Spiking Neurons and Noise

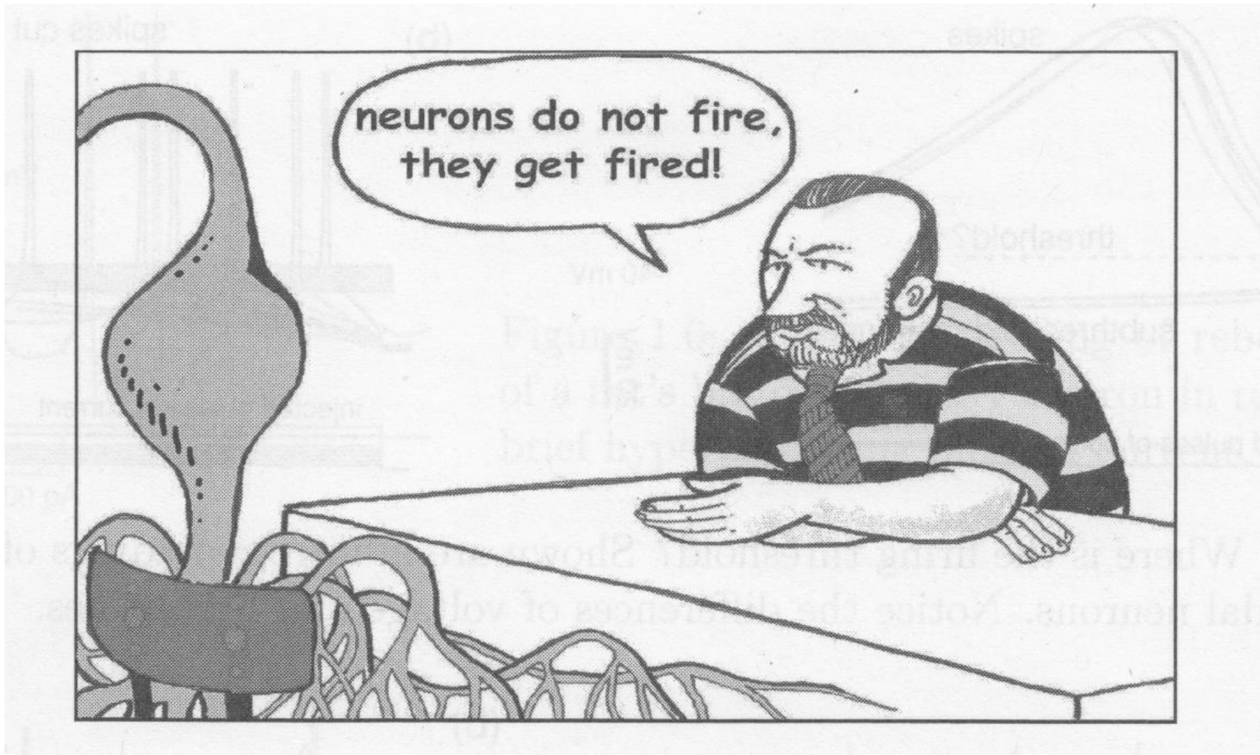

Figure 1.2: What makes a neuron fire? *

Jonathan Tapson
Department of Electrical Engineering
University of Cape Town

* E.M. Izhikevich, *Dynamical Systems in Neuroscience* (2007)

Thanks to:

Ralph Etienne-Cummings
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Mark Vismer

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The National Research Foundation, SA
The University of Sydney
The Institute for Neuromorphic Engineering

Last year…

- Marginalize to eliminate primary Markov property:

$$q_{t_2-t_1}(\tau) = \{\text{Prob that first and second spikes after } t_0 \text{ are separated by } \tau\}$$

$$= \int_{t_0}^{\infty} \prod_{k=1}^{2} \rho_{LP}\left(t_k - t_{k-1} \middle| t_{k-1}\right) dt_1 \text{ for } \mathbf{t} = [t_1, t_1 + \tau]$$

$$= \int_{t_0}^{\infty} \rho_{LP}\left(t_1 + \tau \middle| t_1\right) \rho_{LP}\left(t_1 \middle| t_0\right) dt_1$$

$$= \int_{t_0}^{\infty} \rho(\tau) \rho(t_1 - t_0)(1 + wg(t_1 + \tau))(1 + wg(t_1)) dt_1$$

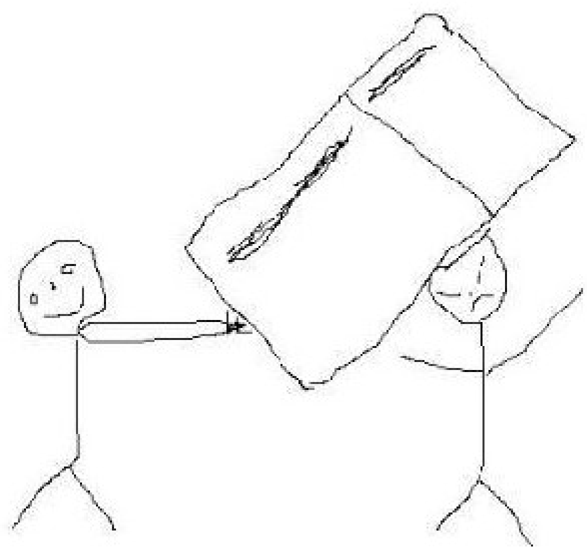
$$= \int_{t_0}^{\infty} \rho(\tau) \rho(t_1 - t_0) dt_1 + w \int_{t_0}^{\infty} \rho(\tau) \rho(t_1 - t_0) g(t_1 + \tau) dt_1$$

$$+ w \int_{t_0}^{\infty} \rho(\tau) \rho(t_1 - t_0) g(t_1) dt_1 + w^2 \int_{t_0}^{\infty} \rho(\tau) \rho(t_1 - t_0) g(t_1 + \tau) g(t_1) dt_1$$

$$q_{t_2-t_1}(\tau) = \rho(\tau) + w^2 \rho(\tau) \int_{t_0}^{\infty} g(t_1 + \tau) g(t_1) dt_1$$

$$= \rho(\tau)\left(1 + w^2 R_{gg}(\tau)\right)$$

This year…



Framework

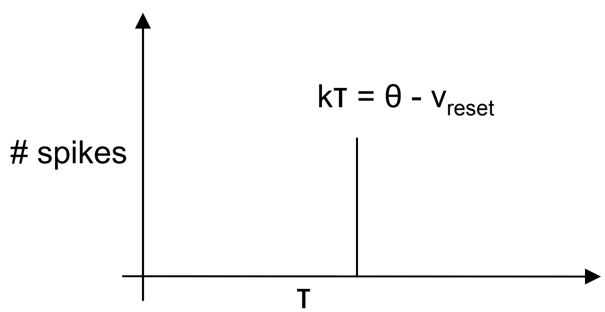
- Build a picture of spiking behavior from the ground up
- Develop a model of input-output functional relationships
- Exploit this relationship in a useful circuit

