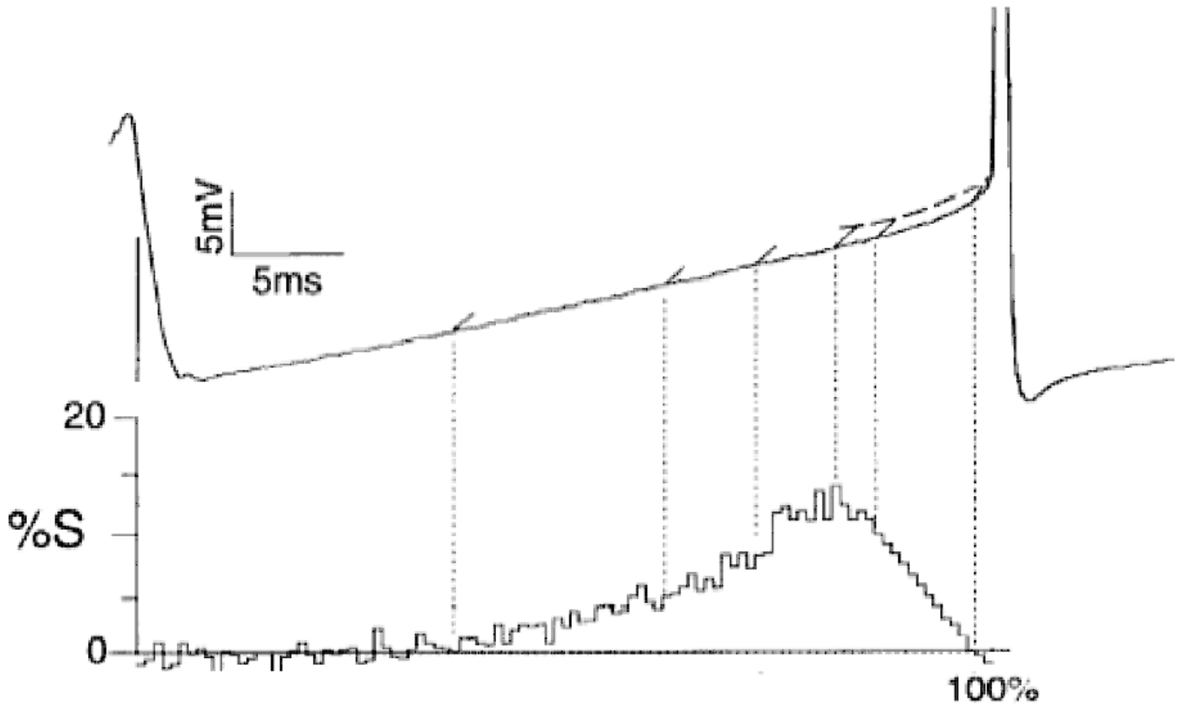
Phase Response



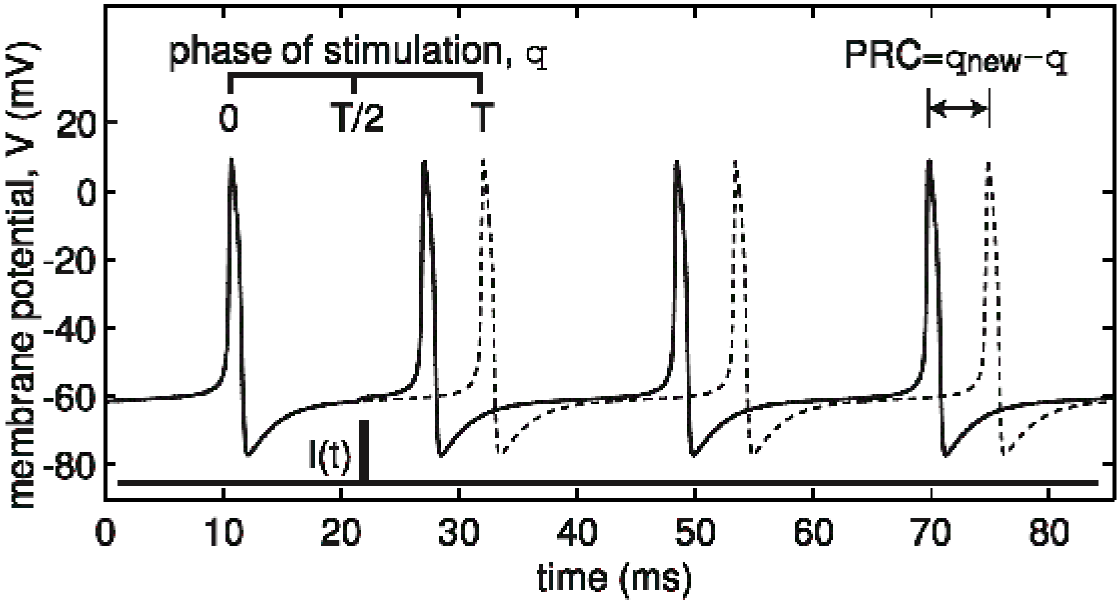
Inward current-pulses decrease a cortical neuron's period (Cat, Layer V). [Fetz93]

