibitory theta-neurons with phase θ_i and tonic excitation b_i, inhibiting itself with slowly decaying inhibition s_i and receiving a periodic excitatory input $\epsilon I(\Phi)$ with period T_I.

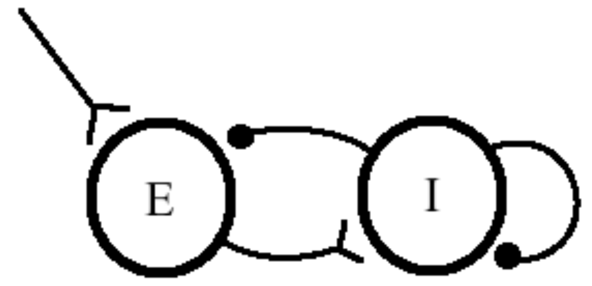


I-population phase:
$$\tau_i \dot{\theta} = 1 - \cos(\theta_i) + (1 + \cos(\theta_i))G_i$$
$$G_i = b_i - g_{ii}s_i + \epsilon I(\Phi), b_i > 0$$

Inhibition: $\dot{s_i} = -s_i/\tau_{s_i}$
When $\theta = \pi$, s_i resets to
$$s_i = c(s_i - 1) + 1$$

Forcing phase: $\dot{\Phi} = 1$

PING is modeled like ING, with the addition of quickly-decaying excitation s_e from synchronous population of excitatory cells with phase θ_e, which triggers the I-population. The E-population receives the forcing $\epsilon I(\Phi)$, and is inhibited by the I-population.



E/I-population phases:
$$\tau_{e/i}\dot{\theta}_{e/i} = 1 - \cos(\theta_{e/i}) + (1 + \cos(\theta_{e/i}))G_{e/i}$$
$$G_e = b_e - g_{ie}s_i + \epsilon I(\Phi), b_e > 0$$
$$G_i = b_i - g_{ii}s_i + g_{ei}s_e, b_i < 0$$

Excitation/Inhibition:
$$\dot{s}_{e/i} = -s_{e/i}/\tau_{s_i}$$
When $\theta_{e/i} = \pi$, $s_{e/i}$ resets to 1.

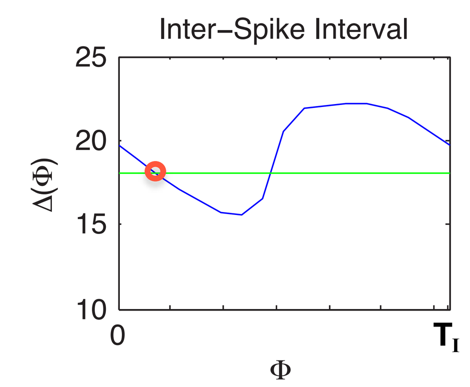
Forcing phase: $\dot{\Phi} = 1$

ING/PING PROPERTIES

Like the **relaxation oscillator** (below), the γ-generating networks maintain a robust natural period while robustly phase-locking to forcing due to **separation of time scales** ($\tau_{s_i} \gg \tau$).

We use the variational equations and return maps for our models (left) to prove two results differentiating them from ordinary relaxation:

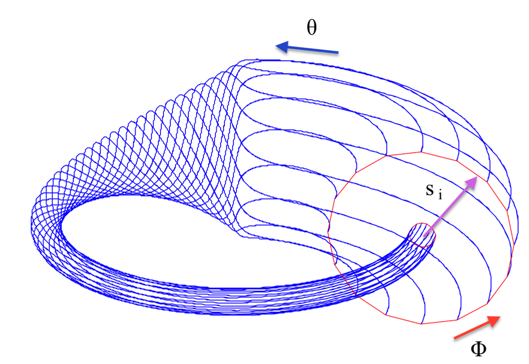
1. Only one phase offset between the **ING** oscillator and pulsatile forcing is stable. We prove this for square pulses.



Left: Phase-locking only occurs where the ISI function crosses the forcing period downwards, which in this case can occur only once.

2. If c is small and/or sufficient time is spent under inhibition each cycle, the system attracts to an invariant torus on which period-doubling and 1:1-2:1 bistability are not possible. .

Right: Given the conditions above, an invariant torus persists under strong forcing. The same applies to the **PING** model if τ_i is small.



PHASE OSCILLATOR LIMITATIONS

The **phase oscillator** is the generic form of a 1D periodically-forced oscillator. By changes of variables, any stable limit cycle under sufficiently weak forcing ($\epsilon < \epsilon^*$ for some $\epsilon^* > 0$) may be written in this form, as may the LIF and QIF neuron models.

$$\dot{\phi} = 1 + g(\phi)(b + \epsilon I(\Phi))$$
$$\dot{\Phi} = 1$$

Restriction to one dimension imposes a tradeoff between robustness of natural period T to changes in tonic drive b and capacity to lock to weak inputs at a wide range of frequencies. At a given forcing strength ϵ, the width W^ϵ of the interval of forcing periods T_I which may evoke stable phase locking is bounded by

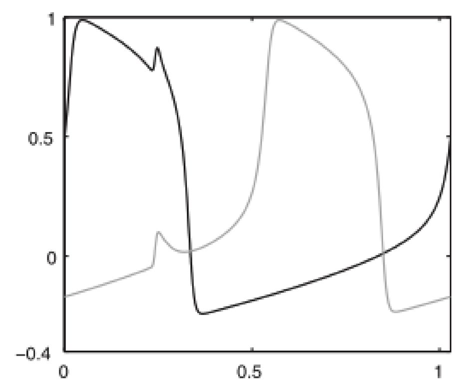
$$W_\epsilon < \sqrt{-\frac{\partial T(0,b,\Phi_0,T_I)}{\partial b}\Big|_{b=0}}\sqrt{\epsilon \sup_{\Phi_0 \in [0,T_I]} \int_0^{T_{0,0}} I(\Phi_0 + t \bmod T_I)dt}$$

A **separation of timescales** can circumvent this problem by making the ϵ^* required for the phase reduction arbitrarily small. Thus, if the ING oscillator has $\tau_{s_i} \gg \tau$, it both maintains a robust natural period T and phase-locks to inputs at a range of forcing periods unbounded by forcing current and sensitivity.

RELAXATION LIMITATIONS

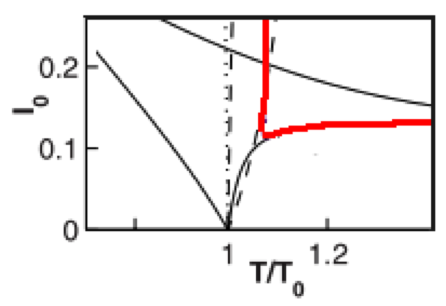
The **separate timescales** of the Fitzhugh-Nagumo **relaxation oscillator** give it a robust period while phase-locking robustly to inputs.

Two distinguishing characteristic properties of the forced phase oscillator are:



Regimes of 1:1 bistability under weak forcing. (**Left:** A bistable pair of 1:1 forced orbits)

Regimes of 1:1-2:1 bistability and period-doubing under stronger forcing. (**Right:** period-doubling bifurcation as forcing strength increases, in red)



Figures and results from (1).

CONCLUSION

The **ING** and **PING** mechanisms are **ideally suited** for responding to upstream γ-rhythms of varying amplitude and frequency by rapidly establishing a **reliable phase-locked relationship**.

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1. H. Croisier *et al.*, *Physical Review E* **79**, 57–59, ISSN: 1539-3755 (Jan. 2009).
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