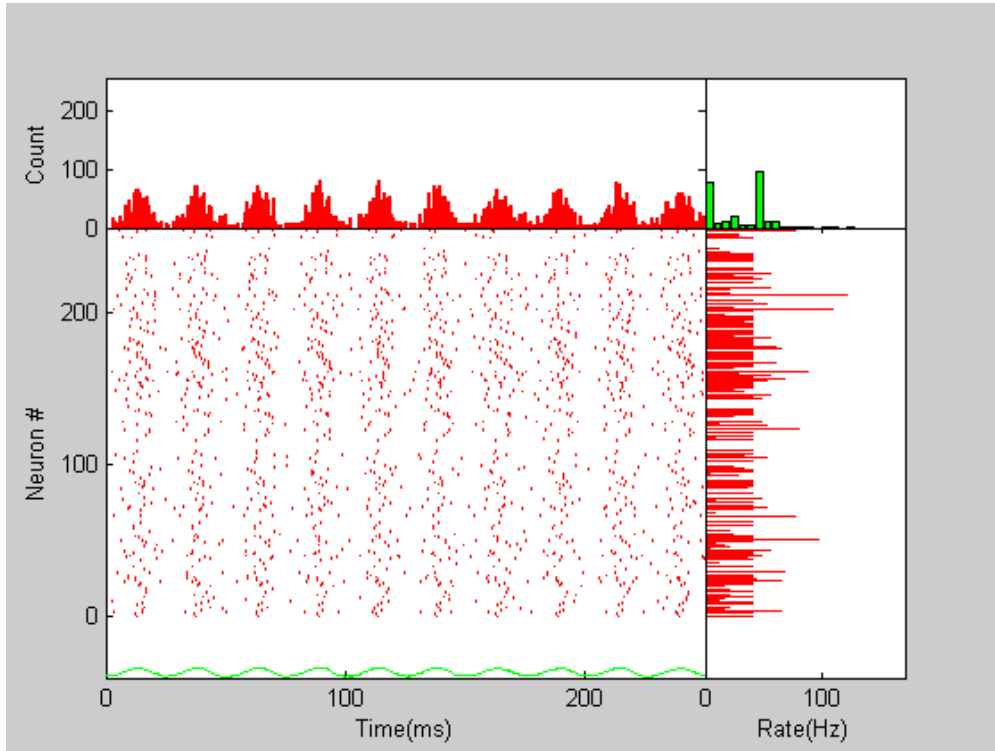
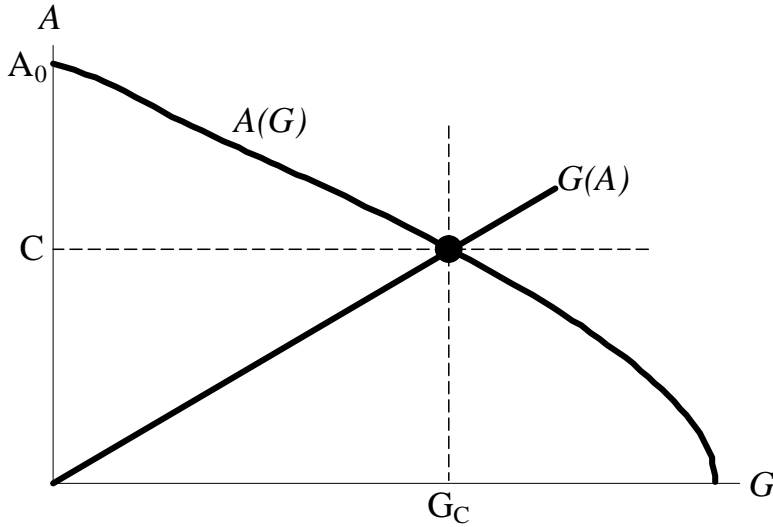


## Synchrony by delayed inhibition



## The asynchronous state



The network rate  $C$  produces inhibition  $G_c$  that makes each neuron spikes at  $C/N$ .  
 The network activity  $A$  gives us the conductance,  $G(A)$ .

$$G[A] \approx N f[G] \Delta g \tau_g$$

The conductance  $G(A)$  gives us each neuron's firing rate,  $C/N$ .