Synaptic input advances (excitatory) or delays (inhibitory) spiking

It is most effective at a particular point in the interspike interval

The phase response curve (PRC) describes this dependence

Measuring the phase-response curve (PRC)



An inward current-pulse ($I(t)$) advances the spike; dashed line shows default [Izhikevich06].

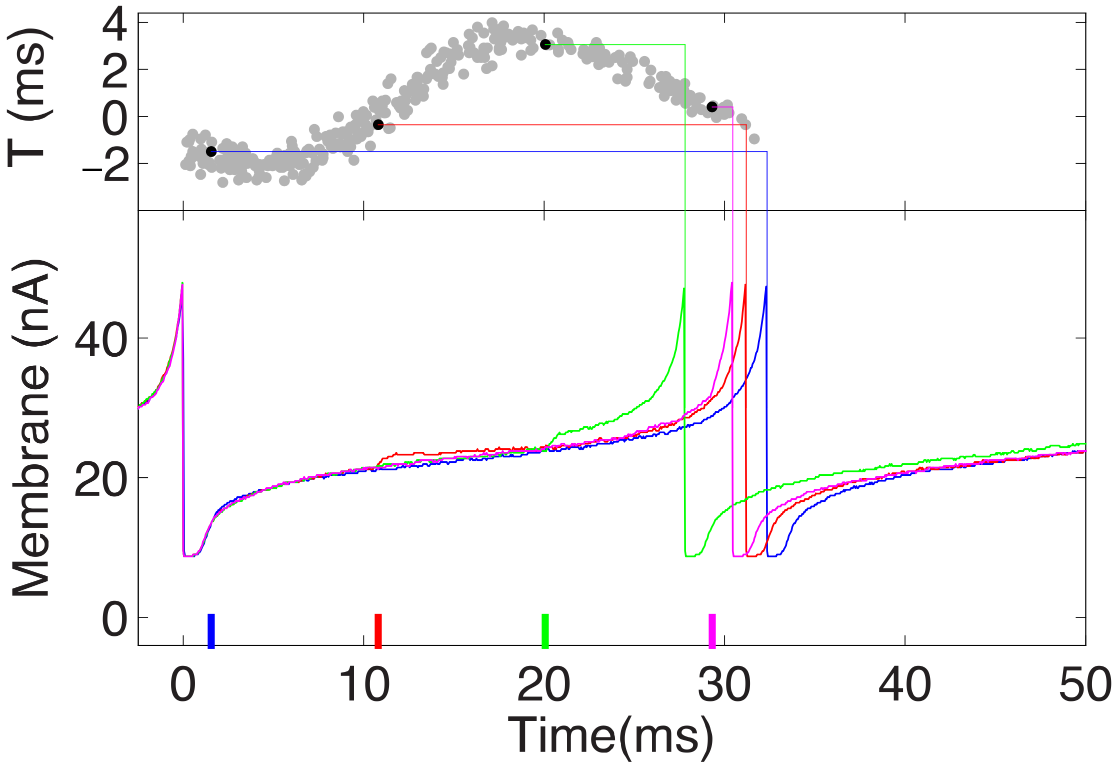
Synaptic input—or a current-pulse—is applied at various points in the interspike interval.

The amount by which the input advances (or delays) spiking is measured.

Plotting this advance (or delay) versus the time relative to the last spike—called the phase—yields the PRC.

The PRC is positive for phase advances (i.e., excitation).

