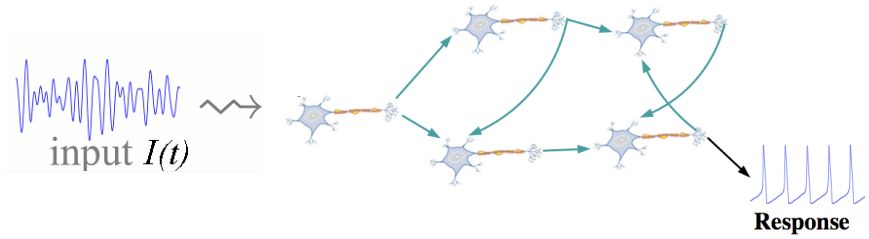
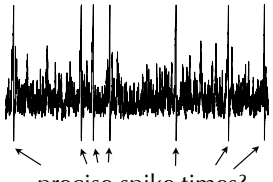
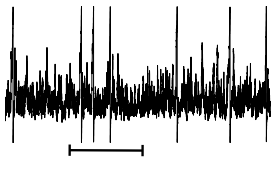
Thanks to Guillaume Lajoie for some of these slides!

Network response to input I(t)



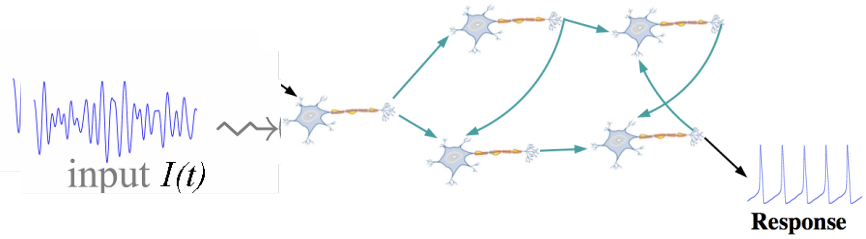
Where's the signal?


precise spike times?


"just" spike rate r(t)?

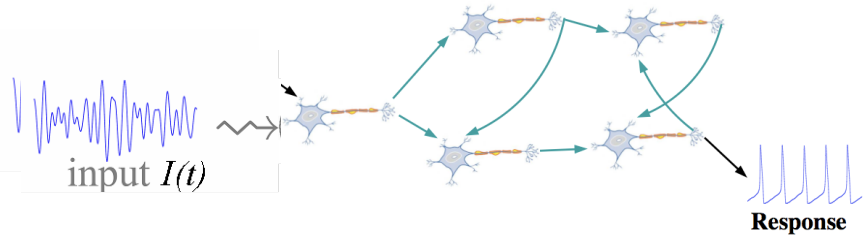
...or something in between?

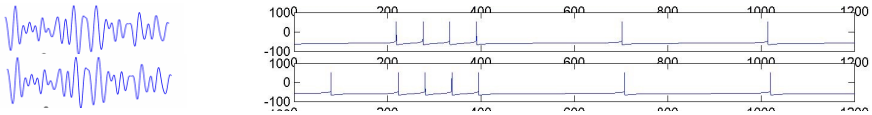
Are spike times repeatable from trial to trial?



Trial 1

Are spike times repeatable from trial to trial?

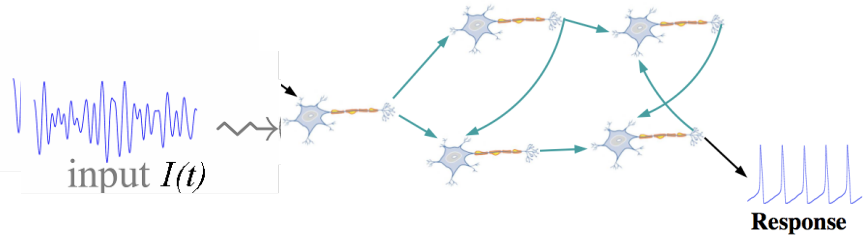


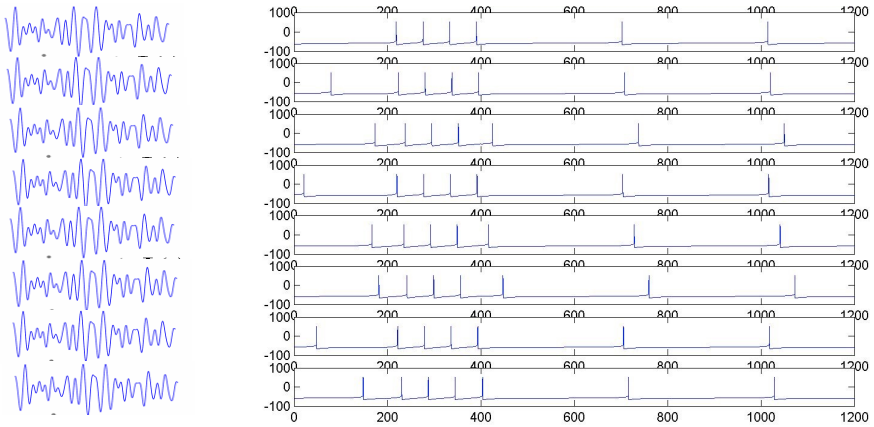


Trial 1

Trial 2

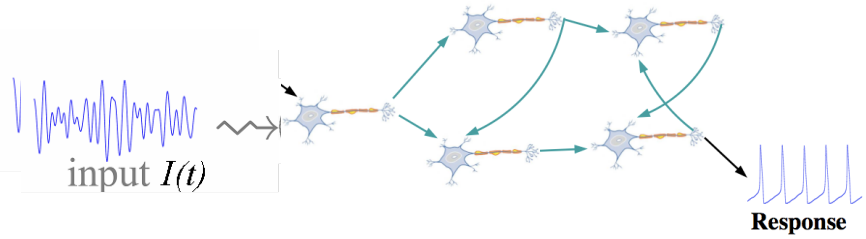
Are spike times repeatable from trial to trial?

