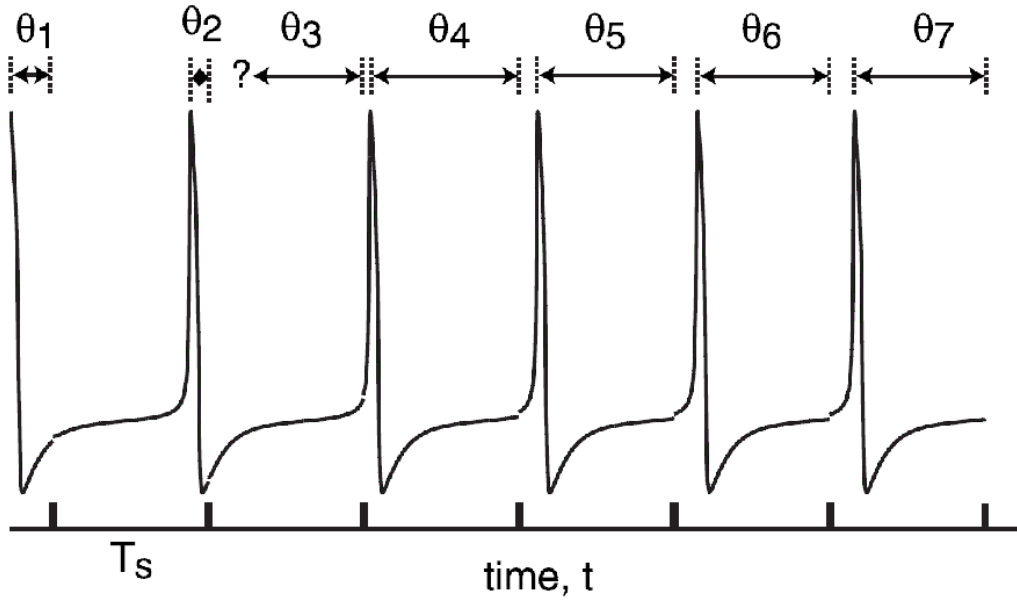


## Phase Locking



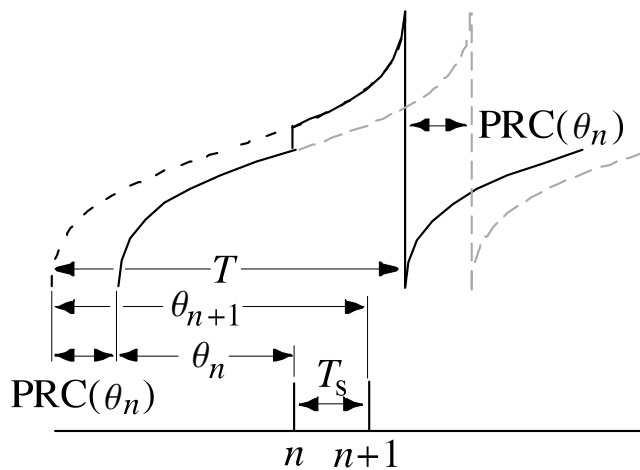
A neuron phase-locks to a periodic input—it spikes at a fixed delay [Izhikevich07].

**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 ( $T_s < T$ )



Stimulus  $n$  advances phase by  $\text{PRC}(\theta_n)$  if it occurs at phase  $\theta_n$ ;  $T$  and  $T_s$  are the neuron's and stimulus' periods, respectively.

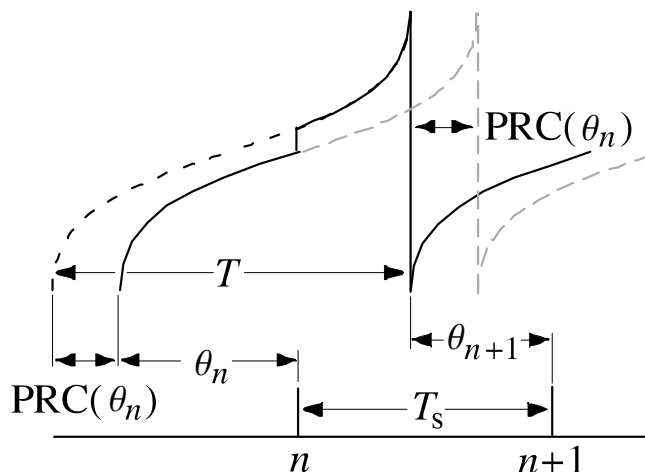
We can find the neuron's phase  $\theta_{n+1}$  just before stimulus  $n + 1$  if we know its phase  $\theta_n$  just before stimulus  $n$ :