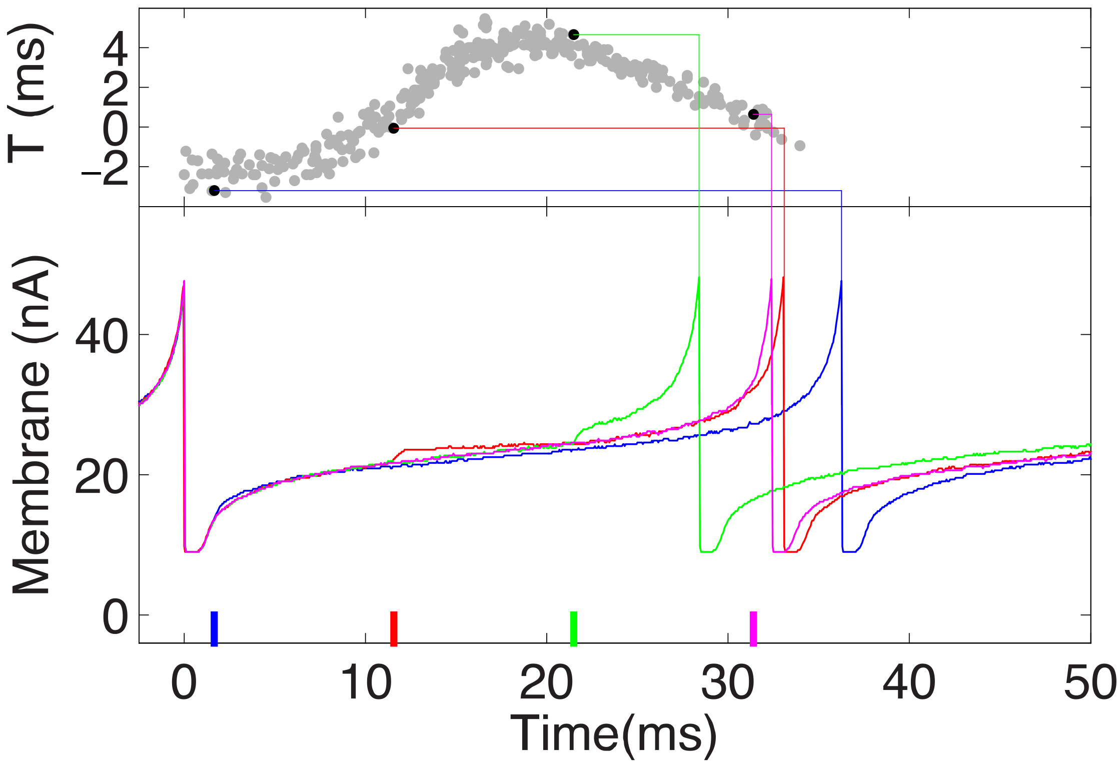
PRC for excitation



Most effective at 17.8ms (0.55*T*), advancing spiking by 3.9ms (0.12*T*).

Rise-time was 0.7ms; time-constant was 1.7ms.