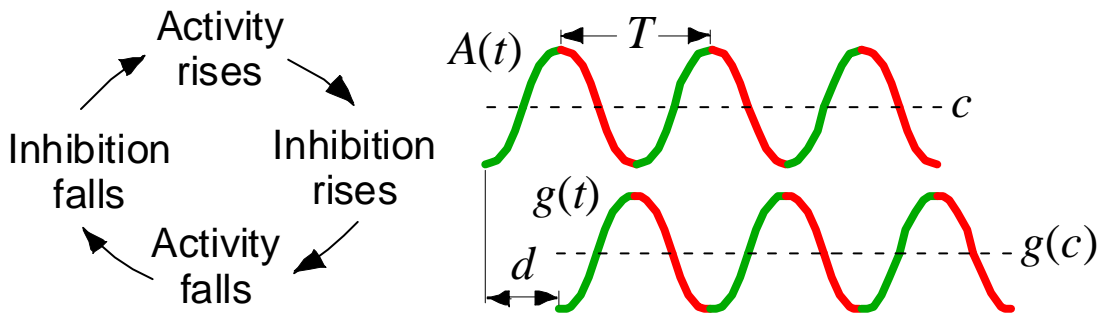
Multiplying  $f(G)$  by the population size  $N$  gives us the activity  $A$ .

The  $A$  we get is the same as the one we started with if

$$A = N f[G[A]]$$

This is the activity level (labeled  $C$  above) in the asynchronous state—neurons distribute their spikes uniformly in time.

## Delayed inhibition destabilizes asynchrony



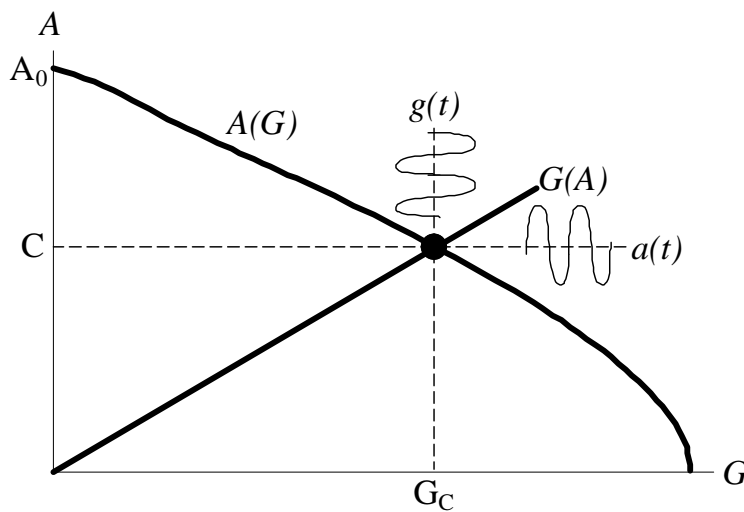
Inhibition overshoots and undershoots repeatedly

Due to  $A(G)$ 's negative slope, excitation falls as inhibition rises—and vice versa—they are exactly half-a-cycle ( $180^\circ$ ) out-of-phase.

Therefore, the network activity oscillates with a period:

$$T = 2d \approx t_p$$

## Synchrony about the synchronous state



The network activity oscillates about its equilibrium

If  $G(A)$ 's slope is greater than the absolute value of  $A(G)$ 's slope, i.e., their product is greater than one, the equilibrium is unstable → If  $A(G)$  deviates from  $C$ ,  $G(A)$  increases enough to push  $A(G)$  to the other side of  $C$ , such that  $A(G)$  is further from  $C$  than it started.

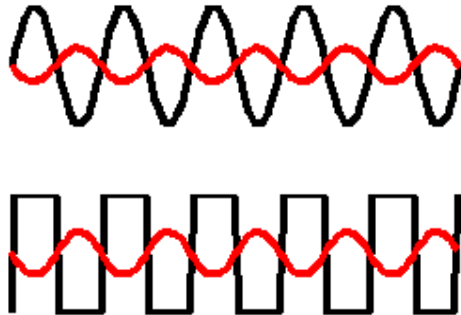
If  $G(A)$ 's slope is less than the absolute value of  $A(G)$ 's slope, any oscillations about  $C$ , are damped decaying to zero amplitude.

During oscillations:

$$A = C + a(t)$$

$$G = G_C + g(t)$$

## Model assumptions



With sinusoidal  $a(t)$  or pulsed  $a(t)$ , inhibition,  $g(t)$ , is similar.  $\tau_p=5\text{ms}$ ,  $\tau=5\text{ms}$

$a(t)$  and  $g(t)$  are sinusoidal.