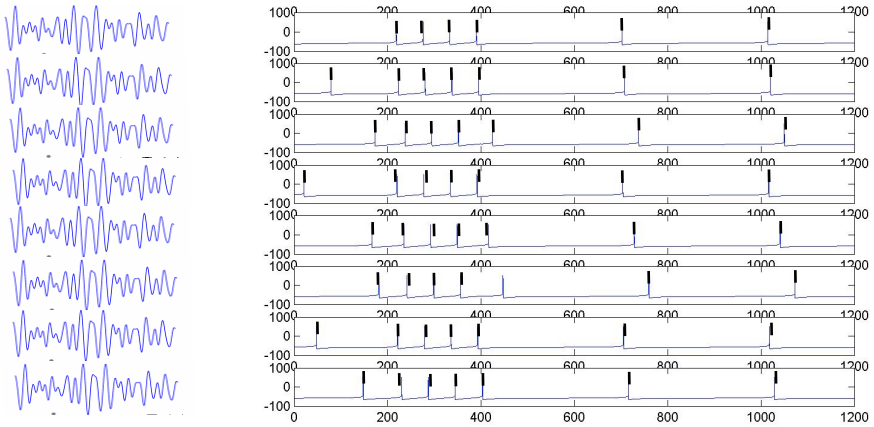




Trial 1
Trial 2
Trial 3
…

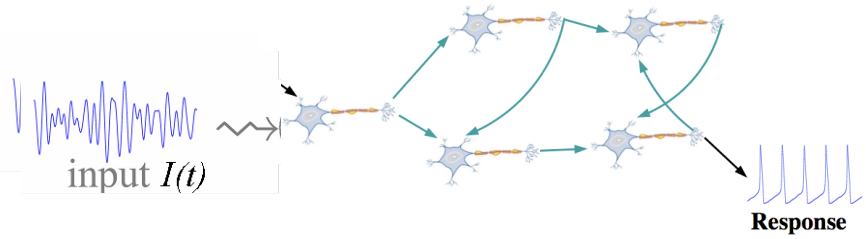
Are spike times repeatable from trial to trial?

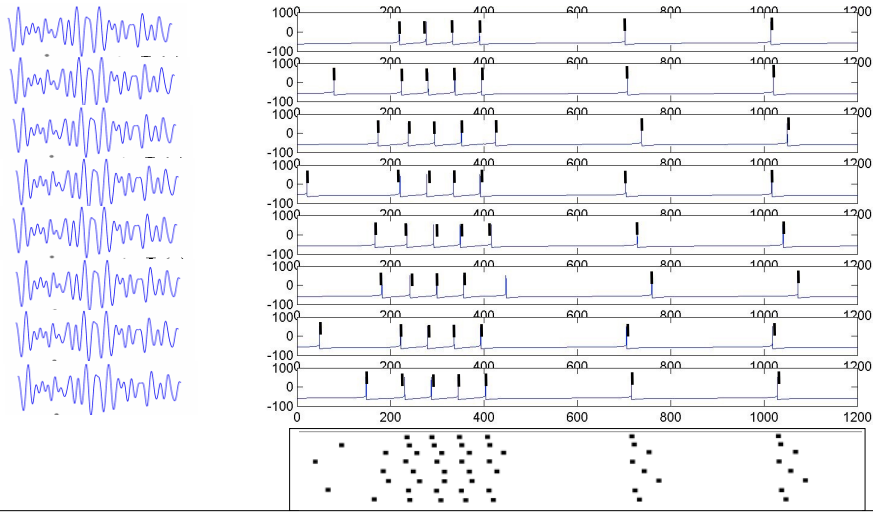




Trial 1
Trial 2
Trial 3
…

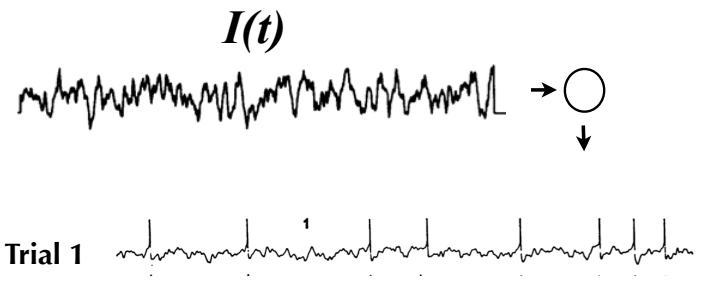
Are spike times repeatable from trial to trial?





- **What do we know from experiments?**

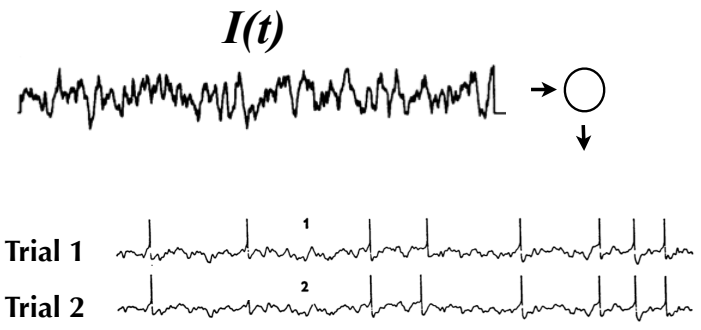
Are spike times **reliable** from trial to trial?



Focus on variability

from Bryant and Segundo, 1976

Are spike times **reliable** from trial to trial?



Focus on variability

from Bryant and Segundo, 1976

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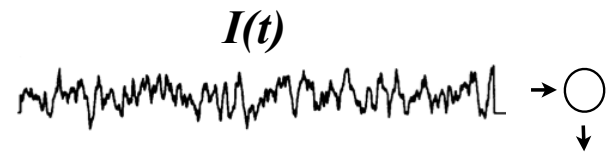
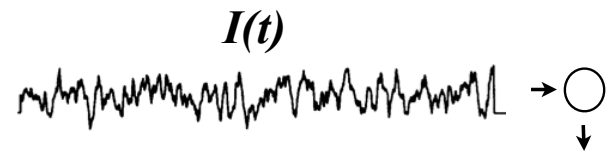
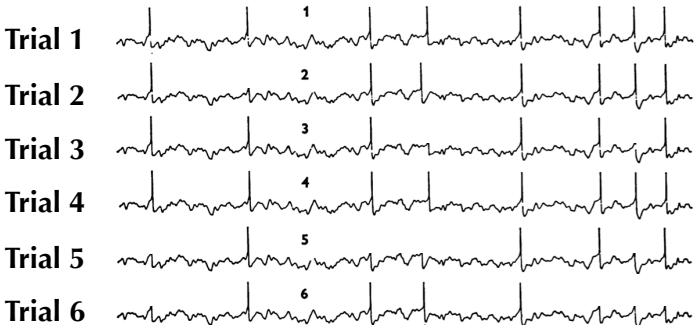


Focus on variability

from Bryant and Segundo, 1976

Are spike times **reliable** from trial to trial?