Stronger excitation

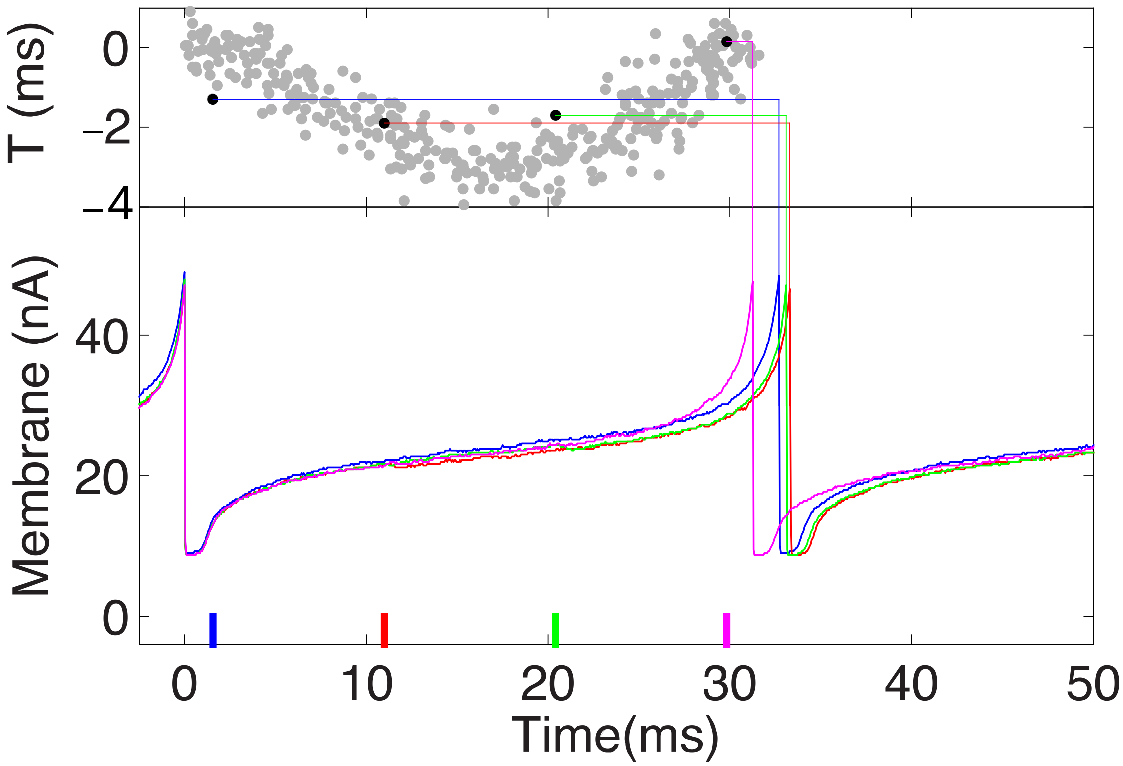


Most effective at 18.8ms (0.55*T*), advancing spiking by 5.1ms (0.15*T*).

Rise-time and time-constant unchanged.

5 of 11

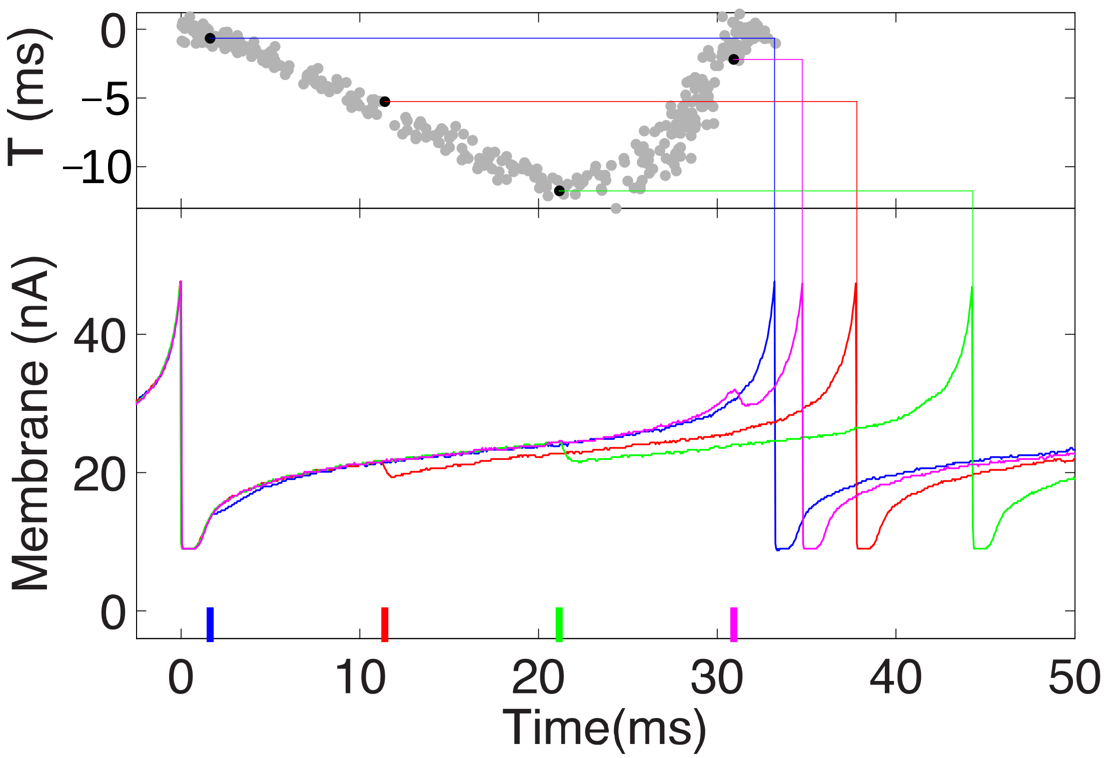
PRC for inhibition



Most effective at 18.2ms (0.57*T*), delaying spiking by 3.9ms (0.12*T*).

Rise-time was 0.4ms; time-constant was 0.6ms.

