Mathematical Foundations of Neuroscience - Lecture 11. Bursting (continued).

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- Recall that bursting in the neuronal context means that the neuron responds to stimuli with a series of spikes instead of just one.
- In more general context a burster is a dynamical system that autonomously alternates between two dynamical regimes. So far we've seen point-cycle bursters, but we may also have cycle-cycle, cycle torus or chaotic bursters.
- When the dynamical system is composed of two parts which operate on different timescale, the burster is said to be of the fast-slow type.
- Fast-slow bursters can be dissected, that is fast and slow part can be analyzed to some extent separately.
- Other bursters are of the hedgehog type, therefore there is a periodic (quasiperiodic, chotic) orbit that passes through different dynamical regimes.

Types of hysteresis loop

- Last time we've seen, that a "neuronal" fast slow burster can driven by the hysteresis loop or the slow wave.
- The hysteresis loop requires bistability, and only two of the plane neuronal models we've seen exhibits bistability - fold/homoclinic and Hopf/Fold Cycle. We noted that other bursters can be achieved only vie the slow wave (at least 2 dimensional slow system)
- There also another way - we can introduce an additional "down" state and therefore achieve bistability and hysteresis loop bursting.

Circle/Circle Bursting

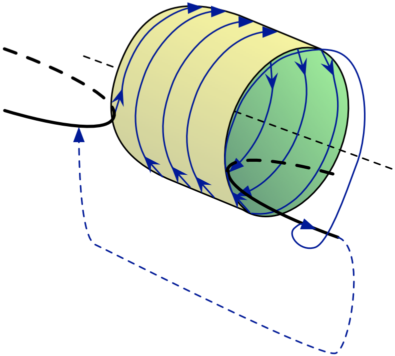


Figure: Circle-circle bursting via a slow wave and via a hysteresis loop with additional stable "down" state.

Circle/Circle Bursting

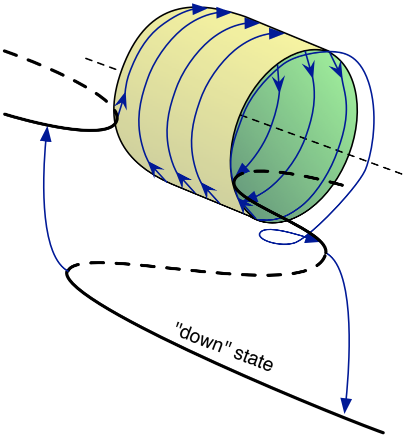


Figure: Circle-circle bursting via a slow wave and via a hysteresis loop with additional stable "down" state.

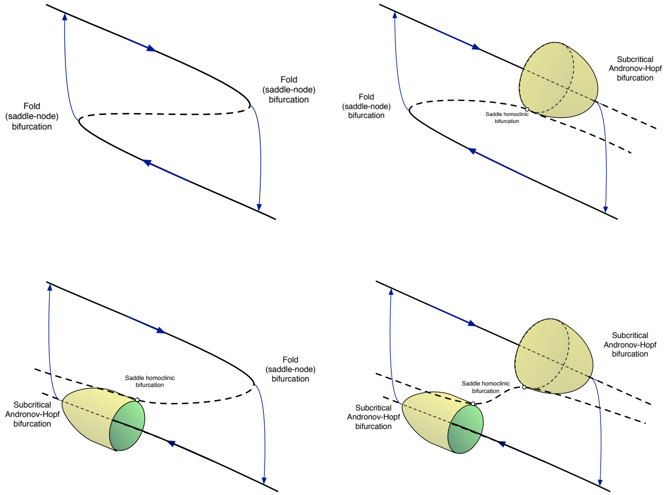


Figure: Different point-point hysteresis loops.

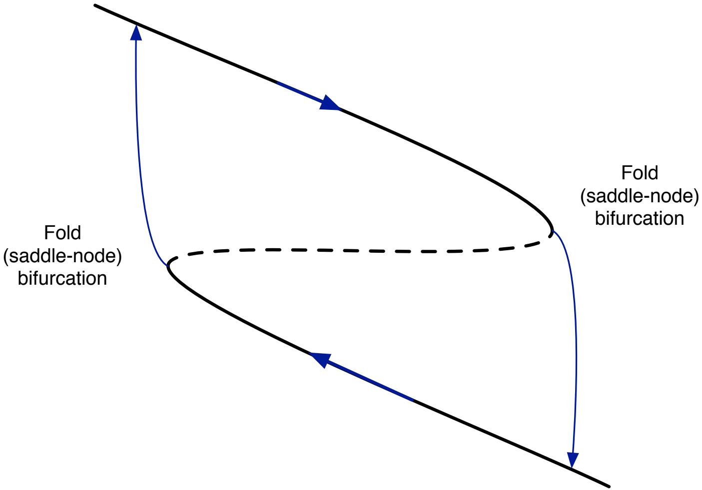


Figure: Fold-fold hysteresis loop.

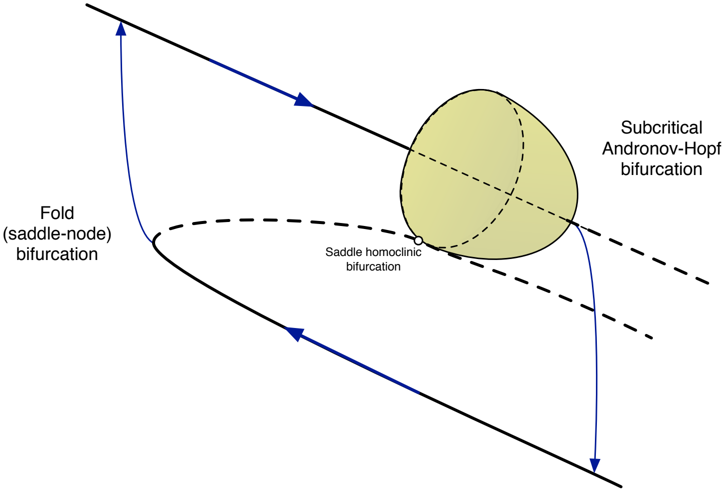


Figure: subHopf-fold hysteresis loop.

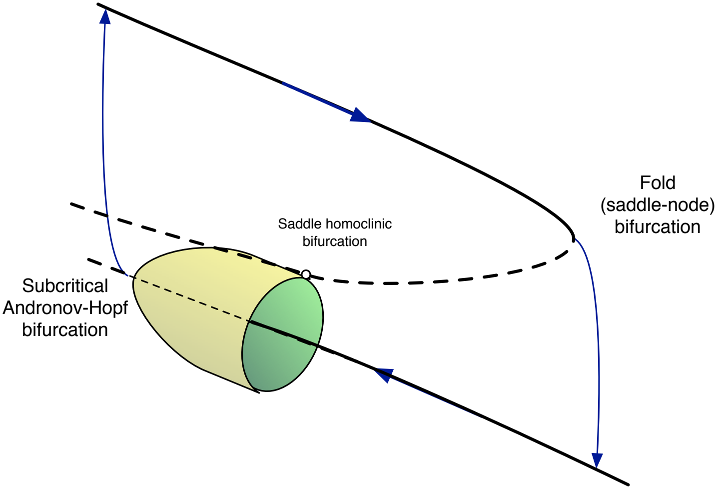


Figure: Fold-subHopf hysteresis loop.

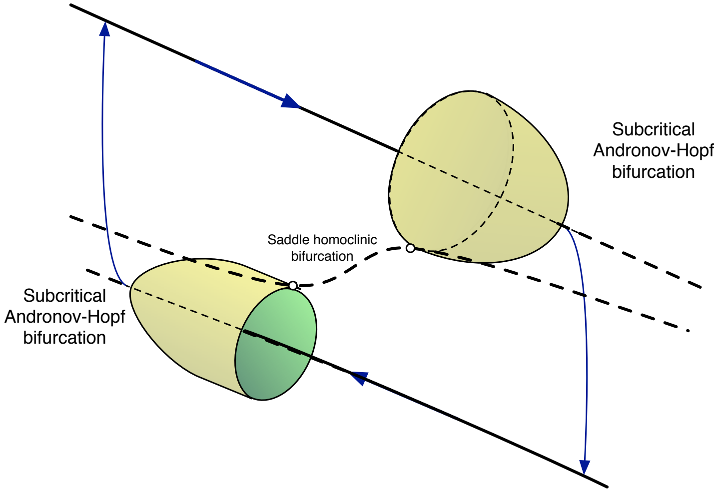


Figure: subHopf-subHopf hysteresis loop.

- There are only four point-point hysteresis loops, but there can be more loops including cycles
- We may have for example Circle/Fold cycle burster via subHopf/fold cycle loop:
  - The "down" rest state looses stability via saddle node on invariant circle bifurcation and begins to spike
  - The limit cycle looses stability via fold cycle bifurcation. The system jumps to the "upper" rest state. Almost immediately the stable limit cycle reappears via another fold cycle bifurcation.
  - The large limit cycle disappears via saddle node on invariant circle bifurcation.
  - The upper rest state looses stability via Subcritical Andronov-Hopf bifurcation, the system jumps to the "down" state.
  - The process repeats...