Focus on variability

from Bryant and Segundo, 1976

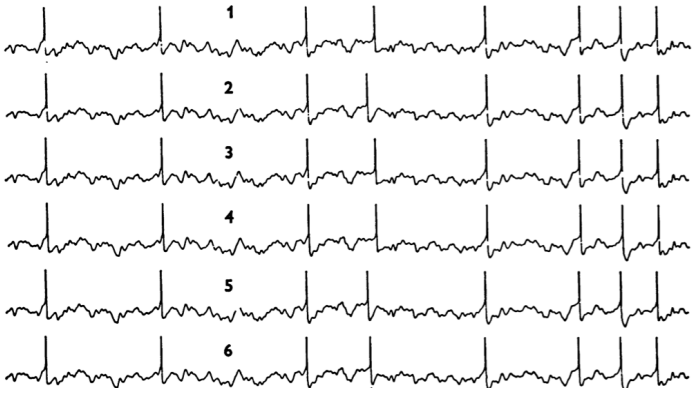
Are spike times **reliable** from trial to trial?

Experiments

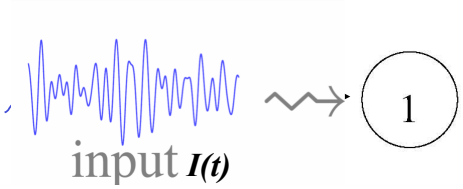
Bryant and Segundo, *1976*

Isolated cells are fairly reliable

(see also Mainen and Sejnowski, *1995*)



Experiments with an *isolated* cell



- Bryant H L, Segundo J P (1976). *J. Physiol.* 260: 279-314.
- Zachary F. Mainen* and Terrence J. Sejnowski

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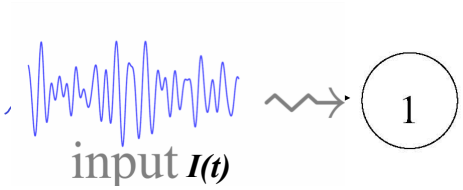
Experiments with an *isolated* cell



Bryant H L, Segundo J P (1976). *J. Physiol.* 260: 279-314.

Zachary F. Mainen* and Terrence J. Sejnowski

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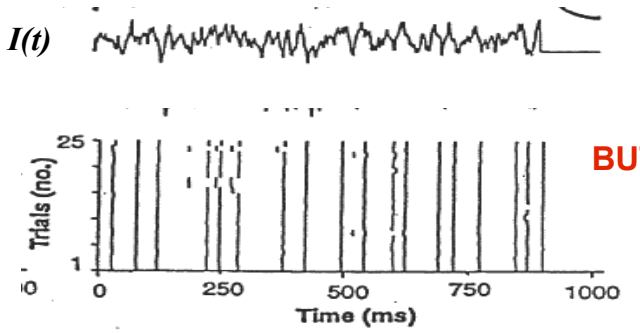
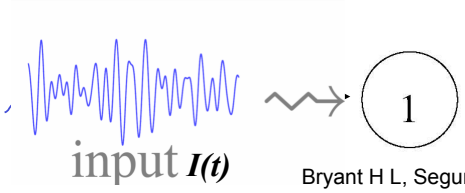


BUT more jitter at lower I(t) amplitudes

Experiments with an *isolated* cell

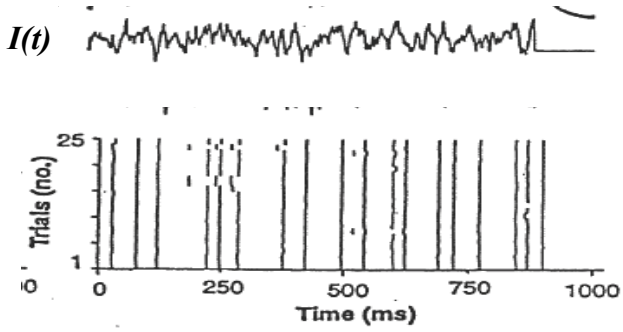


Bryant H L, Segundo J P (1976). *J. Physiol.* 260: 279-314.

Reliability of Spike Timing in Neocortical Neurons

Zachary F. Mainen* and Terrence J. Sejnowski

SCIENCE • VOL. 268 • 9 JUNE 1995

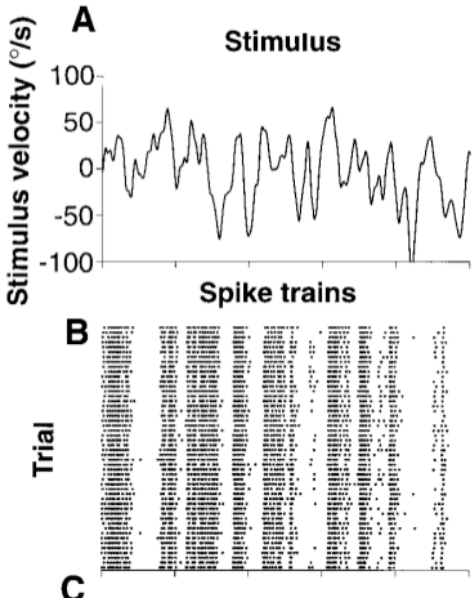


What about experiments with “intact” circuits

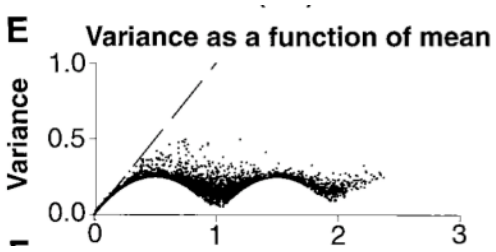
Reproducibility and Variability in Neural Spike Trains

Rob R. de Ruyter van Steveninck, Geoffrey D. Lewen,
Steven P. Strong,* Roland Koberle,† William Bialek