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

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



## Long stimulus intervals ( $T_s > T$ )



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:

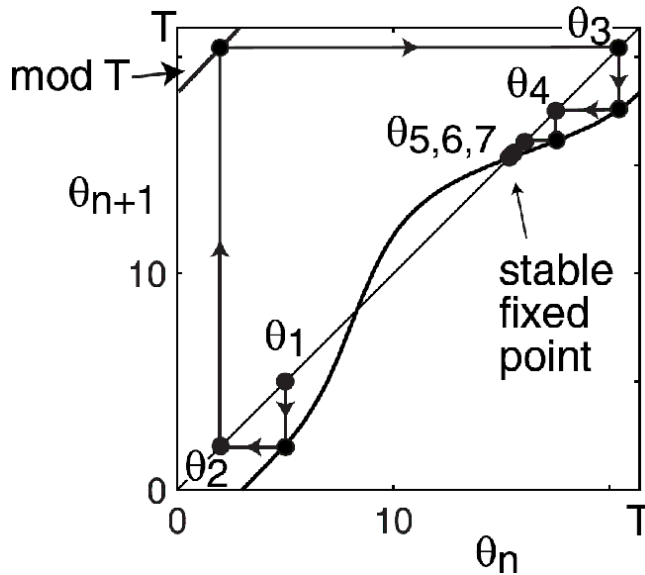
$$\theta_{n+1} = (\theta_n + \text{PRC}[\theta_n] + T_s) - T$$

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

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

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

## Poincare phase map ( $\theta_{n+1} = f(\theta_n)$ )



The phase iteration function and a unity-slope line enables phase updates to be obtained graphically [Izhikevich07].

The Poincare phase map enables phase updates are obtained graphically:

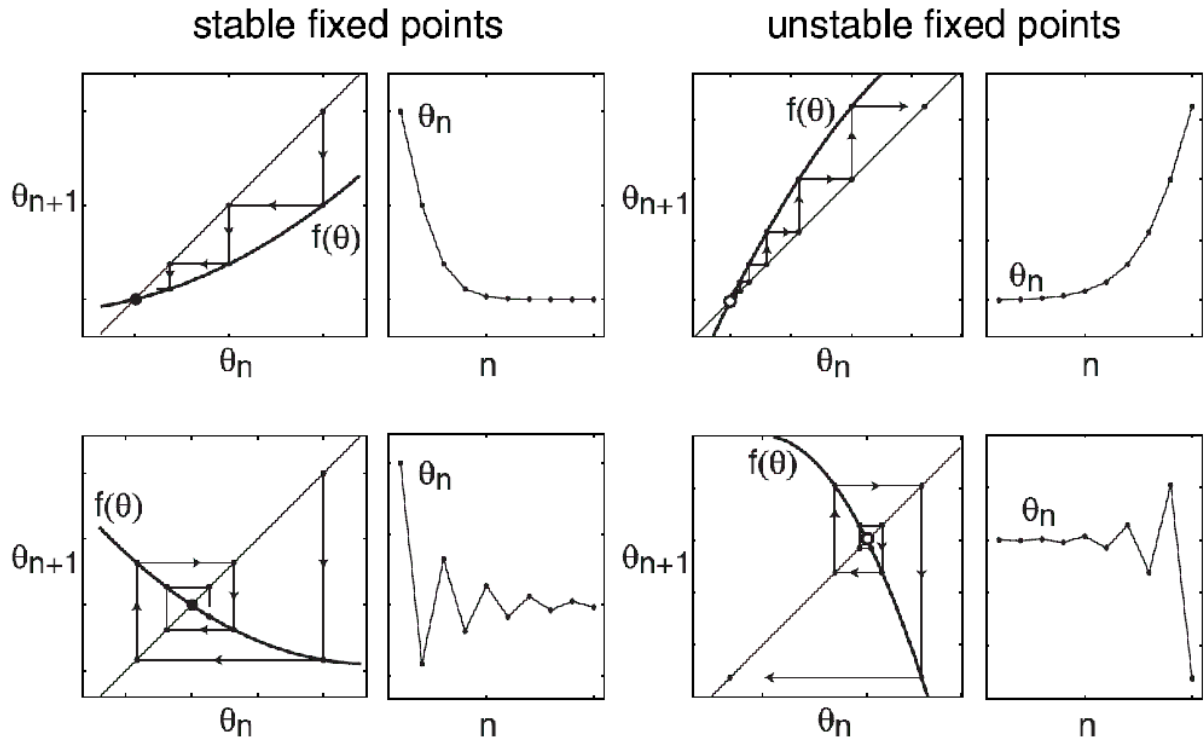
Move vertically from the line ( $\theta_n := \theta_{n+1}$ ) to the curve ( $\theta_{n+1} := f(\theta_n)$ ) to obtain the next value of  $\theta$ .