$a(t)$  leads  $g(t)$  by one half cycle; i.e., the delay,  $d$ , is half of the period,  $T$ .

Inhibition responds to a spike with an exponential ( $\tau$ ) with a rise-time ( $\tau_p$ ); both contribute to delay.

## Contribution of $\tau_p$



$\tau_p$  yields a delay of  $\tau_p/2$ .

$\tau_p$ 's delay is independent of the period,  $T$ .

## Contribution of $\tau$

$\tau$ 's contribution depends on  $T$ .

$g(t)$ 's input, is proportional to  $a(t)$ , we set it to  $\sin(2\pi t/T)$

$$\tau \frac{dg(t)}{dt} + g(t) = \sin(2\pi t/T)$$

We assume a solution of the form:

$$g(t) = g_0 \sin(2\pi(t+s)/T)$$

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## Contribution of $\tau$

We substitute our solution and solve for  $d$ ,  $\tau$ 's contribution to delay:

$$\frac{\tau 2\pi g_0}{T} \cos(2\pi(t+s)/T) + g_0 \sin(2\pi(t+s)/T) = \sin(2\pi t/T)$$

If  $\tau$  is very small, the first term approaches zero:

$$g_0 \sin(2\pi(t+s)/T) = \sin(2\pi t/T)$$

$$s = 0$$

If  $\tau$  is very large, the second term approaches zero:

$$\frac{2\pi\tau g_0}{T} \cos(2\pi(t+s)/T) = \sin(2\pi t/T)$$

$$s = T/4$$

Very large  $\tau$ , contributes only half the necessary delay, which,  $T/2$ .

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## $t_p$ and $\tau$ together

$t_p$  contributes a delay of  $t_p/2$ .

$\tau$  contributes a delay between 0 and  $T/2$ .

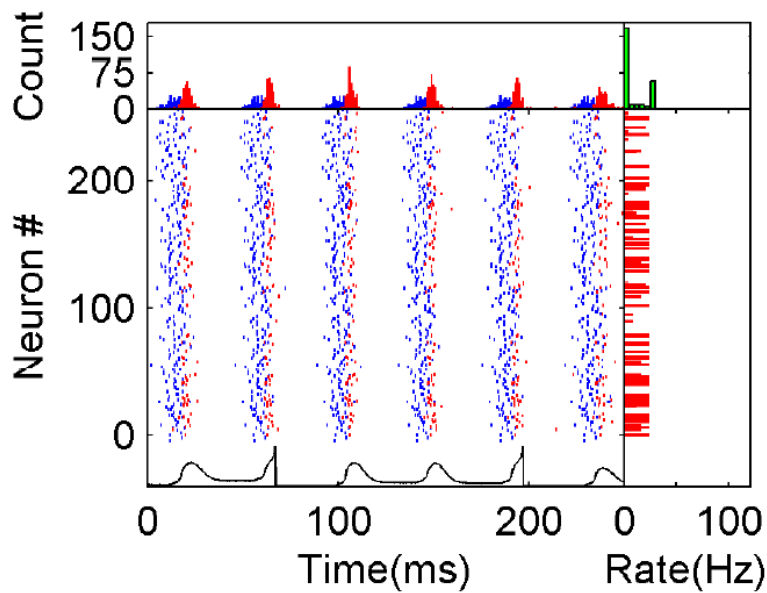
$T$  is twice the total delay, which yields:

$$T = 2(t_p/2 + T/4) \quad \text{- or -} \quad T = 2(t_p/2 + 0)$$

$$t_p < T < 2t_p$$

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## Entrainment



The excitatory population (blue) drives the inhibitory one (red), which inhibits it, shutting down activity until inhibition decays.

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## Entrainment

The excitatory neurons receive constant input current. When they spike they drive the inhibitory interneurons with fast excitation. In turn the inhibitory interneurons inhibit each other and the excitatory neurons, suppressing activity of both populations.

For purely inhibitory interactions, we have:

$$t_p < T < 2 t_p$$

The time between excitatory spiking and inhibitory spiking acts as an additional delay in the system,  $d_{ei}$ .

$$2 (t_p / 2 + d_{ei}) < T < 4 (t_p / 2 + d_{ei})$$