SCIENCE • VOL. 275 • 21 MARCH 1997



Visual stimulus → Fly



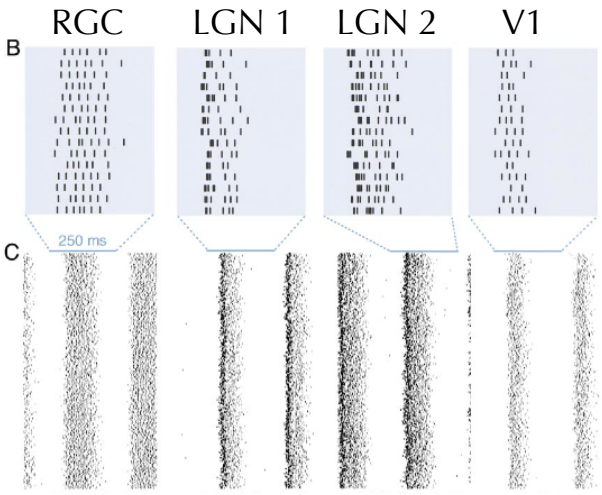
Are spike times **reliable** from trial to trial?

Experiments

Bryant and Segundo, *1976*

Kara, Reinagel and Reid, *2000*

Cat visual system
Reliability gradually degrades deeper into system



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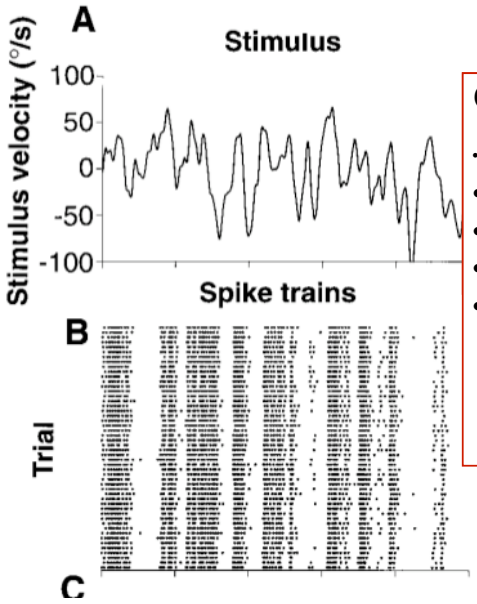


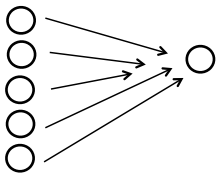
Other 'reliability' experiments…

· Rieke et al, *Spikes* (1997)
• Berry et al, PNAS (1997)
• Bair et al, J. Neurosci. (2001)
• Fellous et al, J. Neurosci. (2004)
• Murphy and Rieke, Neuron (2006)

OVERALL -- reliability to varying degrees

What's behind these results? Many factors limit reliability ...

- **(1) Trial-to-trial noise**
  - **Probabilistic synaptic release**

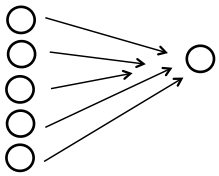


Average away over populations?

presynaptic pops

What's behind these results? Many factors limit reliability ...

- **(1) Trial-to-trial noise**
  - **Probabilistic synaptic release**



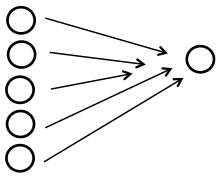
Average away over populations?

- **(2) Trial-to-trial adaptation of system dynamics**

Signal processing strategy?

What's behind these results? Many factors limit reliability ...

- **(1) Trial-to-trial noise**
  - **Probabilistic synaptic release**



Average away over populations?

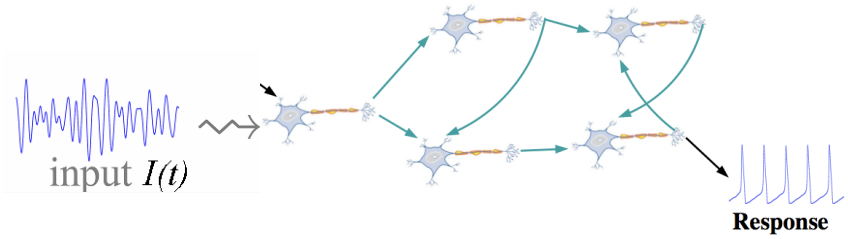
- **(2) Trial-to-trial adaptation of system dynamics**

Signal processing strategy?

- **(3) Trial-to-trial differences in system *initial state***

Our goal is to understand contribution of this factor ... eventually, must see how combines with others ...

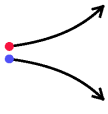
Study *initial condition* effects on reliability in networks



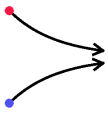
Framework: Lyapunov exponents for driven systems

λ: stability of "typical" trajectories

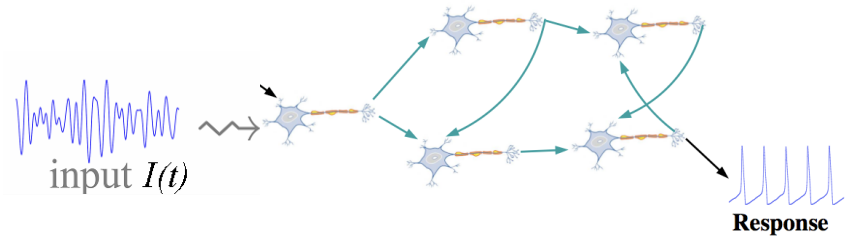
$\lambda > 0 \Rightarrow$ sensitive to initial conditions



$\lambda < 0 \Rightarrow$ insensitive to initial conditions



Preview



How to compute lyapunov exponents

Lyapunov exponents negative for most single neuron models

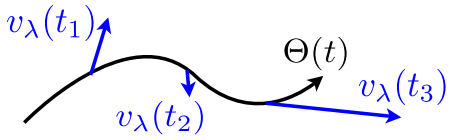
But can easily become positive in networks

Finding λ

Solve variational equation for a randomly chosen unit vector along a trajectory

$$\dot{v}_\lambda = J(t)v_\lambda$$

Jacobian along trajectory



$$\lambda = \lim_{t\to\infty} \frac{\log(\|v_\lambda(t)\|)}{t}$$

For a.e. choice of v_λ, find same $\lambda = \lambda_{max}$

- Have **DICHOTOMY**:

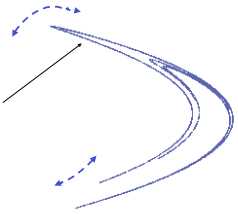
- **Theorem [Le Jan].** If $\lambda_{max} < 0$, then trajectories → random fixed point

All trajectories "collapse"

"Asymptotic reliabilty"

- **Theorem [Ledrappier-Young].** If $\lambda_{max} > 0$, then trajectories → random strange attractor

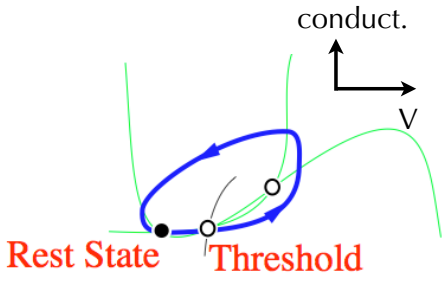
different trajectories=
different initial conditions
(different 'trials')

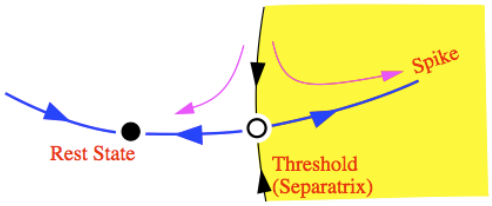


Study *initial condition* effects on reliability in networks

- **First, need single-cell model**

Quadratic Int. + Fire ("Theta") Neuron



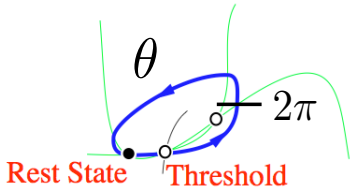


$$\tau \frac{dv}{dt} = \frac{(v - v_R)(v - v_T)}{\Delta v} + \eta$$

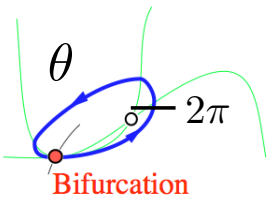
... + reset

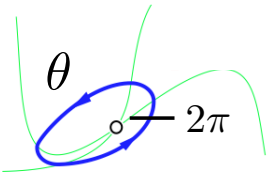
From: Izhikevich, *Int J Bif and Chaos, 2000*

Quadratic Int. + Fire ("Theta") Neuron

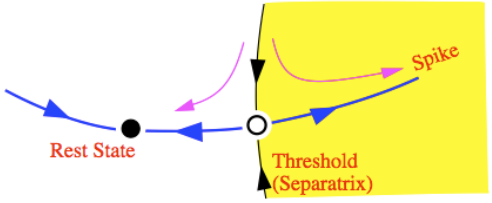


"fluctuation driven"
$\eta < \bar{\eta}$





"mean-driven"
$\eta > \bar{\eta}$



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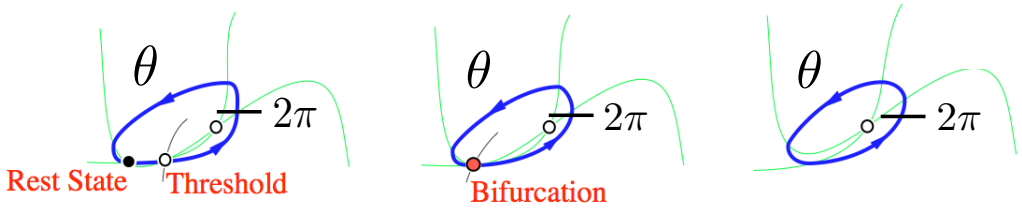
... + reset

From: Izhikevich, *Int J Bif and Chaos, 2000*

Quadratic Int. + Fire ("Theta") Neuron



"fluctuation driven"
$\eta < 0$

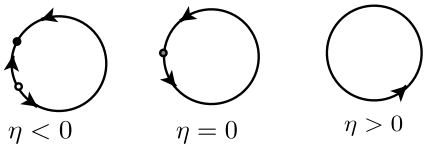
"mean-driven"
$\eta > 0$

(Theta-neuron) **coordinate change**

Ermentrout Neural Comp 1998

$$\dot{\theta} = 1 + cos(2\pi\theta) + \eta(1 - cos(2\pi\theta))$$

$$\theta \in S^1 = \mathbb{R}/\mathbb{Z}$$



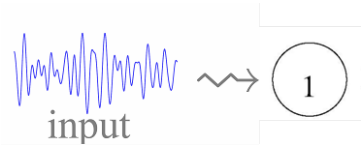
$\eta < 0$ excitable

$\eta = 0$ saddle-node bifurcation

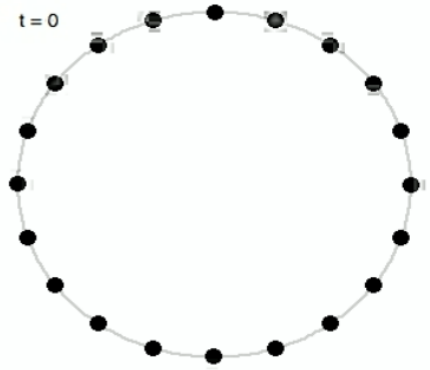
$\eta > 0$ oscillatory

– **Ritt, `03**
– **Pakdaman, `02-`04**
– **Lin, S-B, Young '09 -- Jensen's ineq.**

λ<0 for isolated (phase model) cells



So, "reliable" spiking data is expected:



– Ritt, `03
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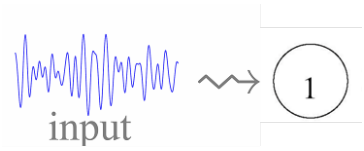

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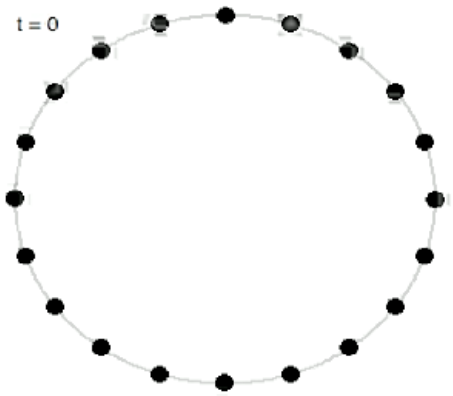
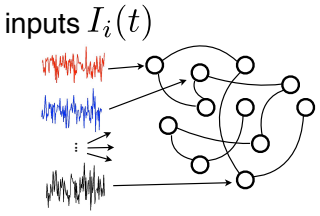