The simplest possible model

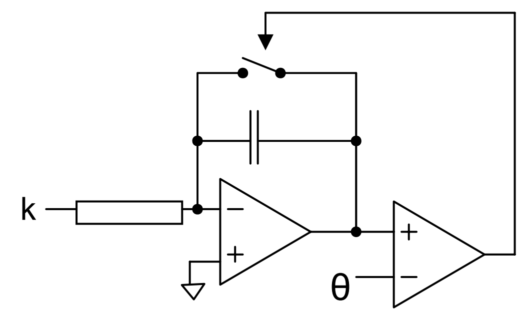
- Integrate and fire, no stimulus, no noise:

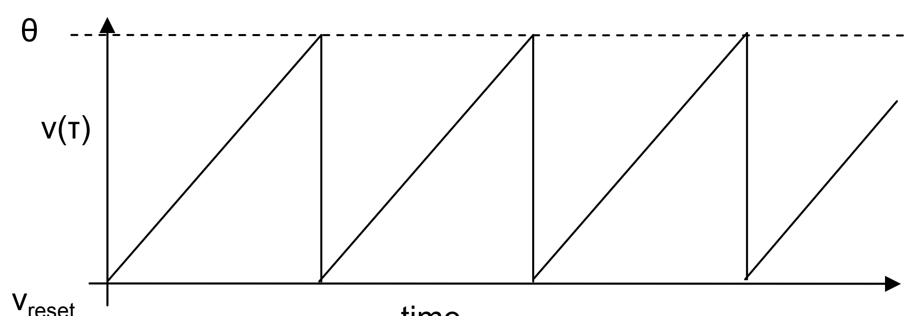
$$v(\tau) = \int_{t_0}^{t_0+\tau} k \, dt$$

$$v(\tau) > \theta : v(\tau) \leftarrow v_{reset}$$



ISIH



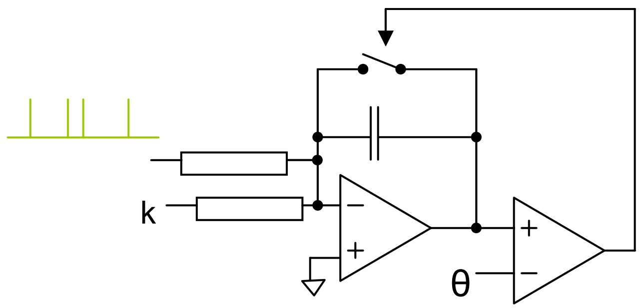


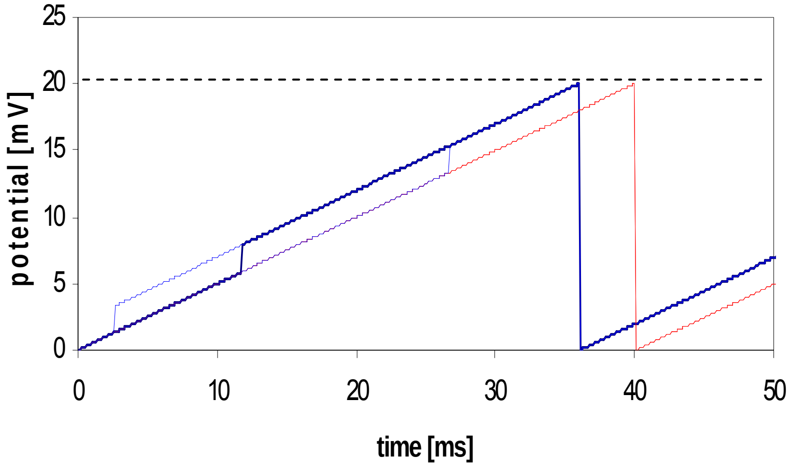
Add a stimulus

- Excitatory synaptic input spikes of constant amplitude *a* at random times *i*:

$$v(\tau) = \int_{t_0}^{t_0+\tau} k + a\delta(t - t_i)\, dt$$

$$v(\tau) > \theta : v(\tau) \leftarrow v_{reset}$$



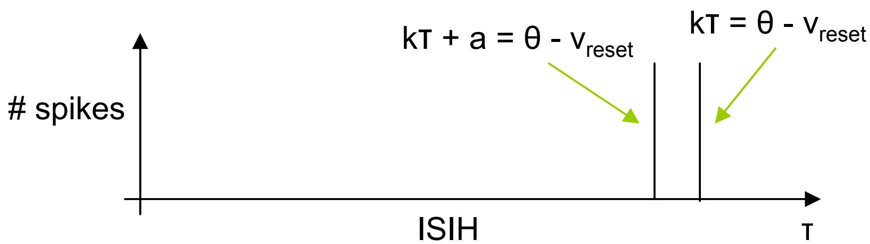


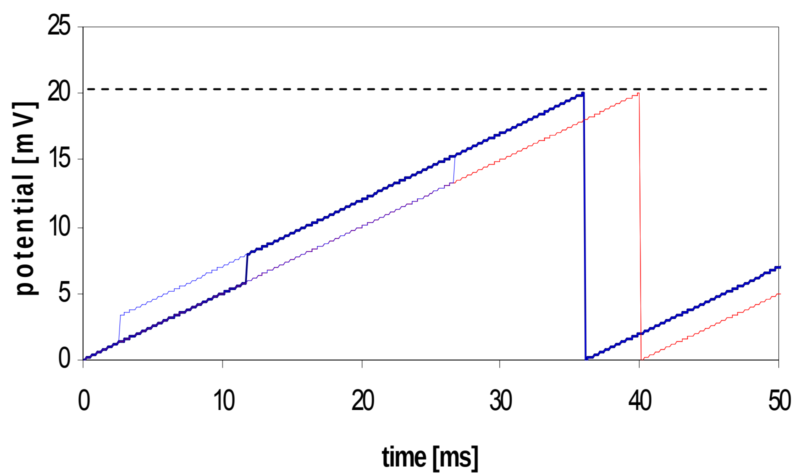
Add a stimulus

- Excitatory synaptic input spikes of constant energy *a* at random times *i*:

$$v(\tau) = \int_{t_0}^{t_0+\tau} k + a\delta(t - t_i)\, dt$$

$$v(\tau) > \theta : v(\tau) \leftarrow v_{reset}$$

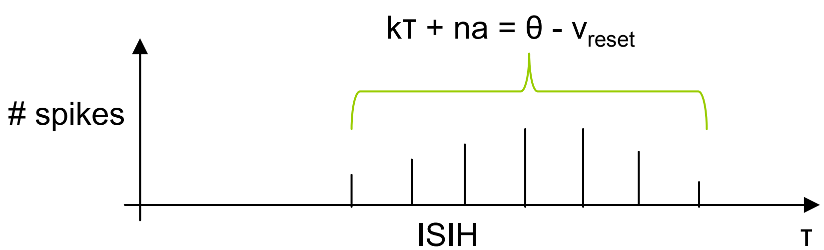


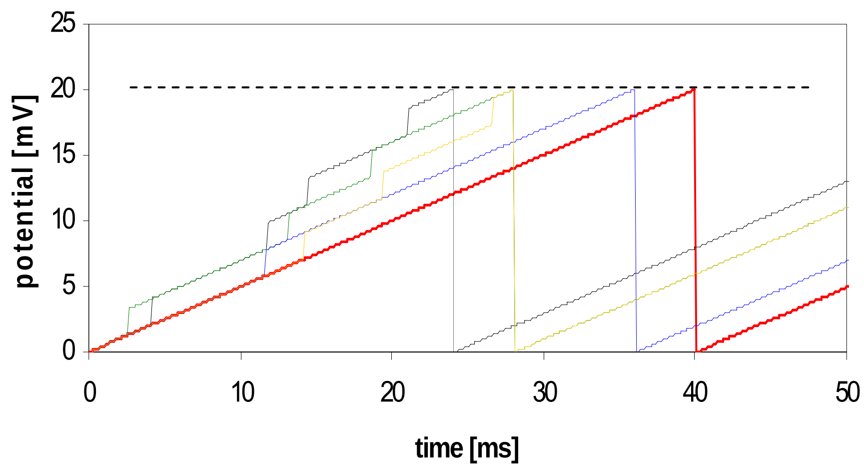


More spikes

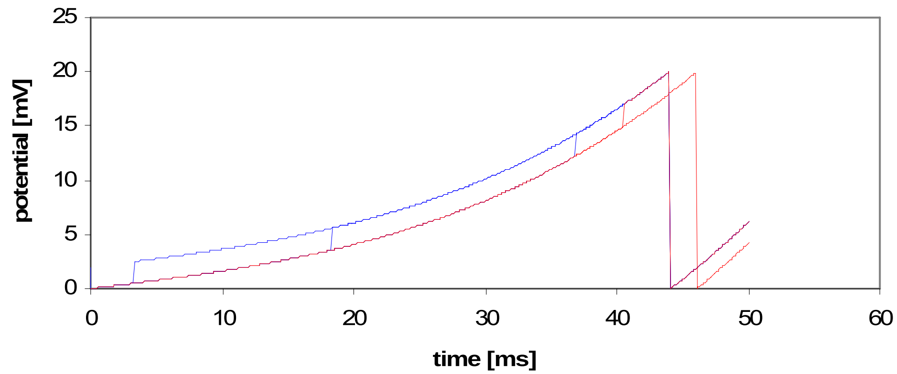
$$v(\tau) = \int_{t_0}^{t_0+\tau} k + a\delta(t - t_i)\, dt$$

$$v(\tau) > \theta : v(\tau) \leftarrow v_{reset}$$



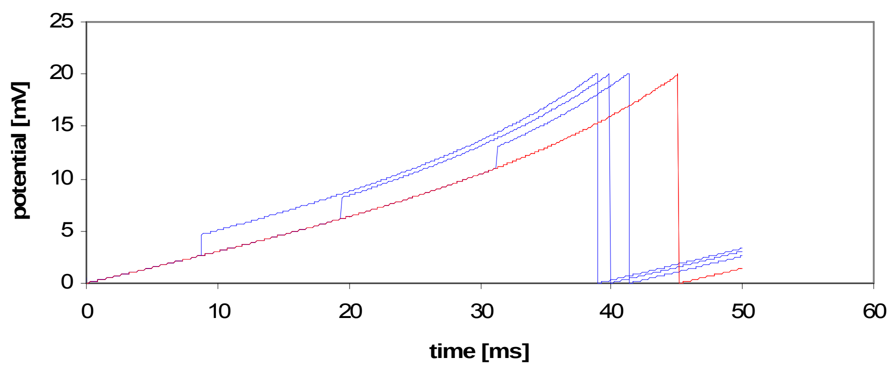


Effect of nonlinearities



Nonlinear in time

$$v(\tau) = \int_{t_0}^{t_0+\tau} k + b\tau + a\delta(t - t_i)\, dt$$



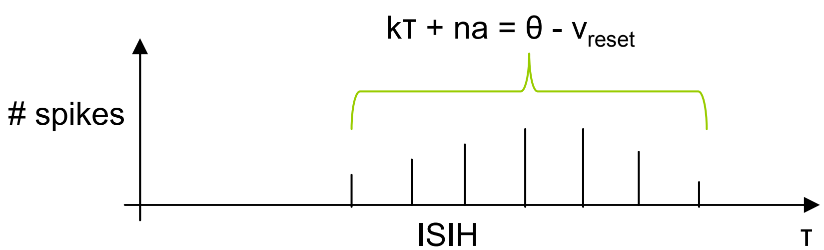
Nonlinear in amplitude

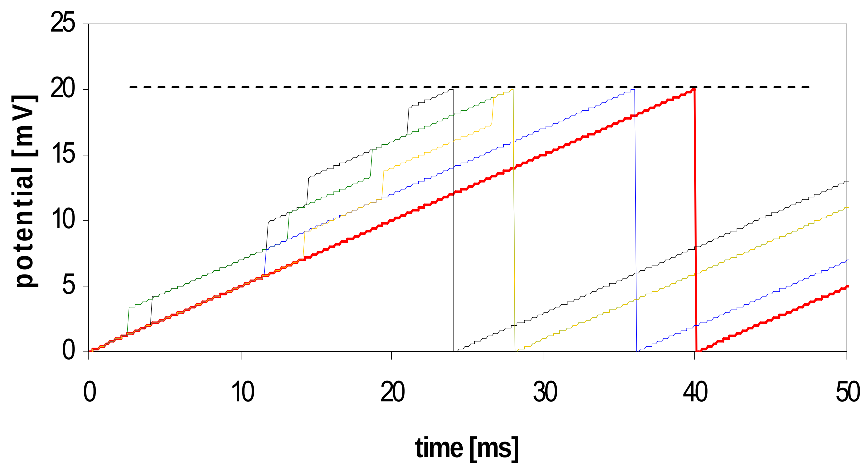
$$v(\tau) = \int_{t_0}^{t_0+\tau} k + bv + a\delta(t - t_i)\, dt$$