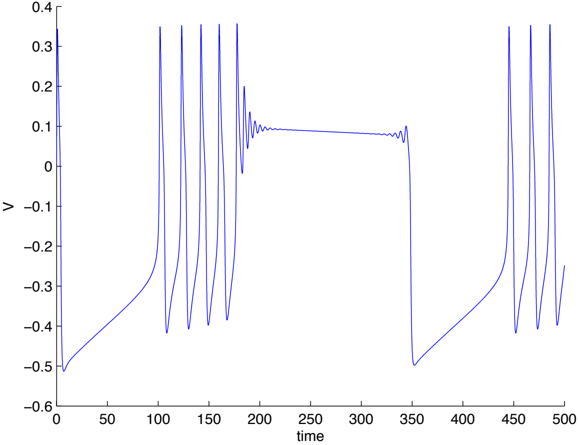


Figure: Circle/Fold Cycle bursting via subHopf/fold cycle hysteresis loop. Morris-Lecar model with parameters as in the next slide.

Morris-Lecar model with slow system (u)

$$\frac{dV}{dt} = -u - g_l(V - E_l) - g_K w(V - E_K) - g_{Ca} m_\infty(V)(V - E_{Ca})$$
$$\frac{dw}{dt} = \lambda(V)(w_\infty(V) - w)$$
$$\frac{du}{dt} = \mu(0.1 + V)$$

$$m_\infty(V) = \frac{1}{2}\left(1 + \tanh\left(\frac{V - V_1}{V_2}\right)\right) \quad w_\infty(V) = \frac{1}{2}\left(1 + \tanh\left(\frac{V - V_3}{V_4}\right)\right)$$

$$\lambda(V) = \frac{1}{3}\cosh\left(\frac{V - V_3}{2V_4}\right)$$

$V_1 = -0.01$, $V_2 = 0.15$, $V_3 = 0.1$, $V_4 = 0.16$, $V_5 = -0.5$, $E_l = -0.5$, $E_K = -0.7$, $E_{Ca} = 1$, $g_l = 0.5$, $g_K = 2$, $g_{Ca} = 1.36$, $\mu = 0.003$

Reassuming we have

- 16 types of fast-slow bursters of neuronal type.
- Each of them can be driven by the slow wave.
- All of them can be driven by a hysteresis loop with additional "down" state
- Some of them can be driven by a hysteresis loop which "reuses" some of the bifurcations that switch on/off bursting (in particular two that we've seen are bistable by default and can drive the hysteresis loop on their own)
- This gives about 100 possible dynamical regimes... unfortunately this is not the end.

Burster classification

- So far we've seen point-cycle bursters, but there are other types possible.
- A strange kind of bursting may appear even when there is no cycle attractor at all, in such a case the "spikes" are simply damped oscillations.
- We may also assume there is a large amplitude cycle (spiking state) and a small amplitude cycle (rest state). This gives additional bursters.
- Since bursters work in 3d, the spiking state could be a torus, while the rest state could just be a slow transition near the cycle ruins.
- Finally there can be chaotic bursters...

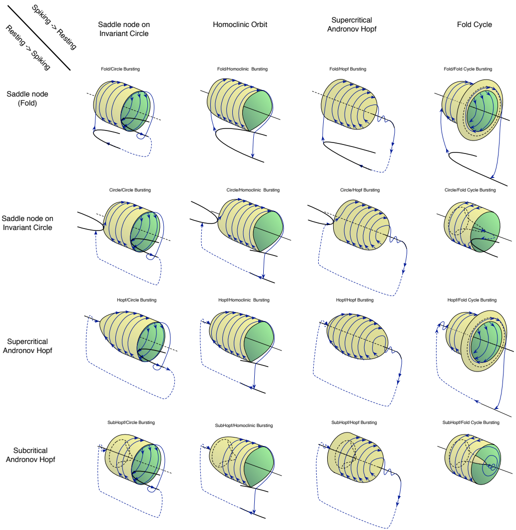


Figure: All planar point-cycle fast-slow bursters (see Izhikevich 2000).

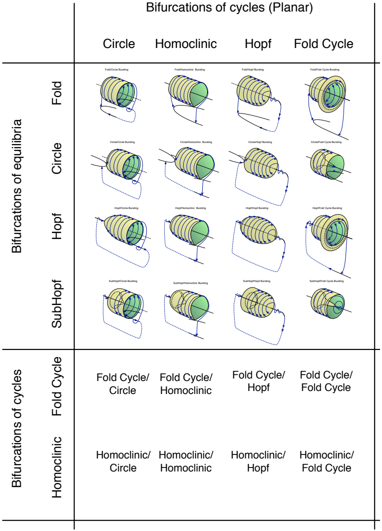
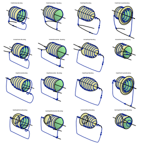
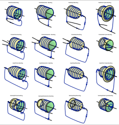


Figure: All planar bursters (including cycle-cycle).



		Bifurcations of cycles (Planar)				Bifurcations of cycles (3d)				
		Circle	Homoclinic	Hopf	Fold Cycle	Subcritical Flip	Subcritical Neimark-Sacker	Saddle Focus Homoclinic	Focus Focus Homoclinic	Blue Sky Catastrophe
Bifurcations of equilibria	Fold					Fold/Flip	Fold/Sacker	Fold/Saddle Focus Homoclinic	Fold/Focus Focus Homoclinic	Fold/Blue Sky
	Circle					Circle/Flip	Circle/Sacker	Circle/Saddle Focus Homoclinic	Circle/Focus Focus Homoclinic	Circle/Blue Sky
	Hopf					Hopf/Flip	Hopf/Sacker	Hopf/Saddle Focus Homoclinic	Hopf/Focus Focus Homoclinic	Hopf/Blue Sky
	SubHopf					SubHopf/Flip	SubHopf/ Sacker	SubHopf/Saddle Focus Homoclinic	SubHopf/Focus Focus Homoclinic	SubHopf/ Blue Sky
Bifurcations of cycles	Fold Cycle	Fold Cycle/ Circle	Fold Cycle/ Homoclinic	Fold Cycle/ Hopf	Fold Cycle/ Fold Cycle	Fold Cycle/ Flip	Fold Cycle/ Sacker	Fold Cycle/ Saddle Focus Homoclinic	Fold Cycle/ Focus Focus Homoclinic	Fold Cycle/ Blue Sky
	Homoclinic	Homoclinic/ Circle	Homoclinic/ Homoclinic	Homoclinic/ Hopf	Homoclinic/ Fold Cycle	Homoclinic/ Flip	Homoclinic/ Sacker	Homoclinic/ Saddle Focus Homoclinic	Homoclinic/ Focus Focus Homoclinic	Homoclinic/ Blue Sky
Bifurcations of cycles (3d)	Subcritical Flip	Flip/ Circle	Flip/ Homoclinic	Flip/ Hopf	Flip/ Fold Cycle	Flip/Flip	Flip/Sacker	Flip/ Saddle Focus Homoclinic	Flip/ Focus Focus Homoclinic	Flip/ Blue Sky
	Subcritical Neimark-Sacker	Sacker/ Circle	Sacker/ Homoclinic	Sacker/ Hopf	Sacker/ Fold Cycle	Sacker/ Flip	Sacker/ Sacker	Sacker/ Saddle Focus Homoclinic	Sacker/ Focus Focus Homoclinic	Sacker/ Blue Sky
	Saddle Focus Homoclinic	Saddle Focus Homoclinic/ Circle	Saddle Focus Homoclinic/ Homoclinic	Saddle Focus Homoclinic/ Hopf	Saddle Focus Homoclinic/ Fold Cycle	Saddle Focus Homoclinic/ Flip	Saddle Focus Homoclinic/ Sacker	Saddle Focus Homoclinic/ Saddle Focus Homoclinic	Saddle Focus Homoclinic/ Focus Focus Homoclinic	Saddle Focus Homoclinic/ Blue Sky
	Focus Focus Homoclinic	Focus Focus Homoclinic/ Circle	Focus Focus Homoclinic/ Homoclinic	Focus Focus Homoclinic/ Hopf	Focus Focus Homoclinic/ Fold Cycle	Focus Focus Homoclinic/ Flip	Focus Focus Homoclinic/ Sacker	Focus Focus Homoclinic/ Saddle Focus Homoclinic	Focus Focus Homoclinic/ Focus Focus Homoclinic	Focus Focus Homoclinic/ Blue Sky
	Blue Sky Catastrophe	Blue Sky/ Circle	Blue Sky/ Homoclinic	Blue Sky/ Hopf	Blue Sky/ Fold Cycle	Blue Sky/ Flip	Blue Sky/ Sacker	Blue Sky/ Saddle Focus Homoclinic	Blue Sky/ Focus Focus Homoclinic	Blue Sky/ Blue Sky

Figure: All (?) cycle-cycle and point-cycle 3d bursters .