Stronger inhibition

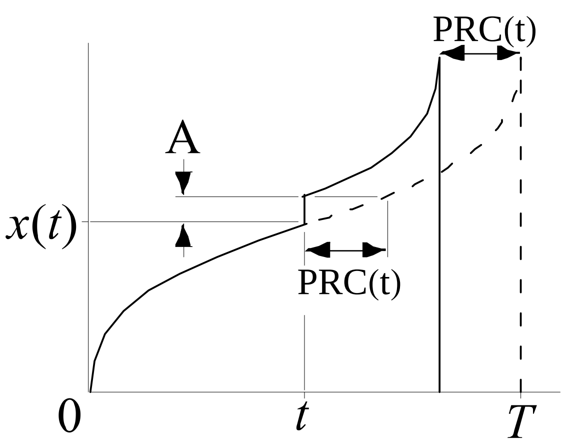


Most effective at 22.1ms (0.65T), delaying spiking by 12.1ms (0.36T).

Rise-time and time-constant unchanged.

7 of 11

Calculating the PRC



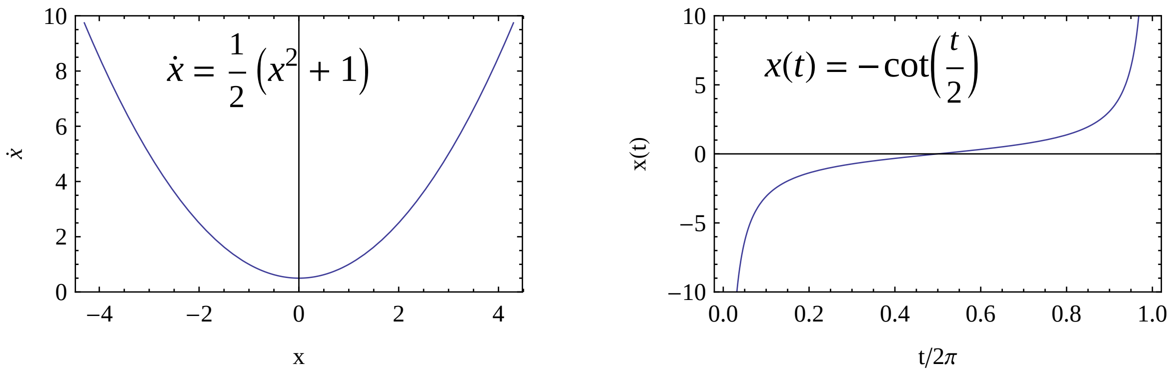
A voltage-increase (A) due to brief excitation at time t advances spiking by PRC(t).

The corresponding point on the membrane-voltage's original trajectory shifts forward by PRC(t), yielding:

```
  x[t + PRC[t]] = x[t] + A
⟺ PRC[t] = x^-1[x[t] + A] - t
```

Thus, we must solve the membrane-voltage's ODE for $x(t)$ and invert this function. Not fun!

Quadratic integrate-and-fire neuron

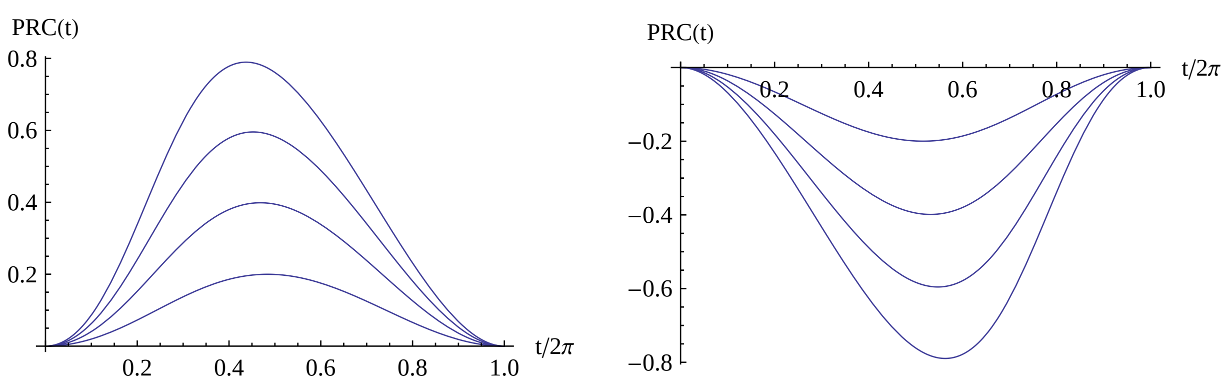


Phase-plot (left) and membrane voltage (right); inflexion-point is at $x = 0$ (due to offset).