The cartoon…

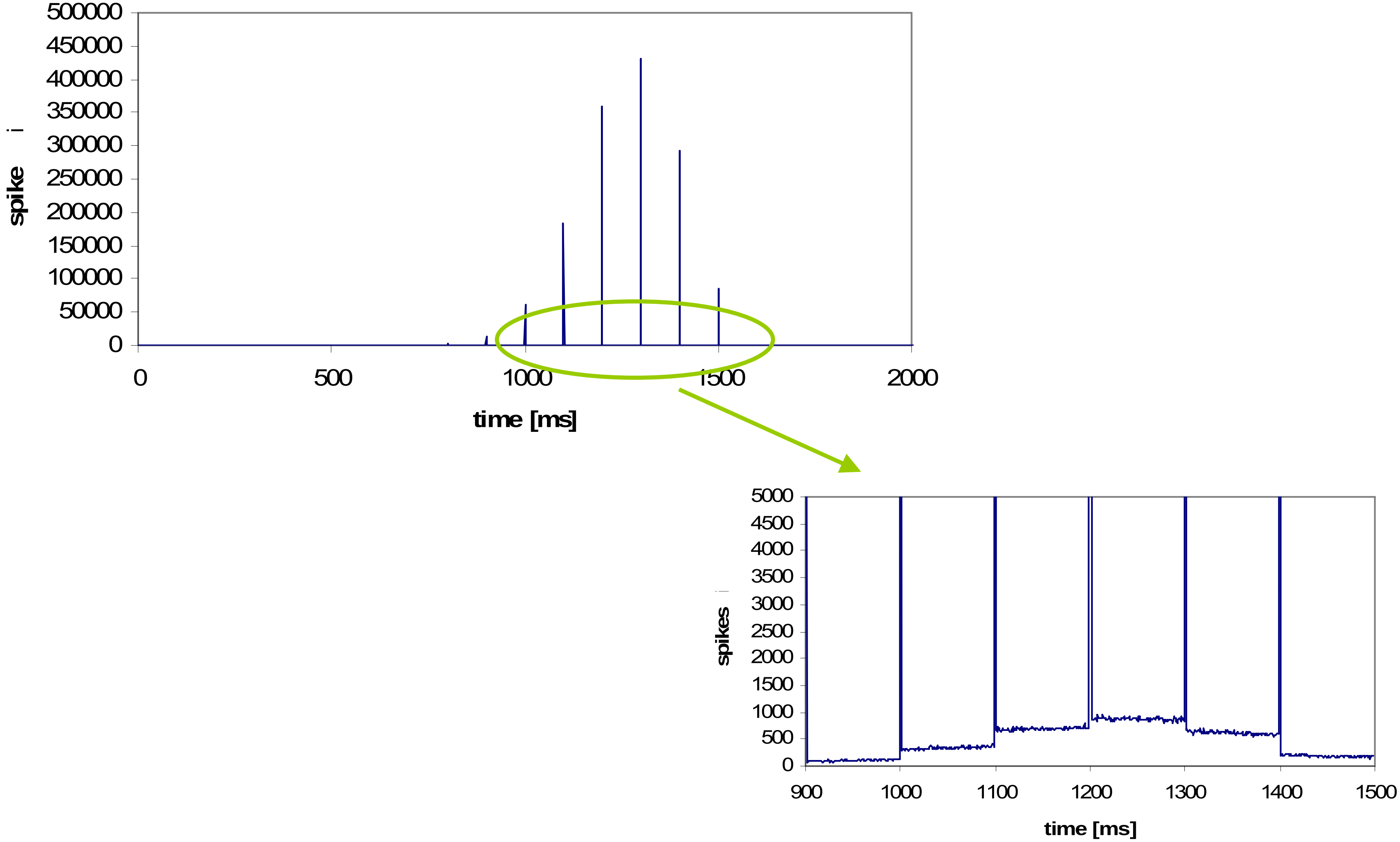
$$v(\tau) = \int_{t_0}^{t_0+\tau} k + a\delta(t - t_i)\, dt$$