Move horizontally from the curve ( $\theta_{n+1} := f(\theta_n)$ ) to the line ( $\theta_n := \theta_{n+1}$ ) to update  $\theta$  to this value.

In our case:

$$f[\theta] = (\theta + \text{PRC}[\theta] + T_s) \bmod T$$

## Stability of fixed-points

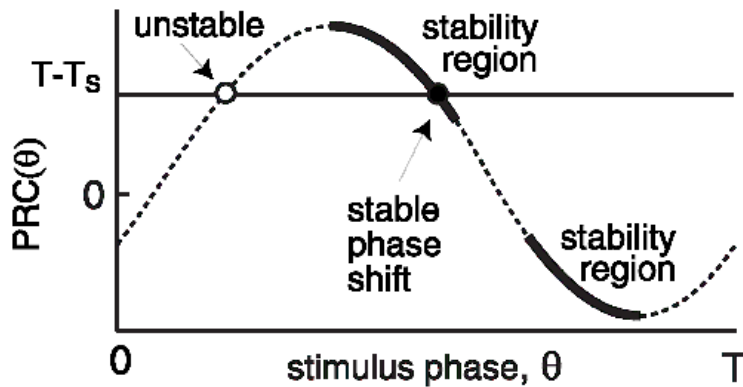


$f(\theta)$ 's slope determines if a fixed-point is stable or not [Izhikevich07].

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

A 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  $|f'(\theta_{fp})| < 1$  predicts yields:

$$\left| \frac{d}{d\theta_{fp}} (\theta_{fp} + \text{PRC}[\theta_{fp}] + T_s - n T) \right| < 1 \implies -2 < \frac{d}{d\theta_{fp}} \text{PRC}[\theta_{fp}] < 0$$

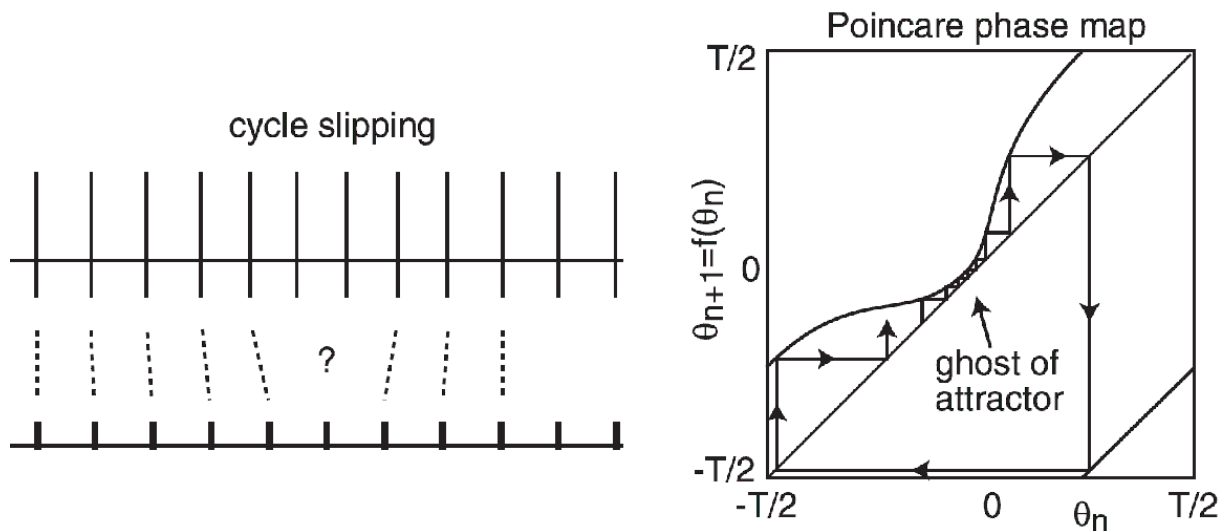
Therefore, the PRC's slope must be between 0 and -2 for stability.