		Bifurcations of cycles (Planar)				Bifurcations of cycles (3d)					
		Circle	Homoclinic	Hopf	Fold Cycle	Subcritical Flip	Subcritical Neimark-Sacker	Saddle Focus Homoclinic	Focus Focus Homoclinic	Blue Sky Catastrophe	Fold Cycle on Homoclinic Torus
Bifurcations of equilibria	Fold					Fold/Flip	Fold/Sacker	Fold/Saddle Focus Homoclinic	Fold/Focus Focus Homoclinic	Fold/Blue Sky	Fold/Torus
	Circle					Circle/Flip	Circle/Sacker	Circle/Saddle Focus Homoclinic	Circle/Focus Focus Homoclinic	Circle/Blue Sky	Circle/Torus
	Hopf					Hopf/Flip	Hopf/Sacker	Hopf/Saddle Focus Homoclinic	Hopf/Focus Focus Homoclinic	Hopf/Blue Sky	Hopf/Torus
	SubHopf					SubHopf/Flip	SubHopf/ Sacker	SubHopf/Saddle Focus Homoclinic	SubHopf/Focus Focus Homoclinic	SubHopf/ Blue Sky	SubHopf/ Torus
Bifurcations of cycles	Fold Cycle	Fold Cycle/ Circle	Fold Cycle/ Homoclinic	Fold Cycle/ Hopf	Fold Cycle/ Fold Cycle	Fold Cycle/ Flip	Fold Cycle/ Sacker	Fold Cycle/ Saddle Focus Homoclinic	Fold Cycle/ Focus Focus Homoclinic	Fold Cycle/ Blue Sky	Fold Cycle/ Torus
	Homoclinic	Homoclinic/ Circle	Homoclinic/ Homoclinic	Homoclinic/ Hopf	Homoclinic/ Fold Cycle	Homoclinic/ Flip	Homoclinic/ Sacker	Homoclinic/ Saddle Focus Homoclinic	Homoclinic/ Focus Focus Homoclinic	Homoclinic/ Blue Sky	Homoclinic/ Torus
Bifurcations of cycles (3d)	Subcritical Flip	Flip/ Circle	Flip/ Homoclinic	Flip/ Hopf	Flip/ Fold Cycle	Flip/Flip	Flip/Sacker	Flip/ Saddle Focus Homoclinic	Flip/ Focus Focus Homoclinic	Flip/ Blue Sky	Flip/ Torus
	Subcritical Neimark-Sacker	Sacker/ Circle	Sacker/ Homoclinic	Sacker/ Hopf	Sacker/ Fold Cycle	Sacker/ Flip	Sacker/ Sacker	Sacker/ Saddle Focus Homoclinic	Sacker/ Focus Focus Homoclinic	Sacker/ Blue Sky	Sacker/ Torus
	Saddle Focus Homoclinic	Saddle Focus Homoclinic/ Circle	Saddle Focus Homoclinic/ Homoclinic	Saddle Focus Homoclinic/ Hopf	Saddle Focus Homoclinic/ Fold Cycle	Saddle Focus Homoclinic/ Flip	Saddle Focus Homoclinic/ Sacker	Saddle Focus Homoclinic/ Saddle Focus Homoclinic	Saddle Focus Homoclinic/ Focus Focus Homoclinic	Saddle Focus Homoclinic/ Blue Sky	Saddle Focus Homoclinic/ Torus
	Focus Focus Homoclinic	Focus Focus Homoclinic/ Circle	Focus Focus Homoclinic/ Homoclinic	Focus Focus Homoclinic/ Hopf	Focus Focus Homoclinic/ Fold Cycle	Focus Focus Homoclinic/ Flip	Focus Focus Homoclinic/ Sacker	Focus Focus Homoclinic/ Saddle Focus Homoclinic	Focus Focus Homoclinic/ Focus Focus Homoclinic	Focus Focus Homoclinic/ Blue Sky	Focus Focus Homoclinic/ Torus
	Blue Sky Catastrophe	Blue Sky/ Circle	Blue Sky/ Homoclinic	Blue Sky/ Hopf	Blue Sky/ Fold Cycle	Blue Sky/ Flip	Blue Sky/ Sacker	Blue Sky/ Saddle Focus Homoclinic	Blue Sky/ Focus Focus Homoclinic	Blue Sky/ Blue Sky	Blue Sky/ Torus
Fold Cycle on Homoclinic Torus		Torus/ Circle	Torus/ Homoclinic	Torus/ Hopf	Torus/ Fold Cycle	Torus/ Flip	Torus/ Sacker	Torus/ Saddle Focus Homoclinic	Torus/ Focus Focus Homoclinic	Torus/ Blue Sky	Torus/ Torus

Figure: All (?) cycle-cycle, point-cycle and cycle/point-torus 3d bursters .

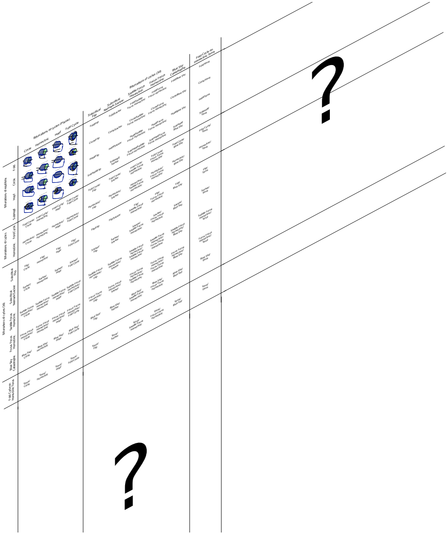


Figure: All (?) fast-slow bursters .

The system

$$\frac{dv}{dt} = v - \frac{v^3}{3} - w$$
$$\frac{dw}{dt} = \varepsilon(a + v - S(w))$$
$$\frac{du}{dt} = 0.01v;$$

where

$$S(w) = \frac{b}{1 + e^{\frac{c-w}{d}}}$$

and $\varepsilon = 1$, $a = 0.77 + \frac{0.33u}{u+0.15}$, $b = 1.65 + u$, $-0.15 + u, d = 0.1$ exhibits cycle-cycle bursting, with low amplitude cycle being the "resting" state.

Homoclinic/Hopf Bursting

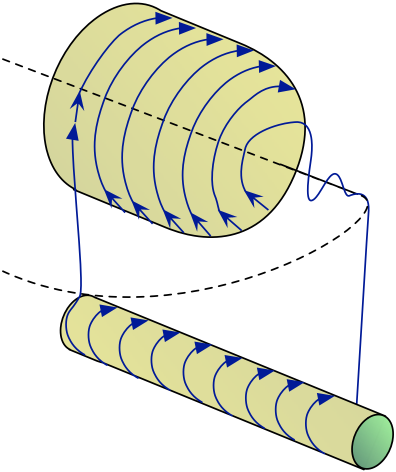


Figure: Homoclinic/Hopf cycle-cycle burster

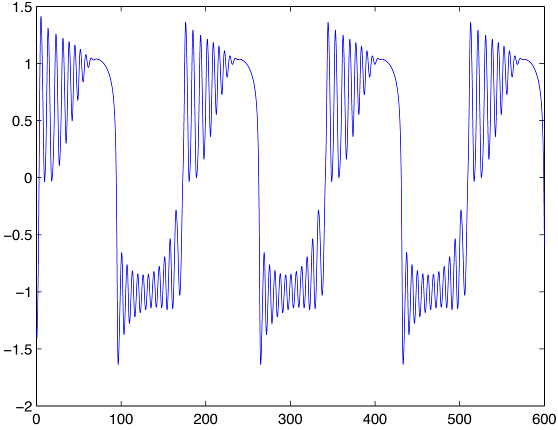


Figure: Cycle-cycle bursting

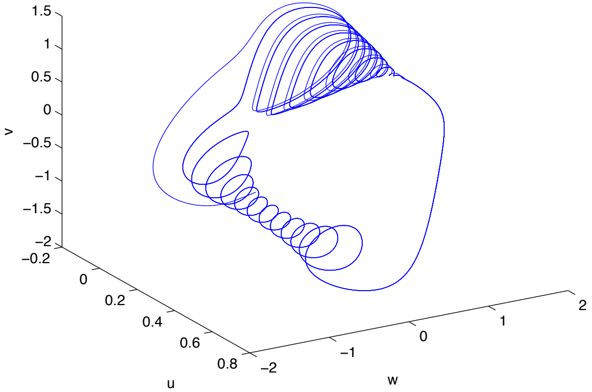


Figure: Cycle-cycle bursting

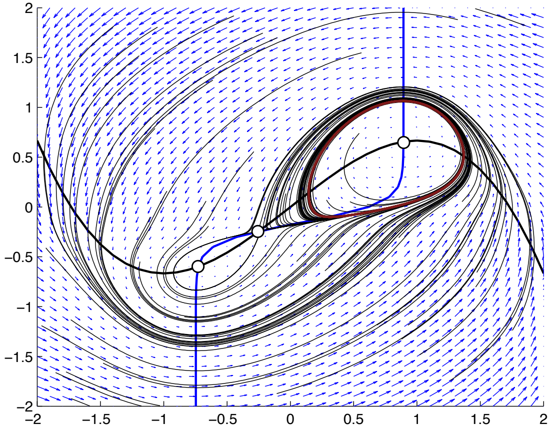
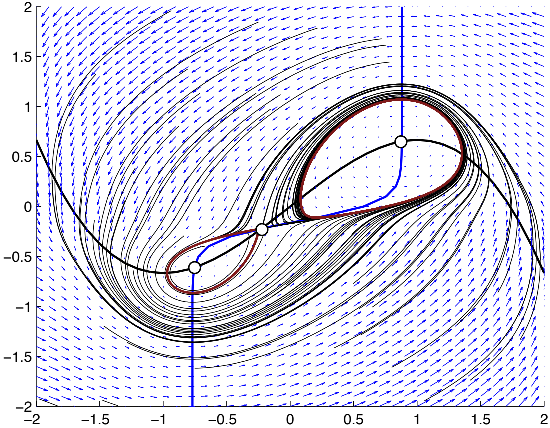