$$v(\tau) > \theta : v(\tau) \leftarrow v_{reset}$$



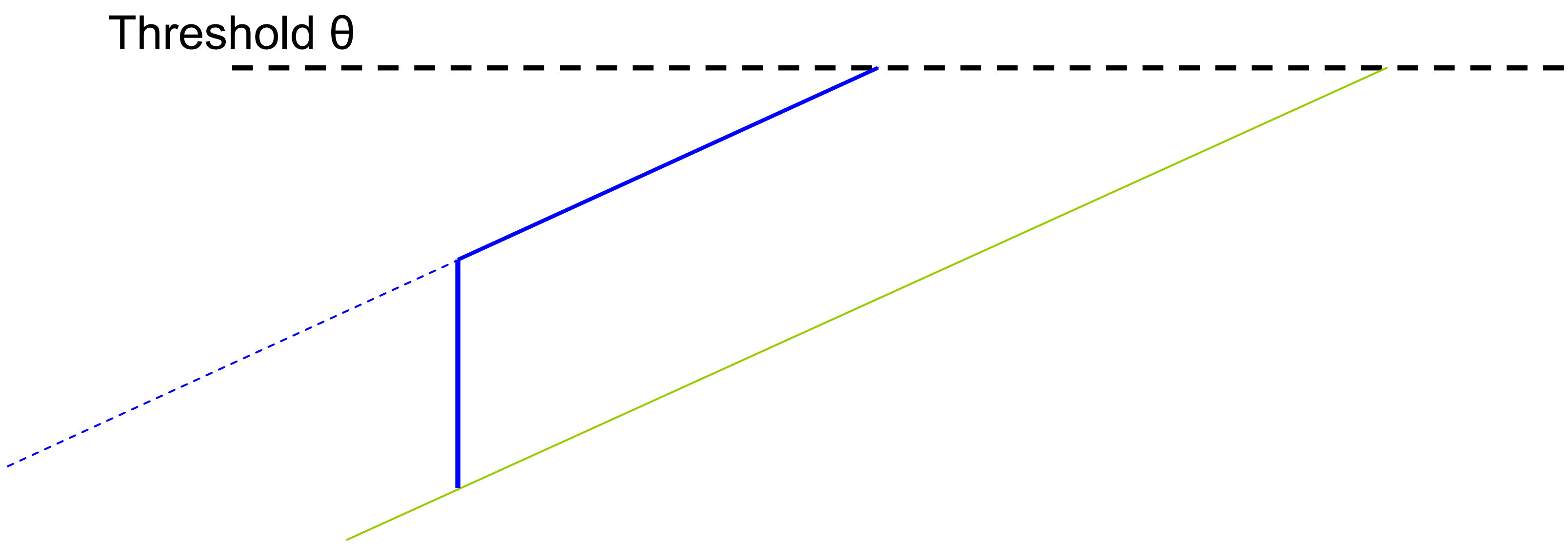


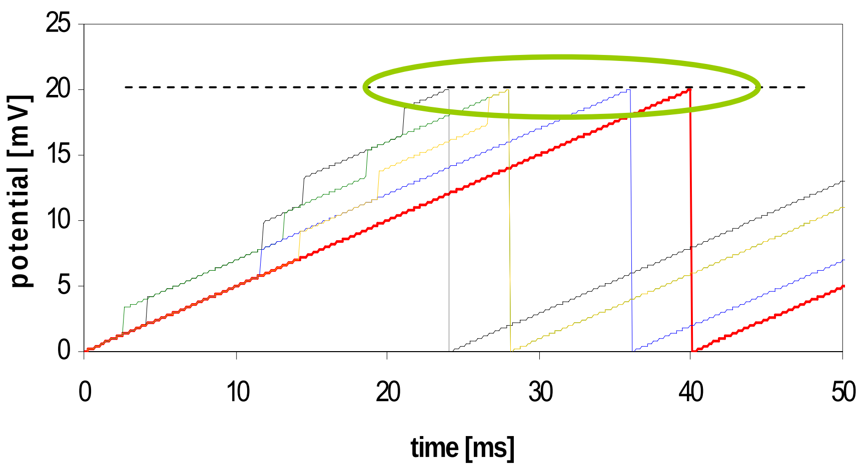
…the reality



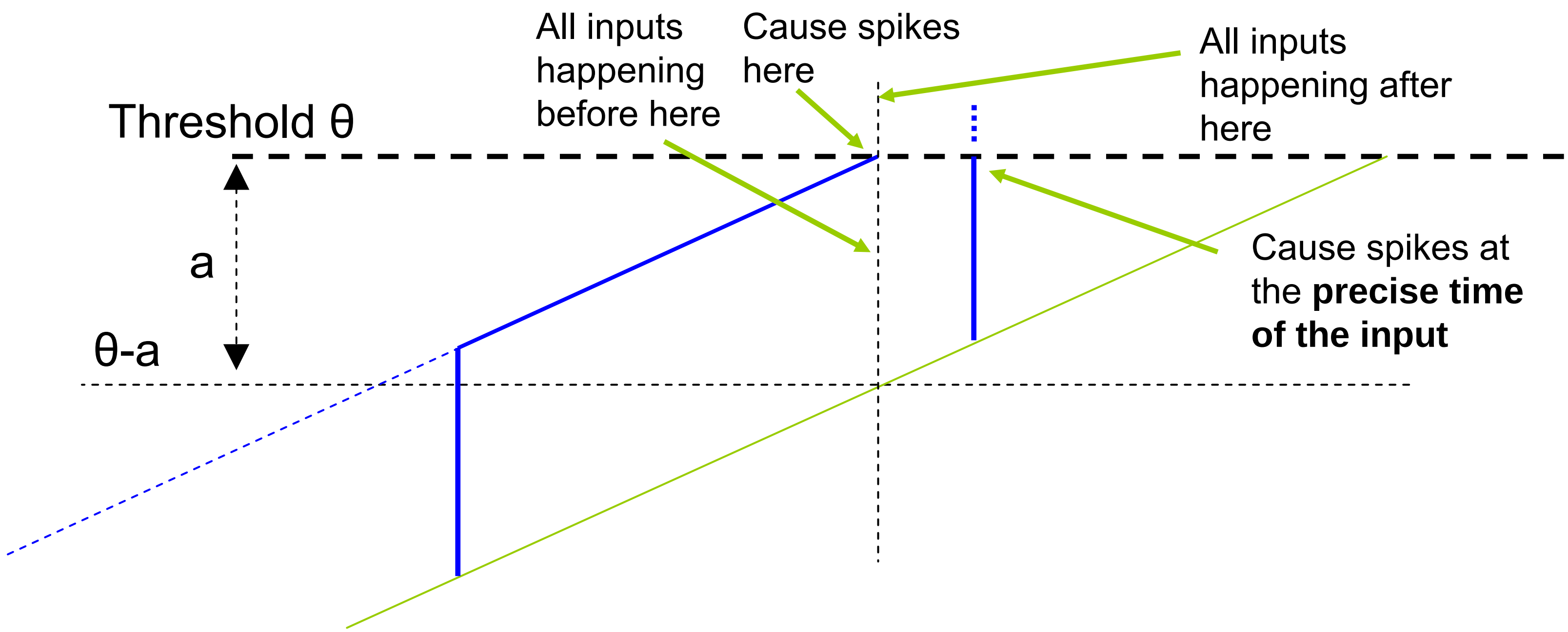
500000
450000
400000
350000
300000
250000
200000
150000
100000
50000
0
spike
0
500
1000
1500
2000
time [ms]
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
spikes
900
1000
1100
1200
1300
1400
1500
time [ms]

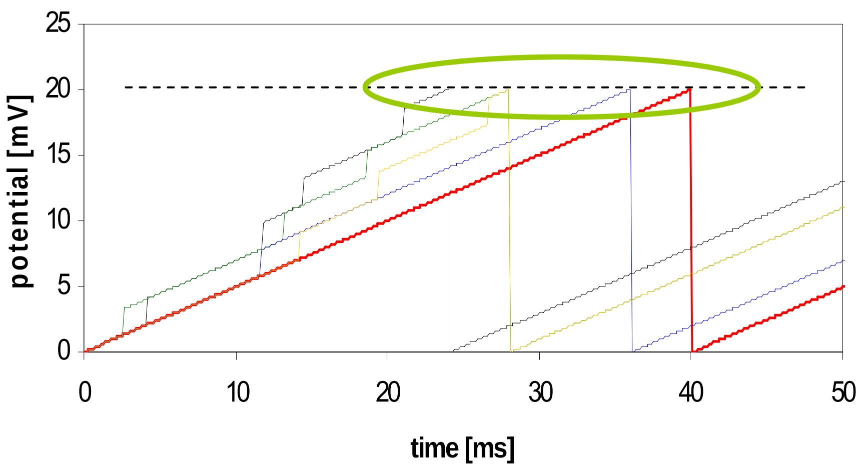
What happens near the threshold?