The PRC also tells us the range of stimulus frequencies that the neuron can phase-lock to. Setting  $\theta_{fp} = f(\theta_{fp})$  tells us that fixed points must satisfy:

$$\theta_{fp} = \theta_{fp} + \text{PRC}[\theta_{fp}] + T_s - n T \implies \text{PRC}[\theta_{fp}] = n T - T_s$$

Therefore, the difference in period between the neuron and the stimulus must be within the PRC's delay range for fixed points to exist.

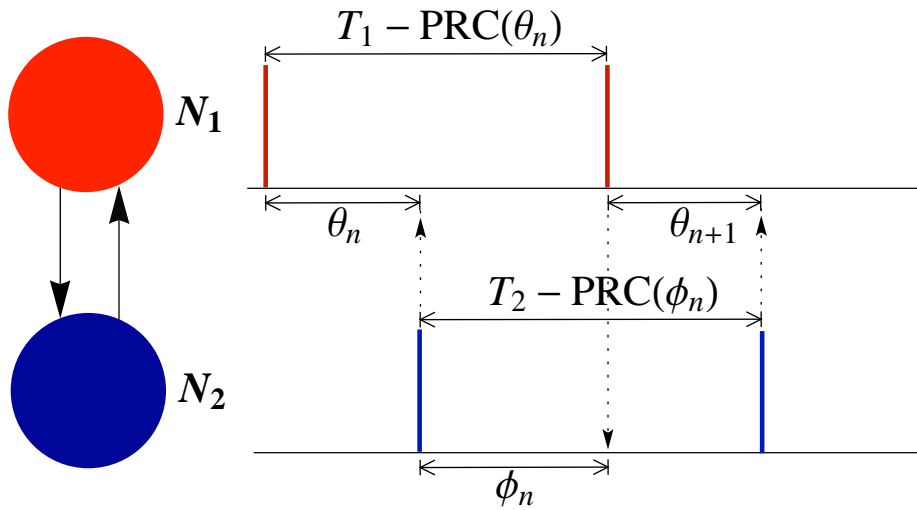
## The ghost of an attractor



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.

## Two coupled neurons



$N_2$  advances  $N_1$ 's spike by  $\text{PRC}(\theta_n)$ ;  $N_1$  advances  $N_2$ 's spike by  $\text{PRC}(\phi_n)$ .

Two neurons,  $N_1$  and  $N_2$ , with different intrinsic periods,  $T_1$  and  $T_2$ , are coupled together. As pictured above,  $N_2$ 's spike arrives at  $N_1$  when the  $N_1$ 's phase is  $\theta_n$  whereas  $N_1$ 's spike arrives at  $N_2$  when  $N_2$ 's phase is  $\phi_n$ . Thus, we have:

$$\begin{aligned} T_1 - \text{PRC}[\theta_n] &= \theta_n + \phi_n \\ T_2 - \text{PRC}[\phi_n] &= \phi_n + \theta_{n+1} \end{aligned}$$

Subtracting the first equation from the second gives:

$$T_2 - T_1 + \text{PRC}[\theta_n] - \text{PRC}[\phi_n] = \theta_{n+1} - \theta_n$$

At a fixed point  $\theta_{n+1} = \theta_n = \theta_{\text{fp}}$ , which requires:

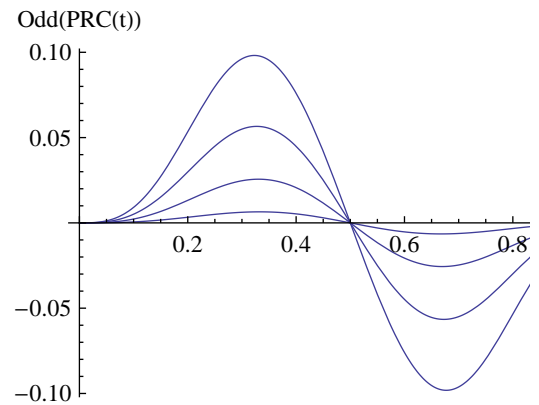
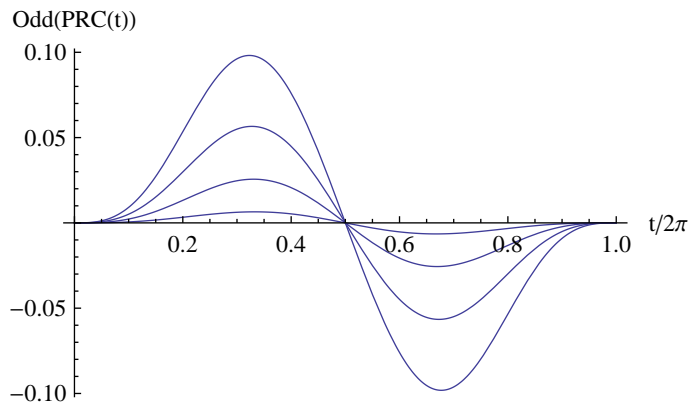
$$T_2 - T_1 + \text{PRC}[\theta_{\text{fp}}] - \text{PRC}[\phi_{\text{fp}}] = 0$$

We can eliminate  $\phi_{\text{fp}}$  by observing that  $\phi_{\text{fp}} + \theta_{\text{fp}} = T$ , where  $T$  is the period the network converges to:

$$\text{PRC}[\theta_{\text{fp}}] - \text{PRC}[T - \theta_{\text{fp}}] = T_1 - T_2$$



## It's the odd part that matters



Odd part of Quadratic Neuron's PRCs for excitation and inhibition ( $A = \pm 0.1, 0.2, 0.3, 0.4$ ).

We can eliminate  $T$  from our previous result by defining the PRC as a periodic function (i.e.,  $\text{PRC}(\theta + T) = \text{PRC}(\theta)$ ):

$$\text{PRC}[\theta_{\text{fp}}] - \text{PRC}[-\theta_{\text{fp}}] = T_1 - T_2$$

The LHS is 0 if the PRC is even (i.e.,  $\text{PRC}(\theta) = \text{PRC}(-\theta)$ ) and is twice the PRC if it is odd (i.e.,  $\text{PRC}(\theta) = -\text{PRC}(-\theta)$ ). If the PRC is neither even nor odd, we can write it as the sum of an odd and an even function (this is true for any function), and drop the even part:

$$2 \text{Odd}[\text{PRC}[\theta_{\text{fp}}]] = T_1 - T_2 \text{ where } \text{Odd}[f[\mathbf{x}]] = (f[\mathbf{x}] - f[-\mathbf{x}]) / 2$$

This equation is identical to that for the single neuron: The odd part of the PRC plays the same role for coupled neurons as the PRC itself plays for a single neuron.

The stability condition is also the same: The neuron's synchronize if

$$-2 < \frac{d}{d\theta_{\text{fp}}} \text{Odd}[\text{PRC}[\theta_{\text{fp}}]] < 0$$

