Phase Locking

A neuron phase-locks to a periodic input—it spikes at a fixed delay [Izhikevich07].

The PRC’s amplitude determines which frequencies a neuron locks to

The PRC’s slope determines if locking is stable

Some neurons (resonators) phase-lock better than others (integrators)
**Short stimulus intervals**

Stimulus $n$ advances phase by $\text{PRC}(\theta_n)$ if it occurs at phase $\theta_n$.

We can find the neuron's phase $\theta_{n+1}$ just before stimulus $n+1$ if we know its phase $\theta_n$ just before stimulus $n$:

$$\theta_{n+1} = \theta_n + \text{PRC}[\theta_n] + T_s$$

Note that, by definition, $\text{PRC}(\theta_n)$ is positive if it advances the spike, negative if it delays it.

**Long stimulus intervals**

Subtract neuron's period ($T$) from previous result for $\theta_{n+1}$.

In this case, we must subtract the neuron's period ($T$) to reset the phase to zero after the spike:
\[\theta_{n+1} = (\theta_n + \text{PRC}[\theta_n] + T_s) - T\]

For arbitrarily long inter-stimulus intervals, we use the modulo function:

\[\theta_{n+1} = (\theta_n + \text{PRC}[\theta_n] + T_s) \mod T\]

This relationship—how the stimulus' phase evolves from period to period—is called the Poincare phase map.

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**Poincare phase map**

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Label the curves and build trace this out on the board---hard to follow otherwise.

Eventually, the phase stops changing—a stable fixed point [Izhikevich07].

Trajectory alternates between moving vertically from the line to the curve \((\theta_{n+1} \equiv f(\theta_n))\) and horizontally from the curve to the line \((\theta_n \equiv \theta_{n+1})\).
Stability of fixed-points

Stability is determined by the slope of \( f(\theta) \) [Izhikevich07].

Fixed-points occur at intersections of the \( f(\theta_n) \) curve and the unity-slope line: \( \theta_{fp} = f(\theta_{fp}) \).

Fixed-point \( \theta_{fp} \) is stable if \( f(\theta) \)'s slope is less than unity (in magnitude) at \( \theta_{fp} \).

Fixed-points from the PRC
Stability is determined by the PRC’s slope [Izhikevich07].

Setting \( \theta_{fp} = f(\theta_{fp}) \) predicts the range of stimulus frequencies that the neuron can phase-lock to:

\[
\theta_{fp} = \theta_{fp} + \text{PRC}[\theta_{fp}] + T_s - n \cdot T \Rightarrow \text{PRC}[\theta_{fp}] = n \cdot T - T_s
\]

The difference in period between the neuron and the stimulus must be within the PRC’s delay range.

Setting \( |f'(\theta_{fp})| < 1 \) predicts whether phase-locking actually occurs:

\[
| \frac{d}{d\theta_{fp}} (\theta_{fp} + \text{PRC}[\theta_{fp}] + T_s - n \cdot T) | < 1 \Rightarrow -2 < \frac{d}{d\theta_{fp}} \text{PRC}[\theta_{fp}] < 0
\]

The PRC’s slope must be between 0 and -2.

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**The ghost of an attractor**

A stimulus frequency at the edge of a neuron's locking range [Izhikevich07].

As the stimulus frequency approaches the edge of the neuron's locking range, a bifurcation occurs: The stable and unstable points annihilate each other and disappear. However, a *ghost attractor* remains that traps trajectories and keeps them near the synchronized state for long periods of time.
Neurons with Class I and II excitability

A Class I neuron’s PRC is mostly positive (left); a Class II neuron’s is not (right). The membrane-voltage (blue) and the K-activation variable’s PRC (dashed) are also shown [Izhikevich07].

Whereas Class I excitability arises from a saddle-node bifurcation, Class II excitability arises from a Hopf bifurcation—a small oscillation appears, grows as the input increases, and leads to spiking. Such neurons are also called resonators, as opposed to integrators (Class I).

Delete V(t) and PRC₂ curves---distracting.
Neurons with Class I and II excitability

Cholinergic action switches a cortical (Layer II) pyramidal cell's PRC from Class I to II [Sejnowski08].

Next week: Synchrony

Interneurons synchronize in gamma band.

Going beyond two neurons, and the PRC, we analyze synchrony in a inhibitory population using a mean firing-rate approximation.