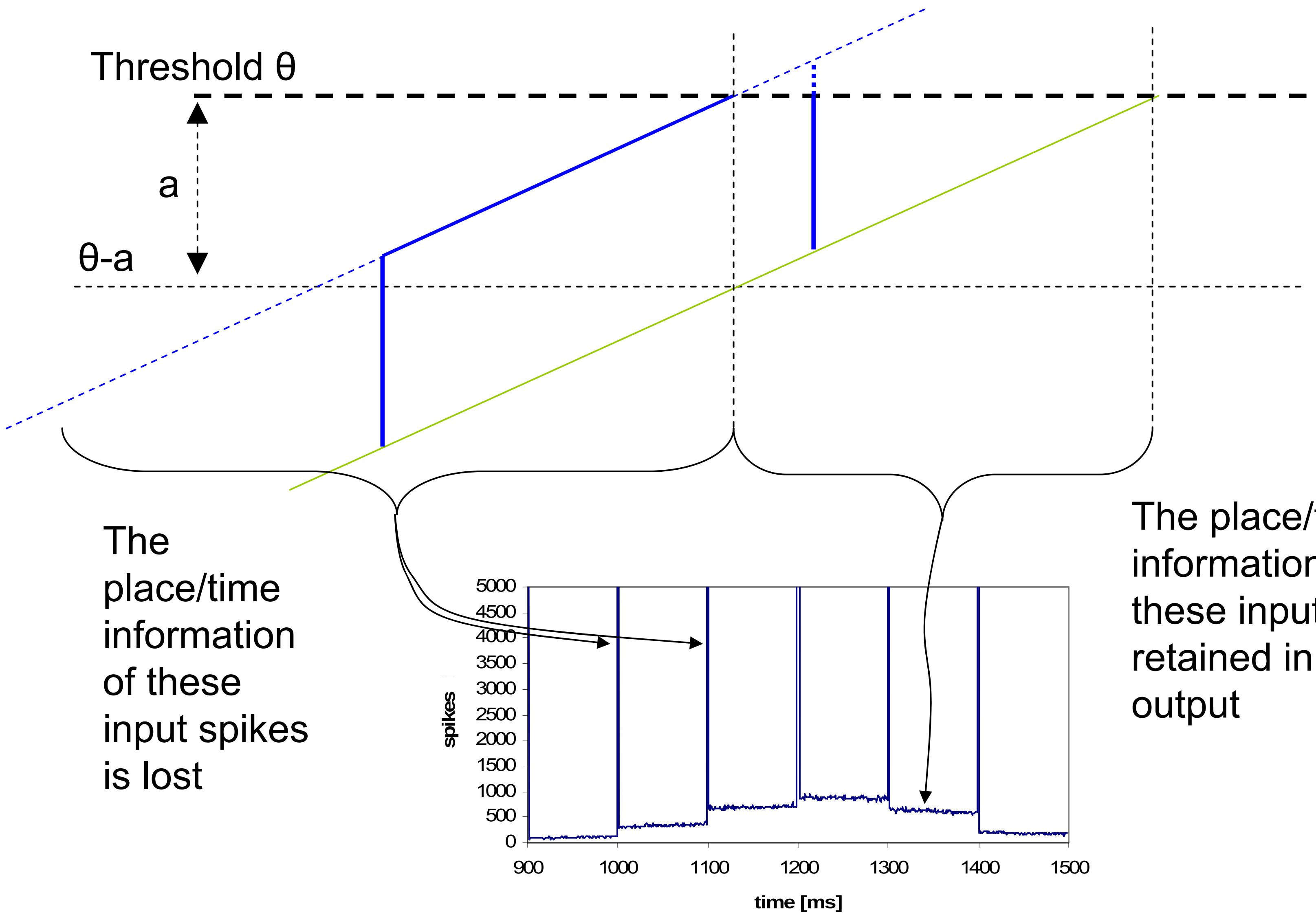


What happens near the threshold?





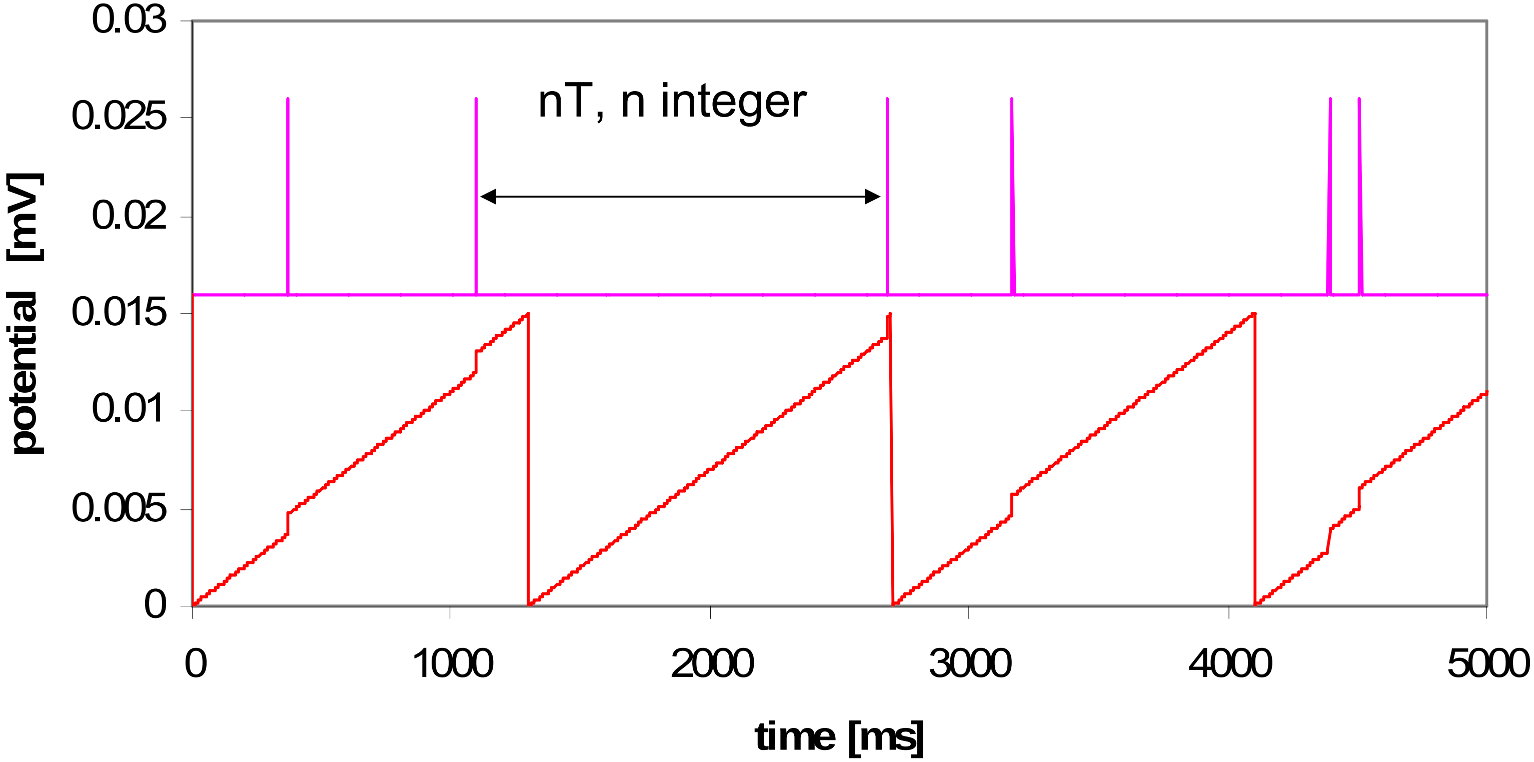
What happens near the threshold?