OUTLINE:

- Intro: Lyapunov exponents and reliability
- (1) Single cells are reliable
- NEXT UP...
- (2) Feedforward networks

Network model

Network of N neurons

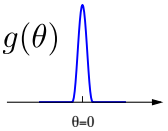


$$\dot{\theta}_i = 1 + \cos 2\pi\theta_i + (1 - \cos 2\pi\theta_i)[\sum_{j=1}^{N} a_{ij} g(\theta_j) + I_i(t)]$$

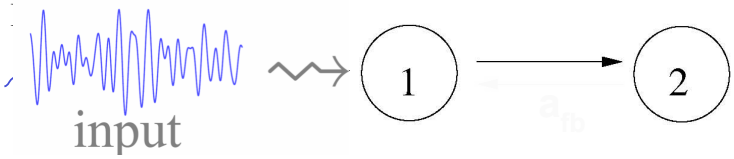
network interactions

$A = \{a_{ij}\}$: coupling matrix

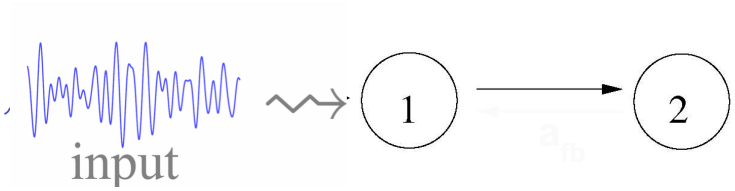
$g(\theta)$: synaptic coupling function with small support centered at 0



A simple feedforward circuit



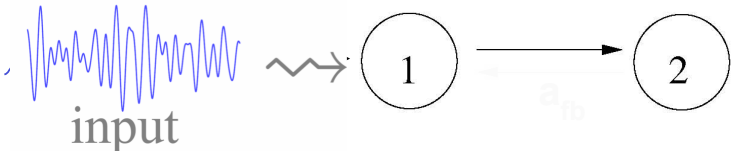
A simple feedforward circuit



λ = **-0.25**

Random fixed point

A simple feedforward circuit



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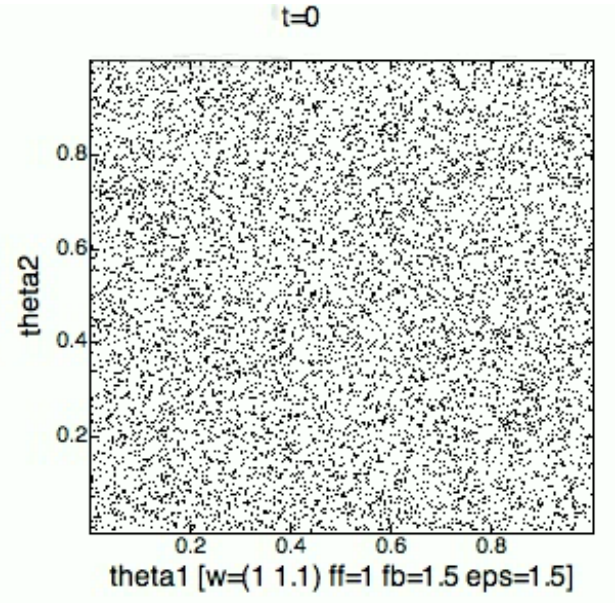
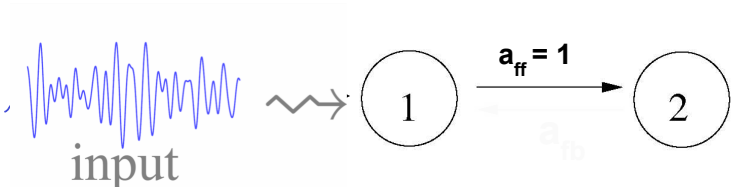


A simple feedforward circuit



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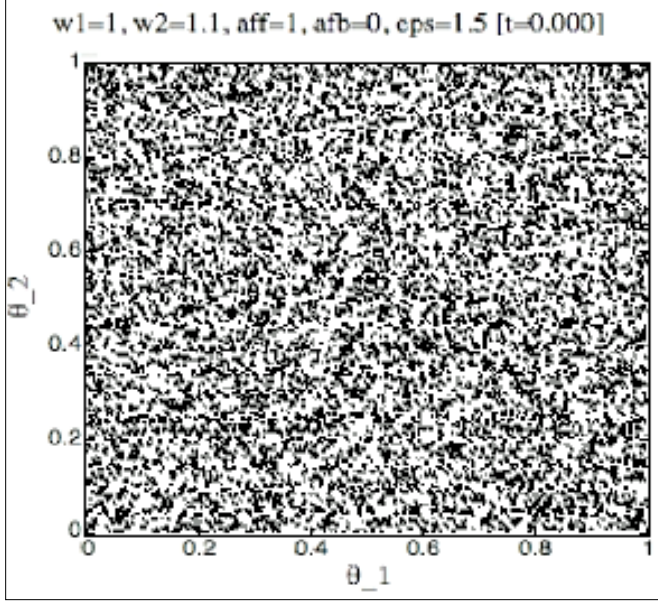
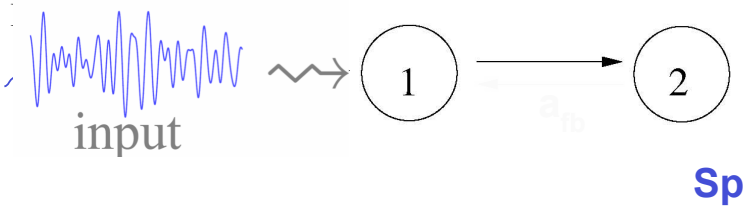