Figure: Point-point bursting



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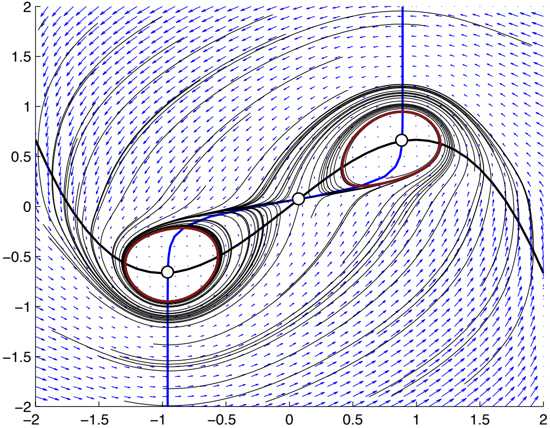

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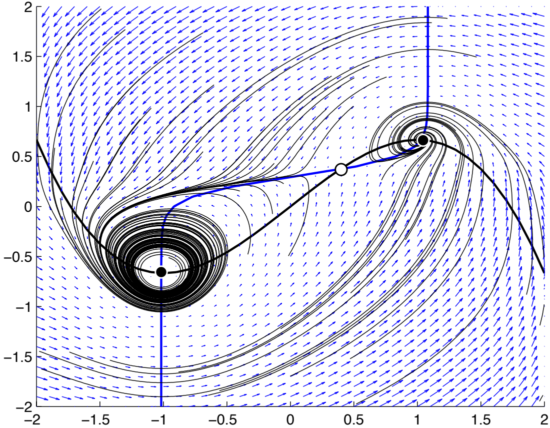

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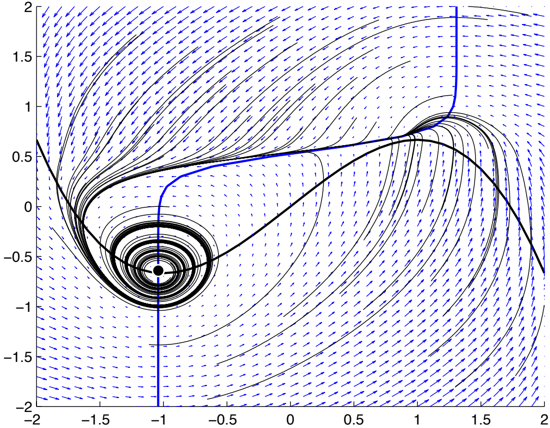


Figure: Point-point bursting

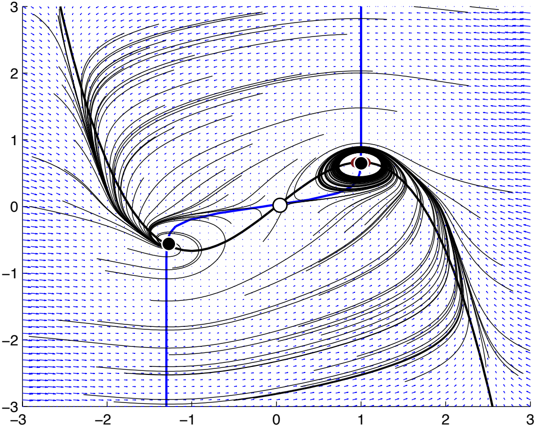
The system

$$\frac{dv}{dt} = v - \frac{v^3}{3} - w$$
$$\frac{dw}{dt} = \varepsilon(a + v - S(w))$$
$$\frac{dc}{dt} = 0.01v$$

where

$$S(w) = \frac{b}{1 + e^{\frac{c-w}{d}}}$$

and $\varepsilon = 0.5$, $a = 1.3$, $b = 2.3$, $d = 0.1$ exhibits a peculiar type of bursting, in which there is not cycle attractor at all! The "spikes" in the active phase are simply damped oscillations around a stable focus, though the rate of convergence to the focus is very slow.



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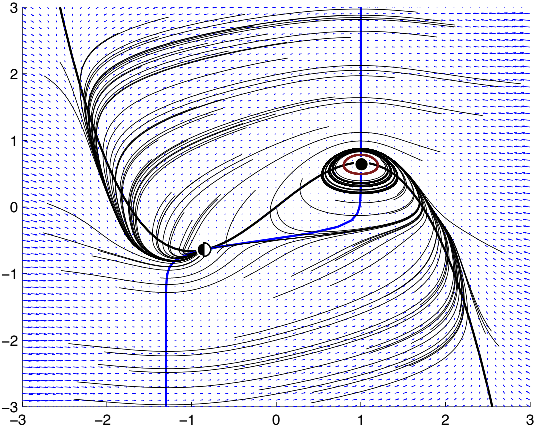

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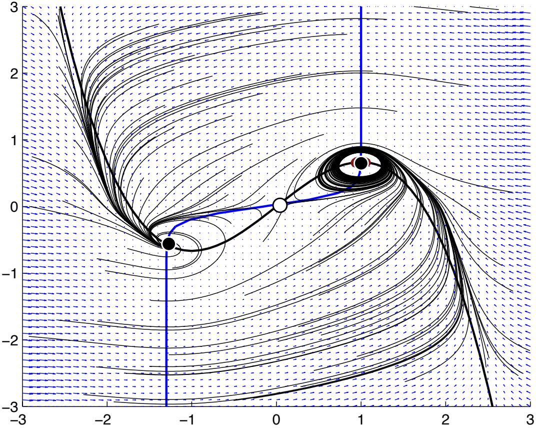

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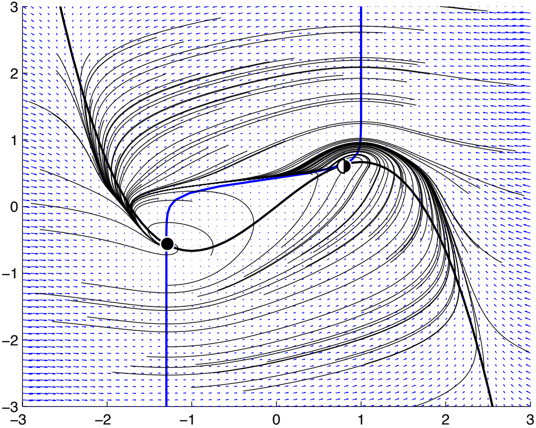

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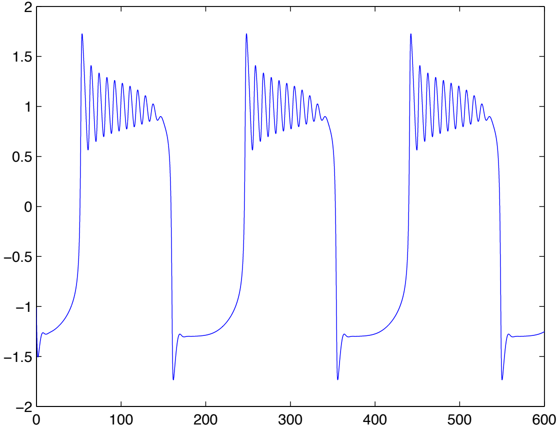

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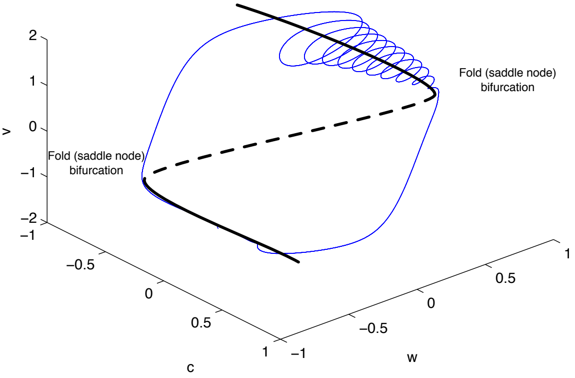


Figure: Point-point bursting

Cycle/Torus

- We we now consider a burster defined on the invariant torus. The burster is 3d, but may be difficult to define in terms of the fast-slow form.
- Assume the torus is close to the fold limit cycle on homoclinic torus bifurcation. In this case, the trajectories are periodic (or quasiperiodic) on the torus.
- However when they pass near the cycle ruins, they significantly slow down. In this case the passage through the external part of the torus corresponds to "active" part of bursting, and the passage near the internal part of the torus corresponds to "quiet" part of the burst.
- The waveform of bursting depends significantly on the position of the limit cycle ruins with respect to the torus.