The place/time information of these input spikes is lost

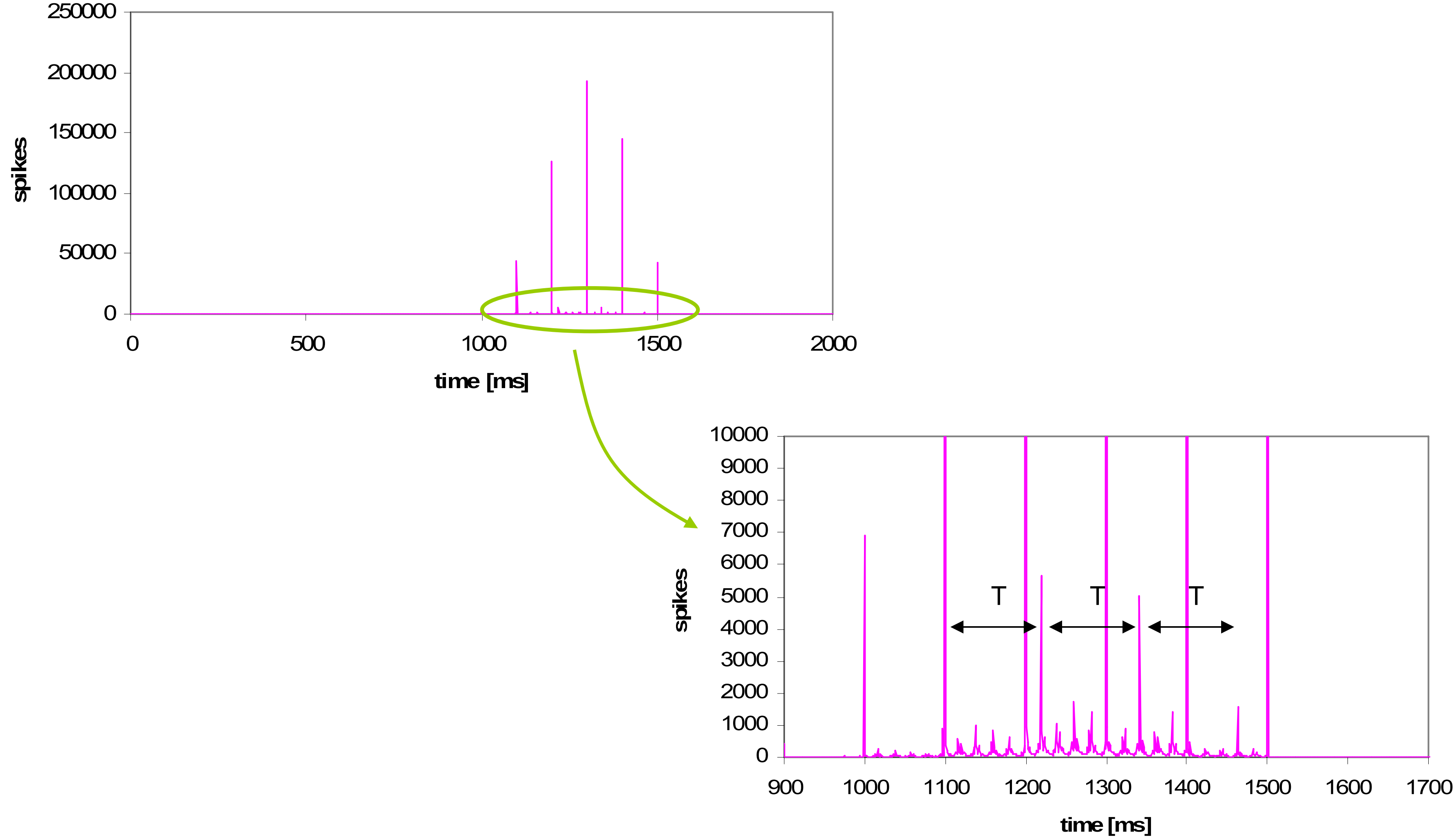
The place/time information of these inputs is retained in the output

This neuron with correlated input spikes



NB Spike amplitude << threshold, so no phase locking

ISIH for correlated input



Introducing randomness

- We can introduce randomness in two obvious ways:
  - Random synaptic weights at input