A simple feedforward circuit



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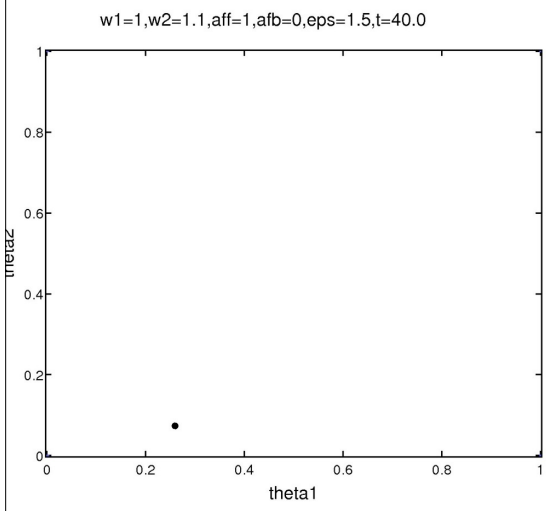
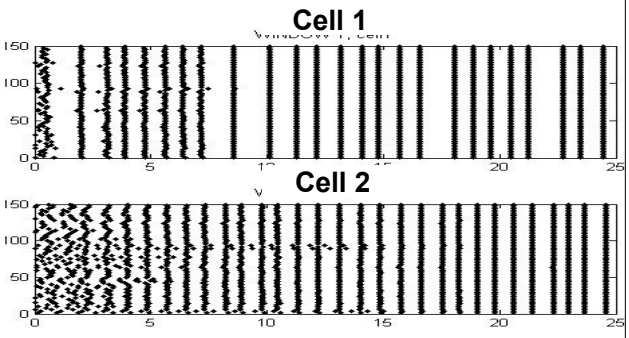
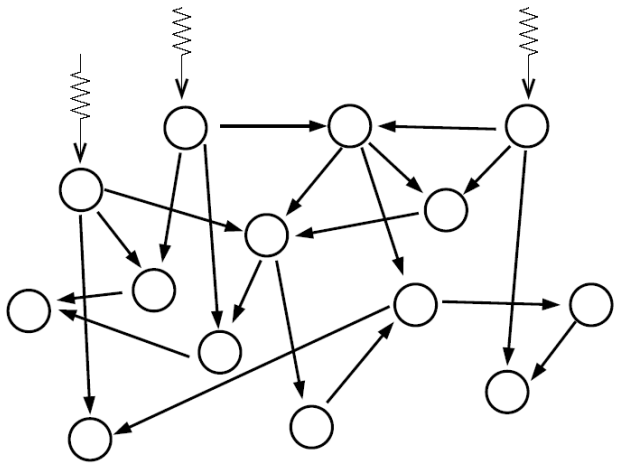
Spike rasters





Generalize → larger networks

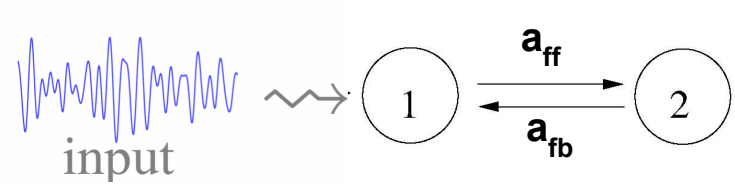
Acyclic feedforward networks are never unreliable ($\lambda_{max} \leq 0$)



OUTLINE

- **Lyapunov exponents and asymptotic reliability**
- **(1) Single cells are reliable**
- **(2) So are acyclic networks**
- **NEXT UP ...**
- **(3) Feedback, unreliability, and chaos**

Feedback from a second cell produces unreliabilty



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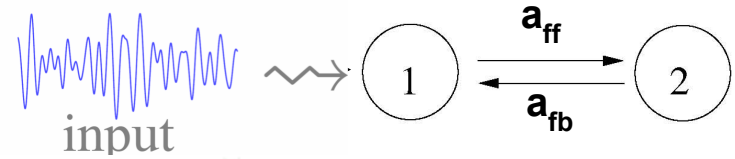
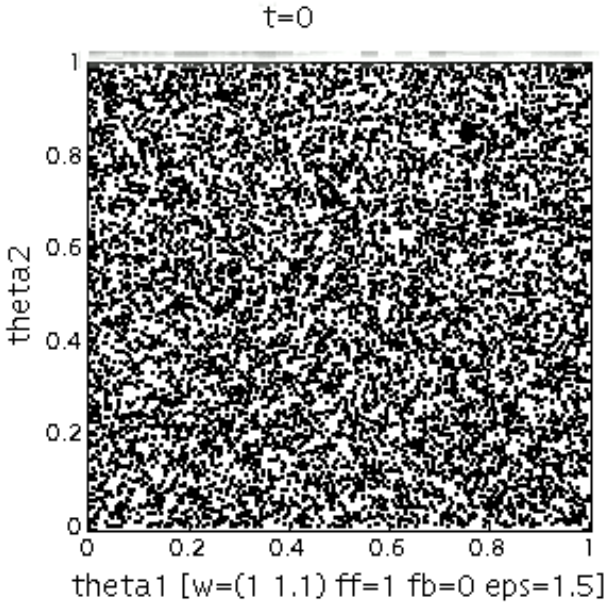


λ = **+0.125**

Random strange attractor



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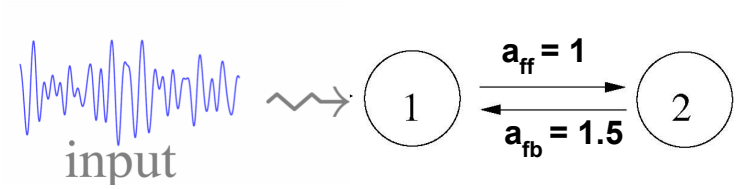

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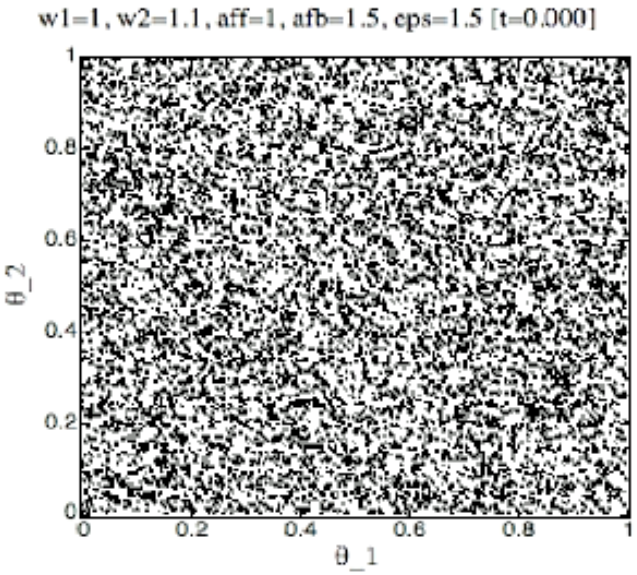