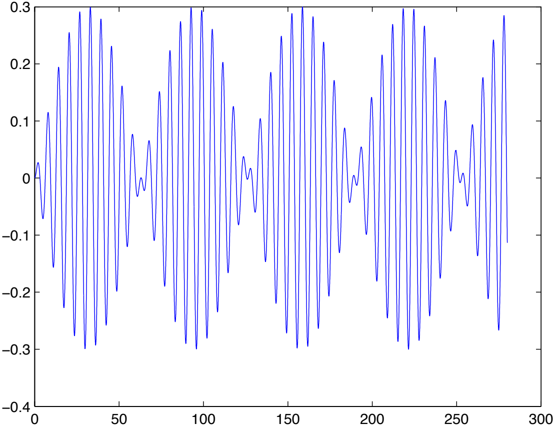


Figure: Quasiperiodic torus bursting

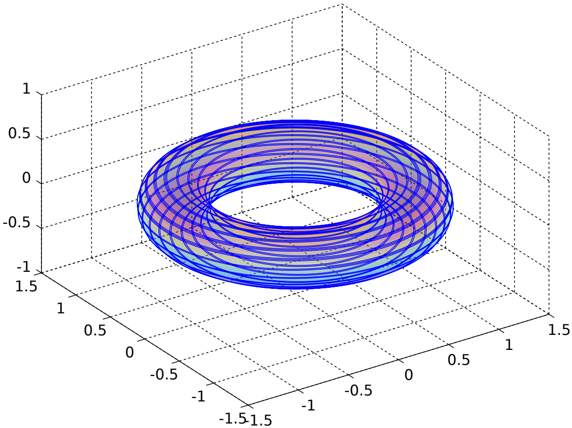


Figure: Quasiperiodic torus bursting

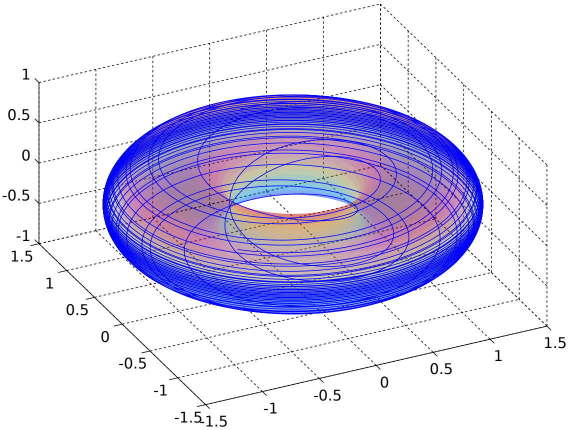
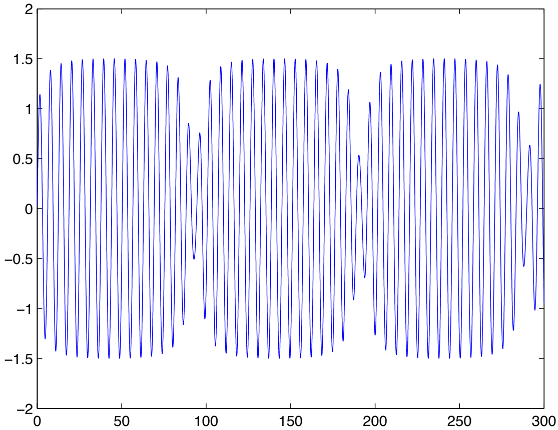


Figure: Various types of quasiperiodic bursting, depending on the locus of cycle ruins in relation to the torus.



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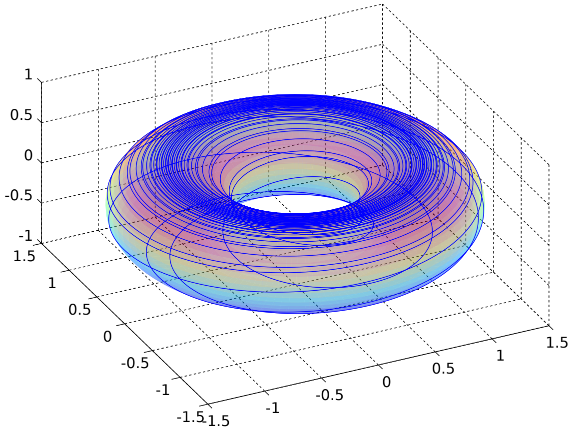

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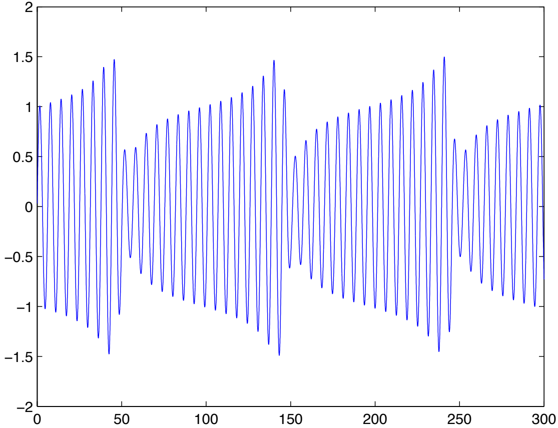

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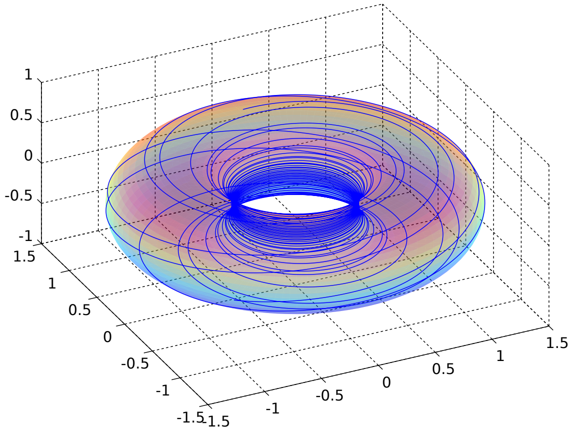

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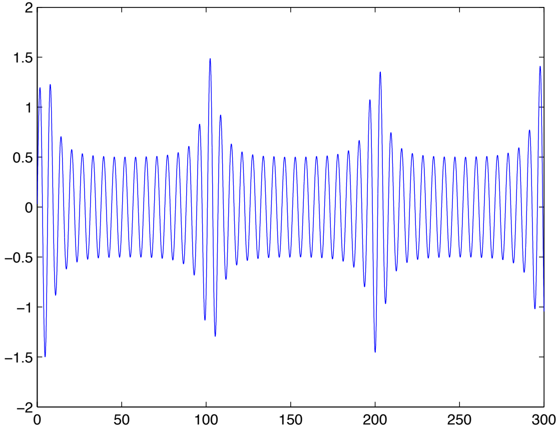

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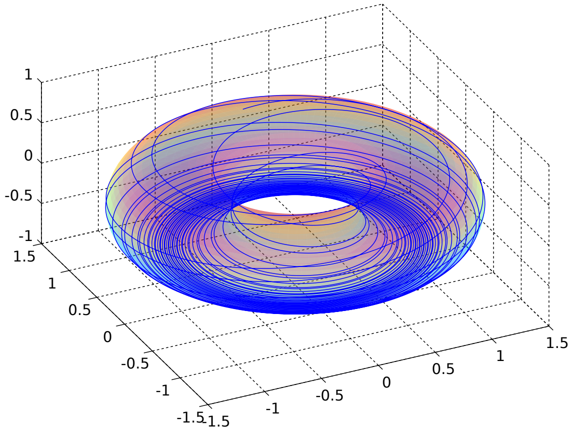

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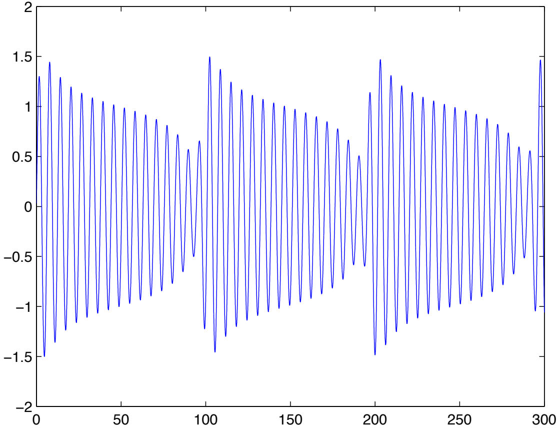


Figure: Various types of quasiperiodic bursting, depending on the locus of cycle ruins in relation to the torus.

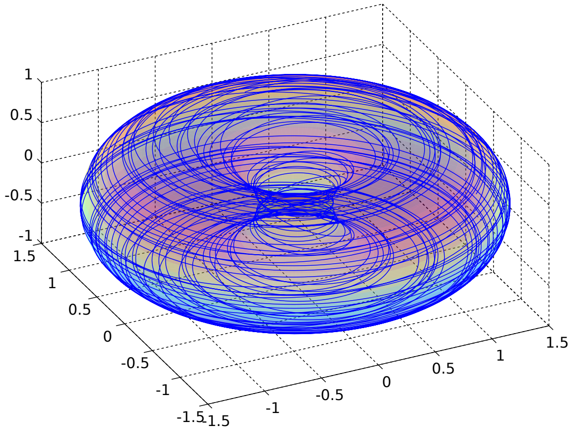


Figure: Trajectories on a torus may become very complex for non autonomous systems...