## Neurons with Class I and II excitability

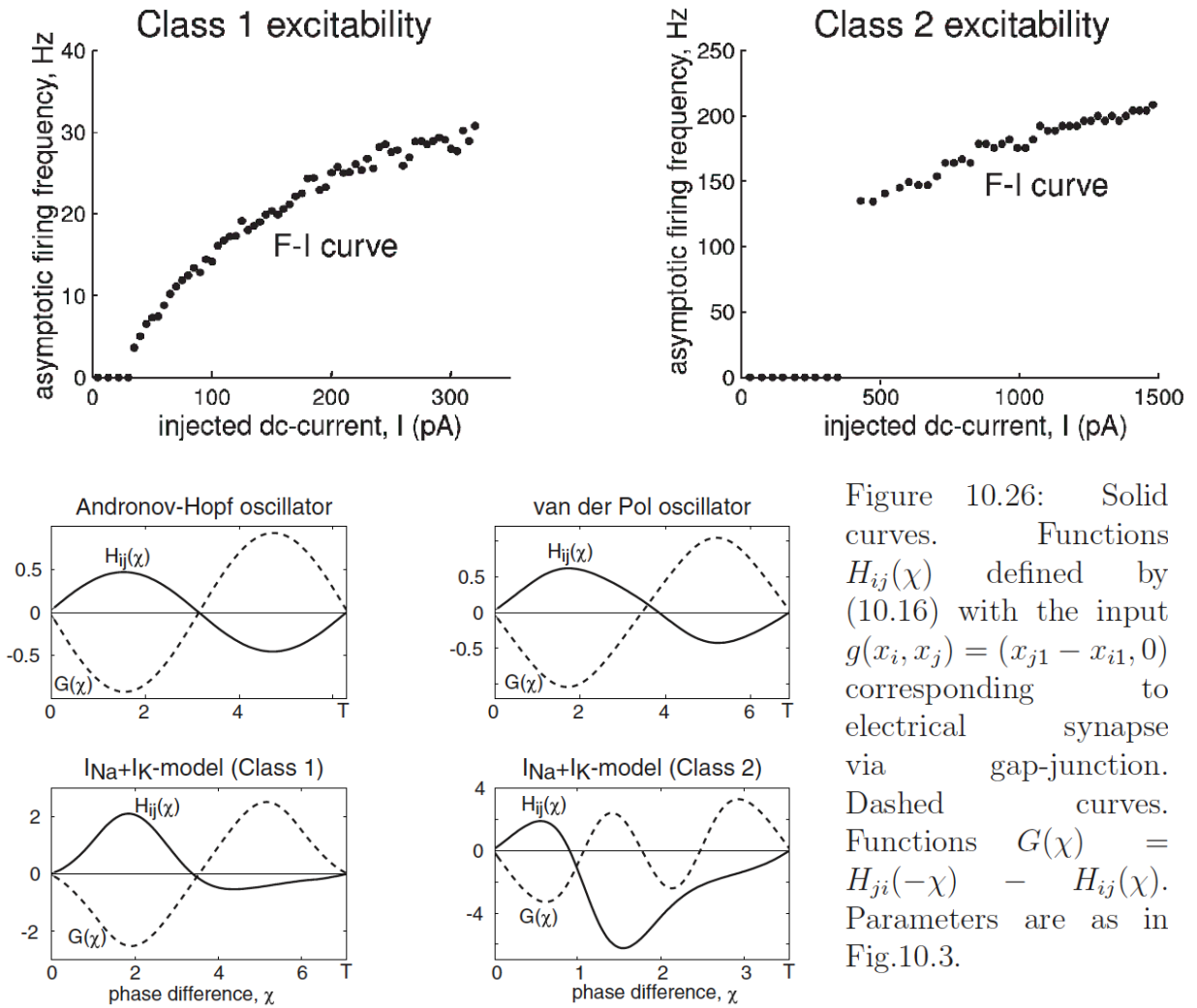


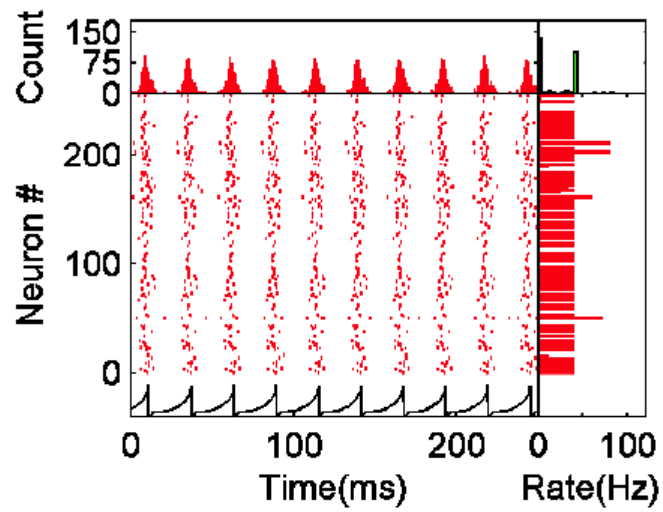
Figure 10.26: Solid curves. Functions  $H_{ij}(\chi)$  defined by (10.16) with the input  $g(x_i, x_j) = (x_{j1} - x_{i1}, 0)$  corresponding to electrical synapse via gap-junction. Dashed curves. Functions  $G(\chi) = H_{ji}(-\chi) - H_{ij}(\chi)$ . Parameters are as in Fig.10.3.

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).



## 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.