This model can be solved analytically:

```
  x[t] = -Cot[t / 2]  with period T = 2 π
⟹ PRC[t] = 2 Cot^-1[Cot[t / 2] - A] - t
```

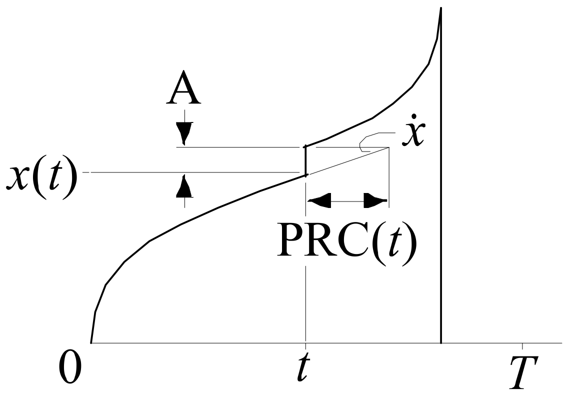

Quadratic I&F neuron's PRCs



PRCs for excitaiton inhibition ($A = \pm 0.1,\ 0.2,\ 0.3,\ 0.4$)

The PRC becomes skewed as A gets large in both cases—skewed to earlier phases for excitation and latter phases for inhibition—the neuron is kicked across the inflexion point in both cases.

Weak limit: A ≪ 1



For small A, $\dot{x}$ yields a good approximation for PRC(t)

Extrapolating $x(t)$ linearly yields:

$$\dot{x}[t]\ \mathrm{PRC}[t] \approx A \Longleftrightarrow \mathrm{PRC}[t] \approx A / \dot{x}[t]$$

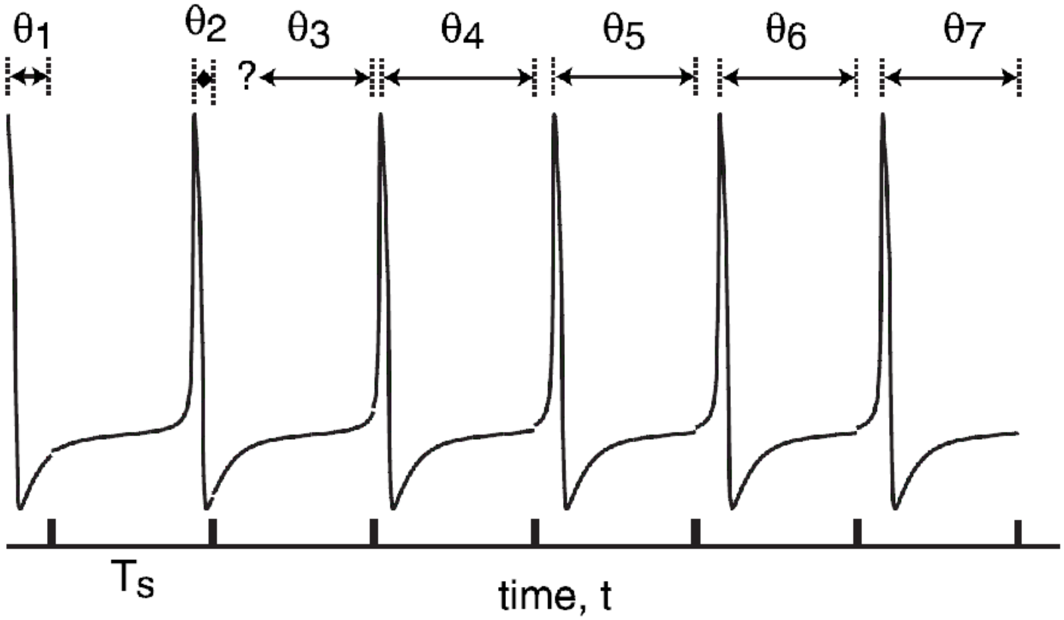
Makes the intuitive prediction that the kick is most effective when $\dot{x}$ is minimum—at the inflexion point.

For the quadratic I&F-neuron, we get :

$$\dot{x}[t] = 1 / \mathrm{Sin}^2[t] \Longrightarrow \mathrm{PRC}[t] \approx A\,\mathrm{Sin}^2[t]$$

This matches the $A = 0.1$ curves in the previous slide.

Next lecture: Phase-locking



Occurs when phase reset matches difference in periods [Izhikevich06].

We use the PRC to predict if one neuron will entrain another.