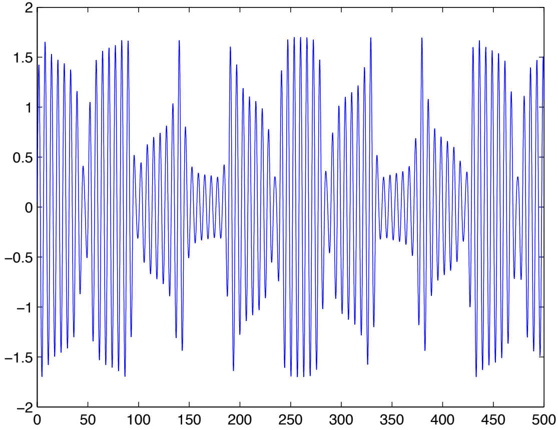


Figure: Trajectories on a torus may become very complex for non autonomous systems...

Lorenz Attractor

The famous Lorenz Attractor

$$\frac{dx}{dt} = \sigma(y - x)$$
$$\frac{dy}{dt} = x(\rho - z) - y$$
$$\frac{dz}{dt} = xy - \beta z$$

For parameters $\rho = 28, \sigma = 10, \beta = 8/3$ is actually a chaotic burster!

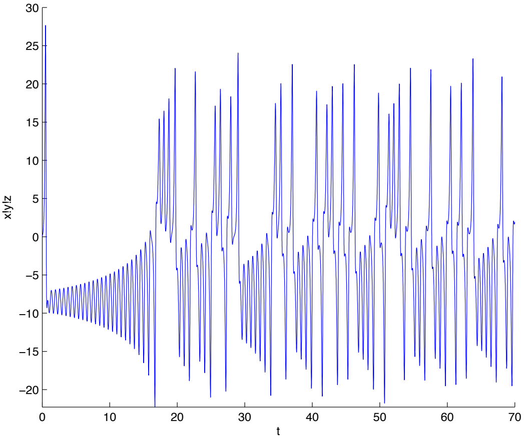


Figure: Chaotic bursting (Lorenz Attractor).

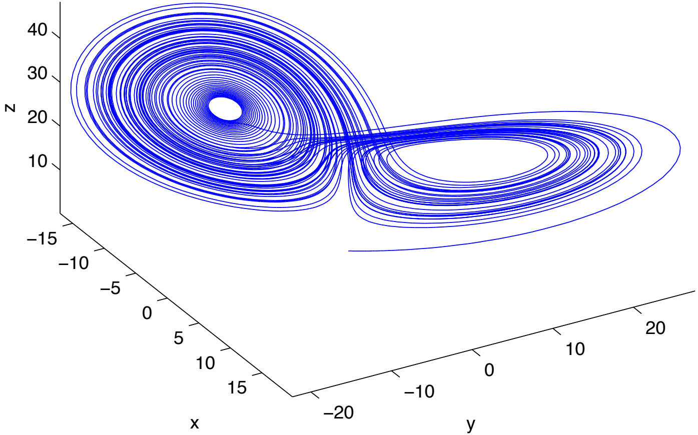


Figure: Chaotic bursting (Lorenz Attractor).

But chaotic bursting does not have to look so "chaotic". In fact chaotic bursting may look very regular, though still the system may be "chaotic". The system:

$$\frac{dx}{dt} = x - \frac{x^3}{3} + I - \Re(u)$$
$$\frac{du}{dt} = 0.1\left(\frac{1}{1+e^{-5x}}(1-10i)u - \frac{u}{2}\right)$$

with $I = 0.75$ exhibits chaotic behavior near saddle homoclinic orbit bifurcation.

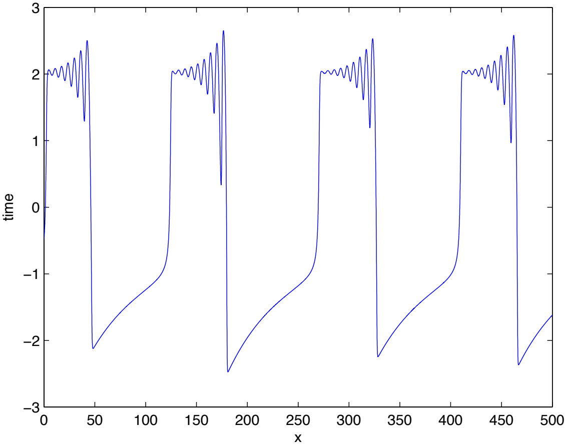


Figure: Chaotic bursting near saddle-focus homoclinic bifurcation.

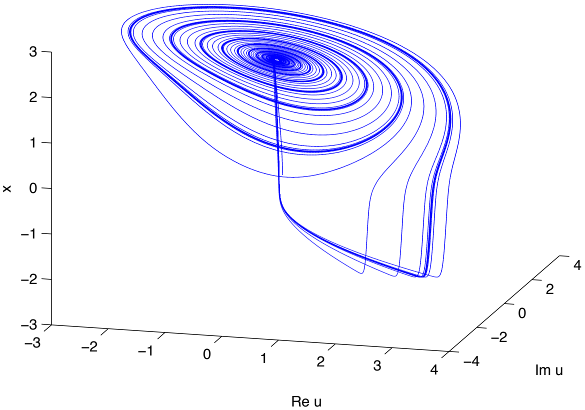


Figure: Chaotic bursting near saddle-focus homoclinic bifurcation.

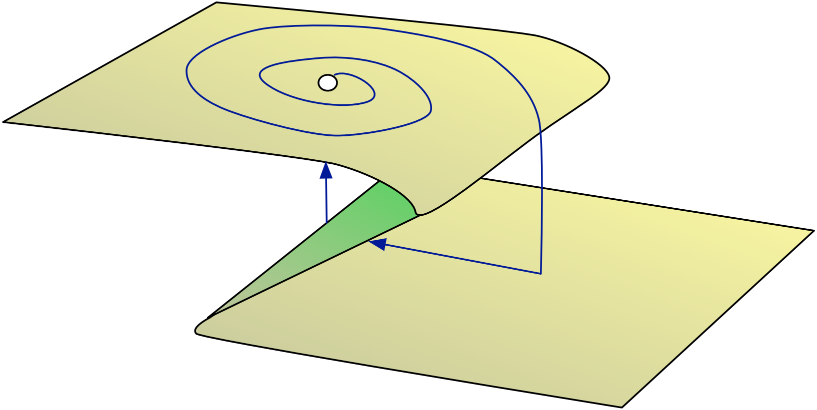


Figure: Chaotic bursting near saddle-focus homoclinic bifurcation.

Some neuronal bursters

- Lets get back to more "neuronal" bursters.
- Conductance based models impose severe conditions on the system, yet many neuronal bursters are possible.
- It is also usual that simple codimension one bifurcations in low dimensional systems are more probable to find in nature than complex high dimensional, high codimension examples
- We know there are 16 types of planar fast-slow bursters of "neuronal" type. Some of these bursters were observed in neuronal recordings, some remain "theoretical".

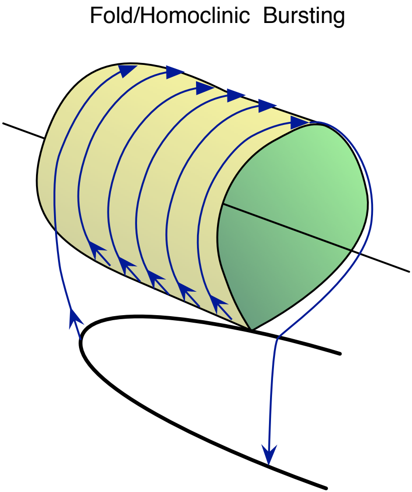


Figure: Fold-Homoclinic bursting diagram. The slow system may be one dimensional due to hysteresis loop..

Fold/Homoclinic burster - $I_{Na,p} + I_K + I_{K(M)}$ model

One can add a slow potassium current to the $I_{Na,p} + I_K$ model:

$$C_m \frac{dV}{dt} = I - g_L(V - E_L) - g_{Na} m_\infty(V)(V - E_{Na}) - g_K n(V - E_K) + \\ - g_{Kslow} n_{slow}(V - E_{Kslow})$$

$$\frac{dn}{dt} = (n_\infty(V) - n)/\tau_n(V)$$

$$\frac{dn_{slow}}{dt} = (n_{\infty slow}(V) - n_{slow})/\tau_{slow}(V)$$

With $C_m = 1$, $E_L = -80$, $\tau_n(V) = 0.152$ $g_L = 8$, $g_{Na} = 20$, $g_K = 9$, $g_{Kslow} = 5$, $E_{Na} = 60$, $E_K = -90$, $E_{Kslow} = -90$, $\tau_{slow}(V) = 20$, $m_\infty(V) = \frac{1}{1+e^{\frac{-20-V}{15}}}$, $n_\infty(V) = \frac{1}{1+e^{\frac{-25-V}{5}}}$, $n_{\infty slow}(V) = \frac{1}{1+e^{\frac{-20-V}{5}}}$

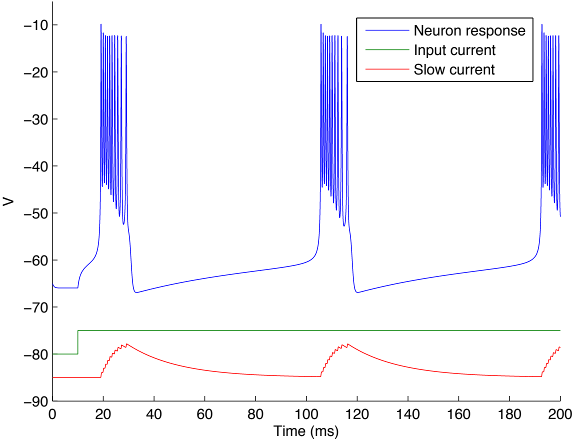


Figure: Fold-homoclinic burster via a hysteresis loop.