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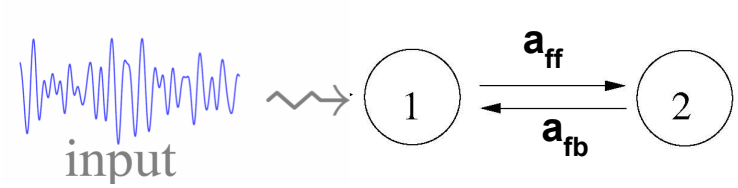

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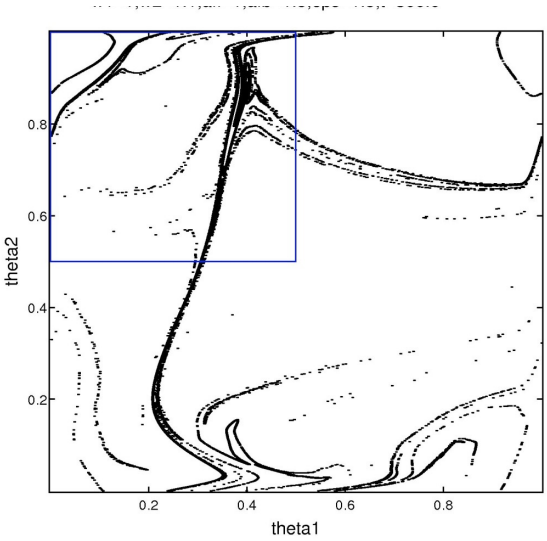
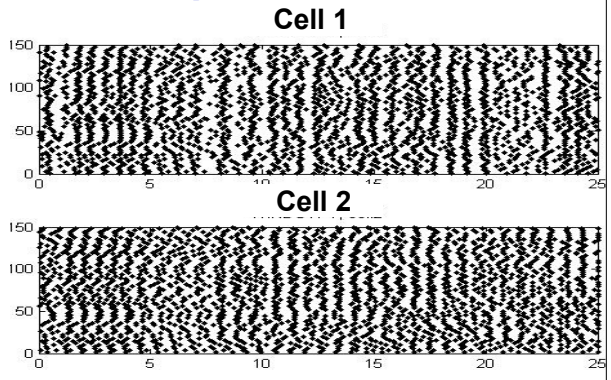
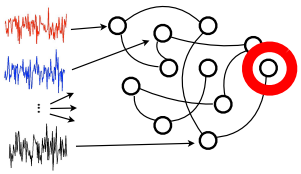
Spike rasters

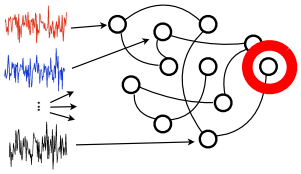






Finally, consider a LARGE network with ~10^3 neurons.

Results: Spike output



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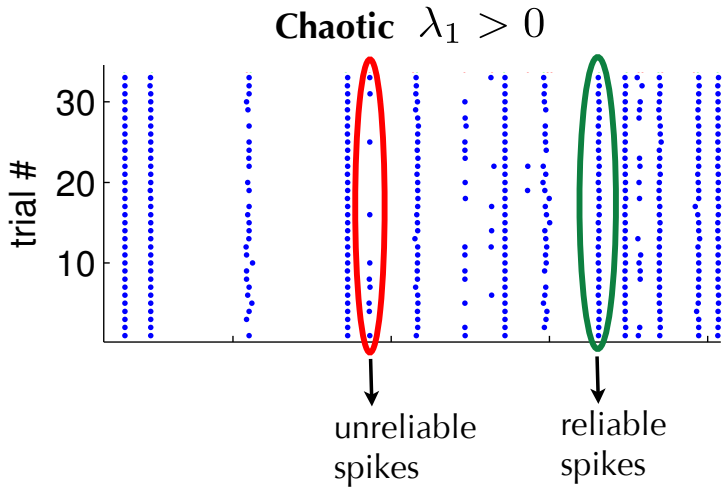
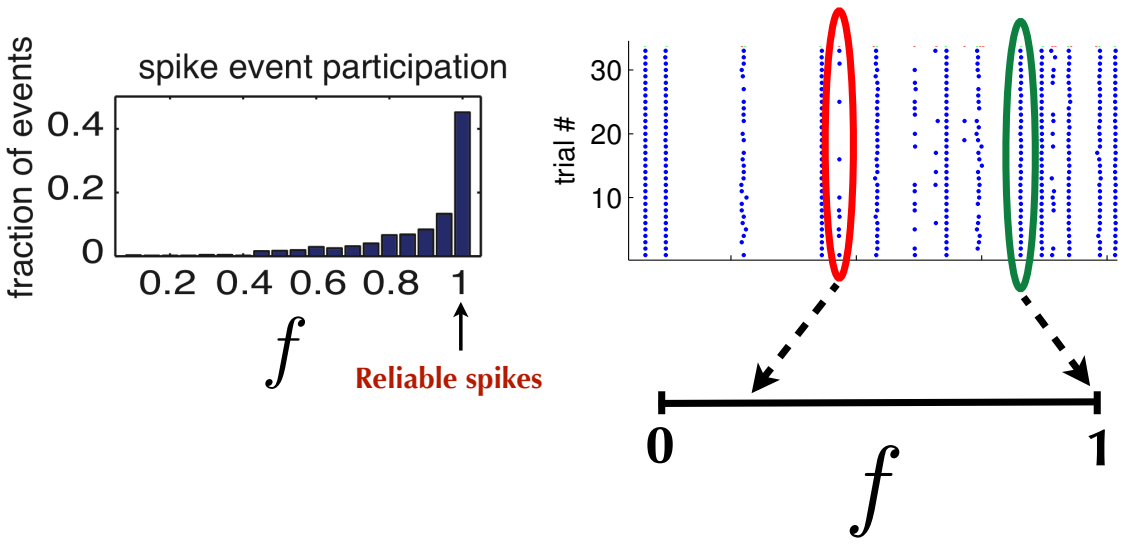


… but see reliable spikes anyway!

Results: Quantifying spike-time reliability



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