Canonical model of Fold/Homoclinic bursting

- Any fold/homoclinic burster via a continuous change of variables can be transformed into:

$$\frac{dv}{dt} = I + v^2 - u$$
$$\frac{du}{dt} = -\mu u$$

with after spike reseting $v \leftarrow 1$, $u \leftarrow u + d$ where I, d and $\mu << 1$ are parameters.

- Note how this model resembles the simple spiking model by Izhikevich. Therefore the bursting exhibited by the simple model is of the Fold/Homoclinic type.

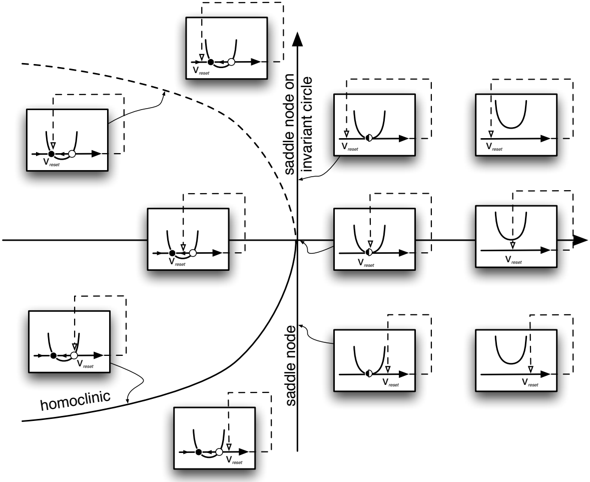


Figure: Saddle-node homoclinic orbit bifurcation diagram and corresponding canonical models with reset value.

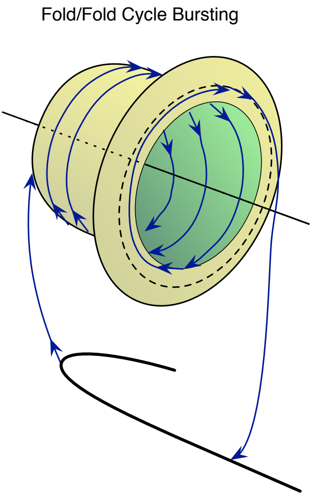


Figure: Fold/Fold Cycle bursting diagram.

Fold/Fold Cycle burster - Wilson-Cowan model

The Wilson-Cowan oscillator with a slow system (u) defined as:

$$\frac{dx}{dt} = -x + S((-4.76 + u) + ax - by)$$
$$\frac{dy}{dt} = -y + S((-9.7 + 0.3u) + cx - dy)$$
$$\frac{du}{dt} = 0.1(0.5 - x)$$

where

$$S(x) = \frac{1}{1 + e^{-x}}$$

and $a = 10$, $b = 10$, $c = 10$, $d = -2$ exhibits Fold/Fold Cycle bursting

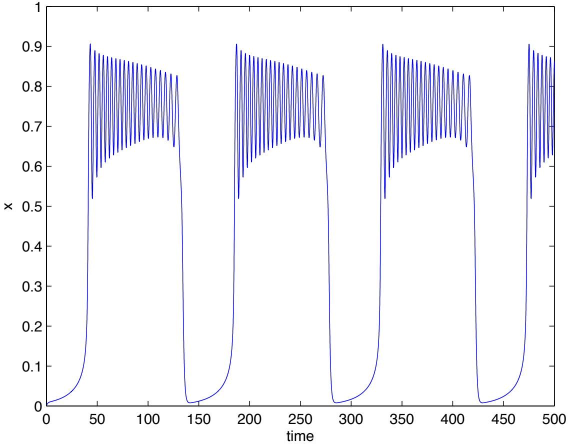


Figure: Fold/fold cycle burster in Wilson-Covan oscillator.

Circle/Circle burster - $I_{Na,p} + I_K +$ slow wave model

$$C_m \frac{dV}{dt} = I - g_L(V - E_L) - g_{Na} m_\infty(V)(V - E_{Na}) - g_K n(V - E_K) + \\ - g_{K\ slow} n_{slow}(V - E_{K\ slow}) - g_{Na\ slow} m_{slow}(V - E_{Na\ slow})$$

$$\frac{dn}{dt} = (n_\infty(V) - n)/\tau_n(V)$$

$$\frac{dn_{slow}}{dt} = (n_{\infty slow}(V) - n_{slow})/\tau_{K\ slow}(V)$$

$$\frac{dm_{slow}}{dt} = (m_{\infty slow}(V) - m_{slow})/\tau_{Na\ slow}(V)$$

With $I = 5$, $C_m = 1$, $E_L = -80$, $\tau_n(V) = 1$, $g_L = 8$, $g_{Na} = 20$, $g_K = 9$, $g_{K\ slow} = 20$, $E_{Na} = 60$, $E_K = -90$, $E_{K\ slow} = -90$, $E_{Na\ slow} = 60$, $g_{Na\ slow} = 3$, $\tau_{K\ slow}(V) = 20$, $\tau_{Na\ slow}(V) = 50$, $m_\infty(V) = \frac{1}{1+e^{\frac{-20-V}{15}}}$, $n_\infty(V) = \frac{1}{1+e^{\frac{-25-V}{5}}}$, $n_{\infty slow}(V) = \frac{1}{1+e^{\frac{-20-V}{5}}}$, $m_{\infty slow}(V) = \frac{1}{1+e^{\frac{-40-V}{5}}}$

Circle/Circle Bursting

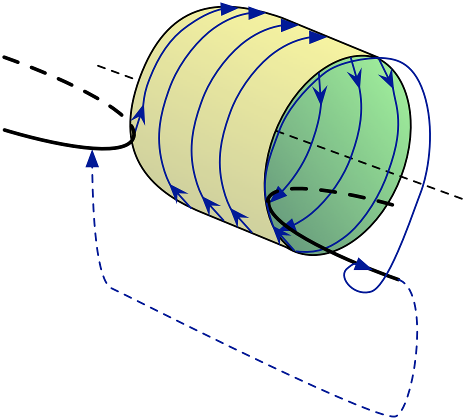


Figure: Circle-Circle bursting diagram.

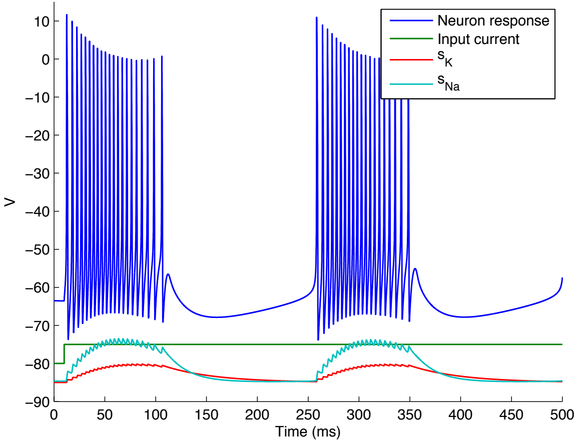


Figure: Circle-circle burster via a slow wave.

Note that the slow system:

$$\frac{dn_{\text{slow}}}{dt} = (n_{\infty\text{slow}}(V) - n_{\text{slow}})/\tau_{\text{K slow}}(V)$$
$$\frac{dm_{\text{slow}}}{dt} = (m_{\infty\text{slow}}(V) - m_{\text{slow}})/\tau_{\text{Na slow}}(V)$$

is uncoupled, so it cannot oscillate when $V = \text{const}$. So the slow wave is only possible when voltage changes! The slow system alone is worthless!

SubHopf/Fold Cycle Bursting

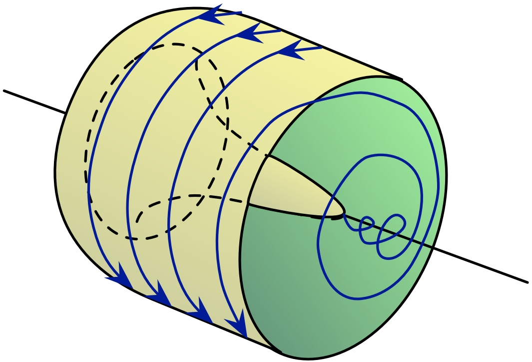


Figure: Subcritical Andronov-Fold Cycle bursting diagram. The slow system may be one dimensional due to hysteresis loop.

SubHopf/Fold Cycle burster - $I_{Na,p} + I_K + I_{K(M)}$ model

The $I_{Na,p} + I_K$ model:

$$C_m \frac{dV}{dt} = I - g_L(V - E_L) - g_{Na} m_\infty(V)(V - E_{Na}) - g_K n(V - E_K) + \\ - g_{Kslow} n_{slow}(V - E_{Kslow})$$

$$\frac{dn}{dt} = (n_\infty(V) - n)/\tau_n(V)$$

$$\frac{dn_{slow}}{dt} = (n_{\infty slow}(V) - n_{slow})/\tau_{slow}(V)$$

With $I = 55$, $C_m = 1$, $E_L = -78$, $\tau_n(V) = 1$ $g_L = 1$, $g_{Na} = 4$, $g_K = 4$, $g_{Kslow} = 1.5$, $E_{Na} = 60$, $E_K = -90$, $E_{Kslow} = -90$, $\tau_{slow}(V) = 60$, $m_\infty(V) = \frac{1}{1+e^{\frac{-30-V}{7}}}$, $n_\infty(V) = \frac{1}{1+e^{\frac{-45-V}{5}}}$, $n_{\infty slow}(V) = \frac{1}{1+e^{\frac{-20-V}{5}}}$ exhibits Subcritical Andronov-Hopf/Fold Cycle bursting

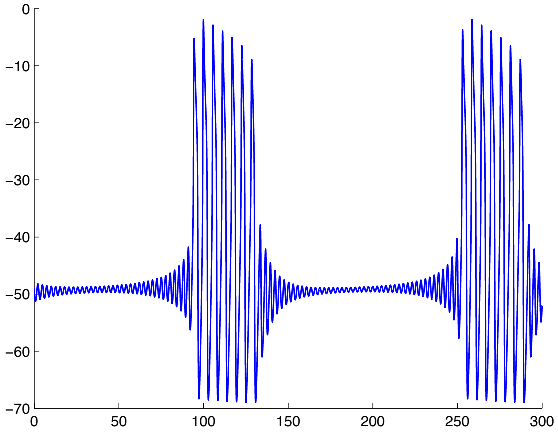


Figure: SubHopf - Fold Cycle burster via the hysteresis loop.

Synchronization of bursters

There are at least four ways in which two bursters may synchronize

- Spike (de)synchronization
- Burst (de)synchronization
- Burst and spike synchronization
- Burst synchronization, spike desynchronization

Depending on a type of bursters various synchrony regimes can be obtained by excitatory/inhibitory coupling.

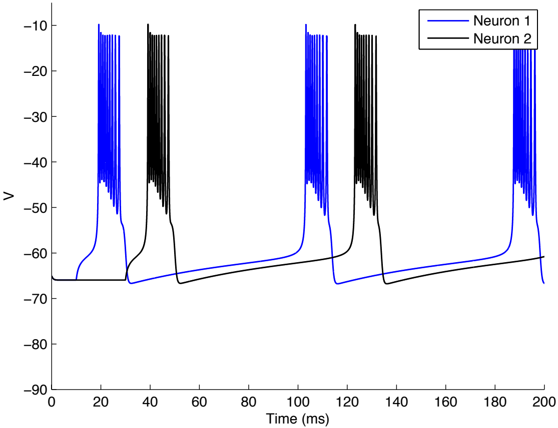
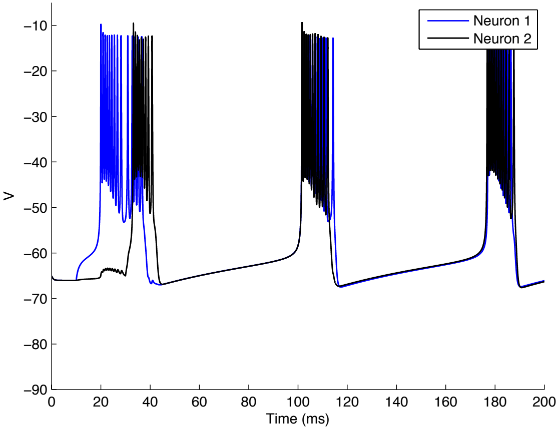


Figure: Uncoupled fold/homoclinic burster (first pic) and coupled via excitatory connection (second pic). Excitatory connection causes burst synchronization. Spikes are synchronized at the beginning of the burst, but then desynchronize.



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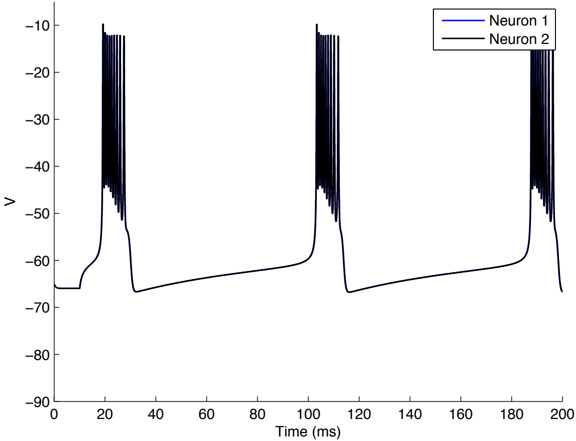
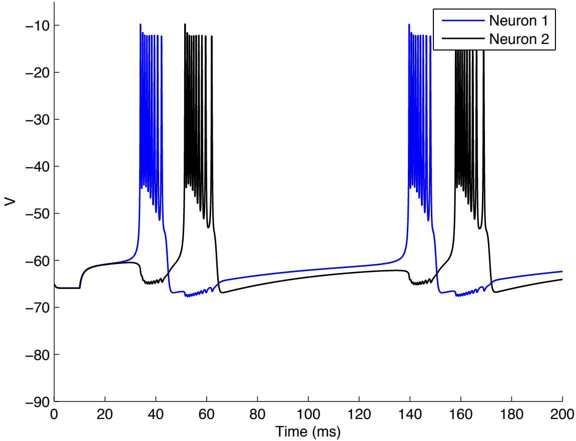


Figure: Uncoupled and synchronized fold/homoclinic burster (first pic) and coupled via inhibitory connection (second pic). Inhibitory connection causes burst desynchronization.



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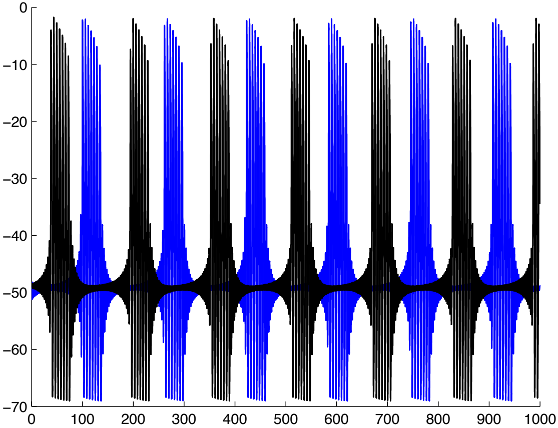
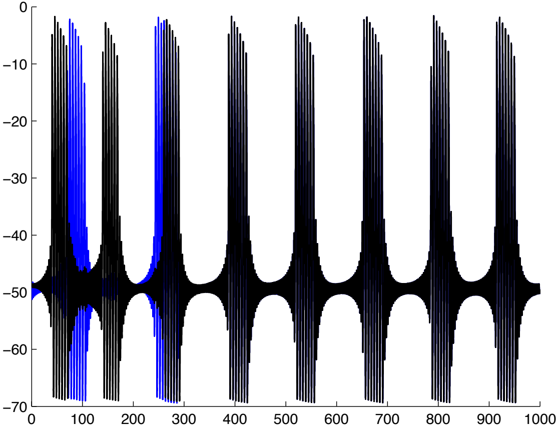


Figure: Uncoupled SubHopf/Fold Cycle burster (first pic), coupled via excitatory and inhibitory connections (second and third pic respectively). Both types of connections result in burst synchrony, but the latter desynchronizes spikes.



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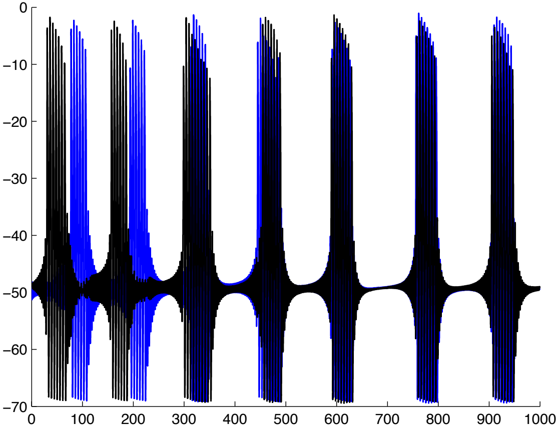

Figure: Uncoupled SubHopf/Fold Cycle burster (first pic), coupled via excitatory and inhibitory connections (second and third pic respectively). Both types of connections result in burst synchrony, but the latter desynchronizes spikes.

Recapitulation

- There are 16 planar fast-slow point-cycle bursters, 24 planar fast-slow bursters, 120 known 2d/3d fast slow bursters up to date
- Some bursters are not fast-slow type, but hedgehog type, blue sky or torus structure
- There are also chaotic bursters
- Bursters synchronize on various ways - spike sync, burst sync, etc. Depending on the burster type sign of coupling may result in one or the other synchronization regime.
- More on bursting can be found here: http://izhikevich.org/publications/nesb.htm