$$v(\tau) = \int_{t_0}^{t_0+\tau} k + a_i \delta(t - t_i)\, dt$$

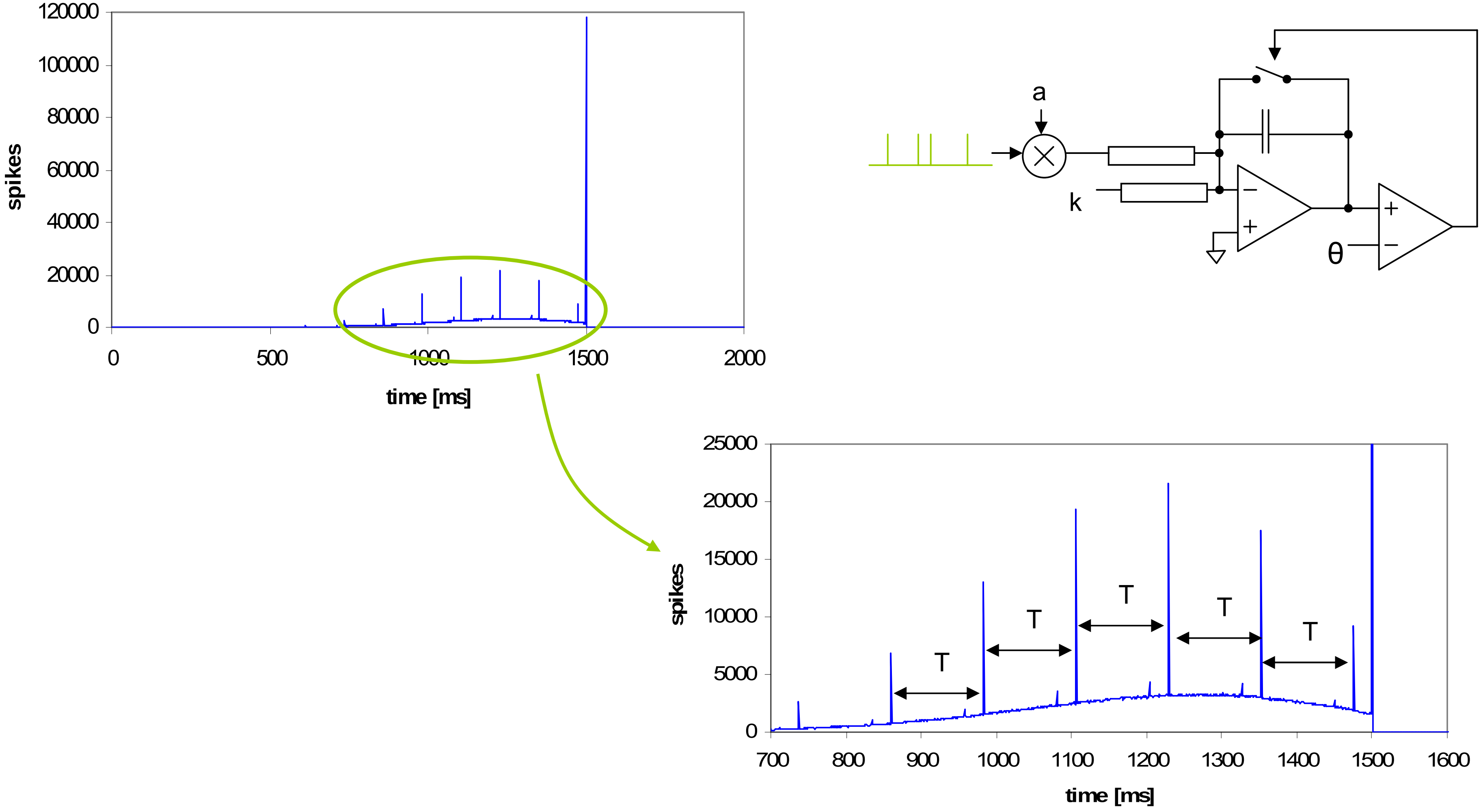
Where a_i is a random variable

  - Noisy drift current

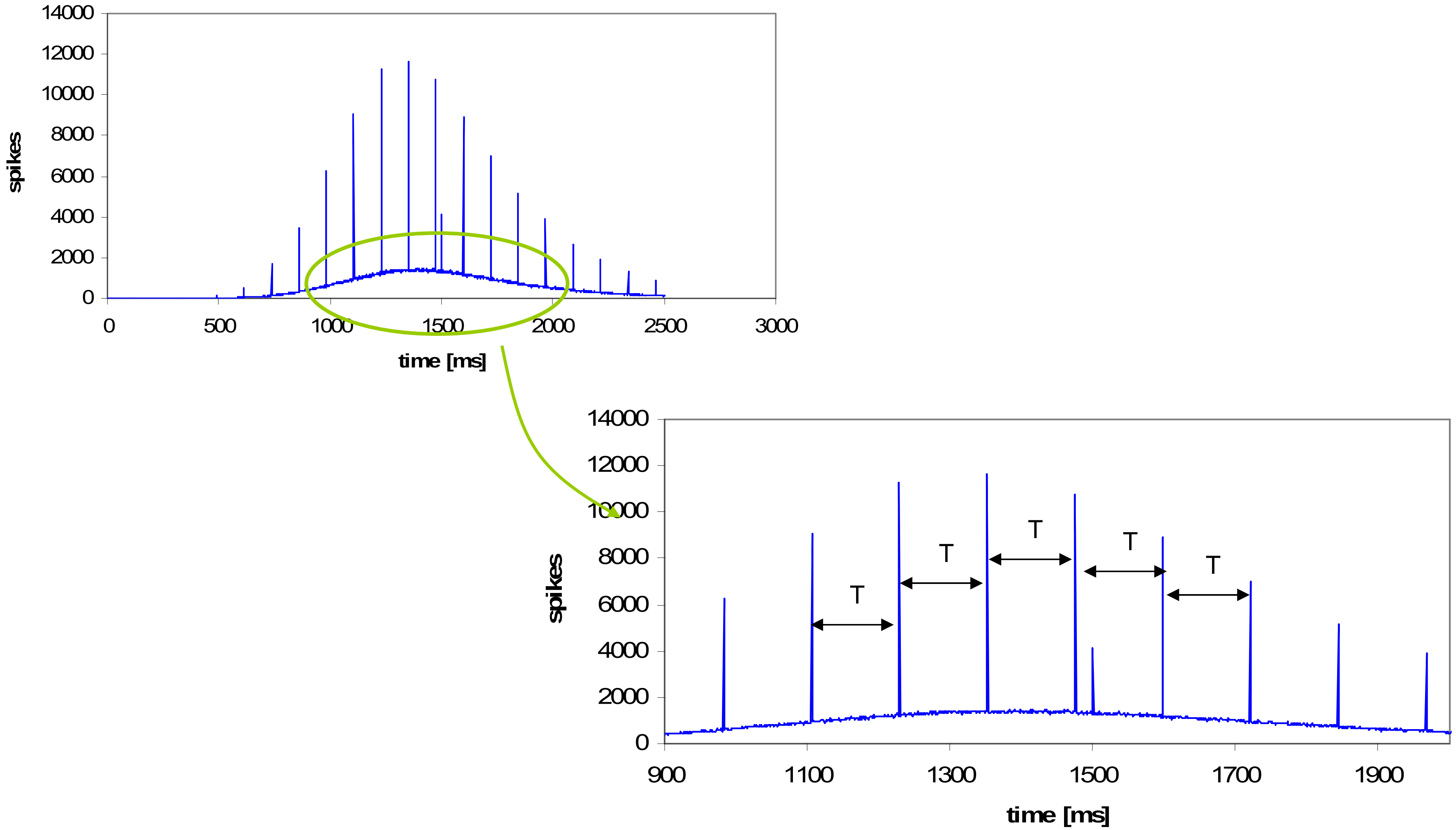
$$v(\tau) = \int_{t_0}^{t_0+\tau} k + \varsigma(t) + a\delta(t - t_i)\, dt$$

Where ζ is a noise process, e.g. AWGN

ISIH for correlated input, monopolar stochastic synaptic transmission



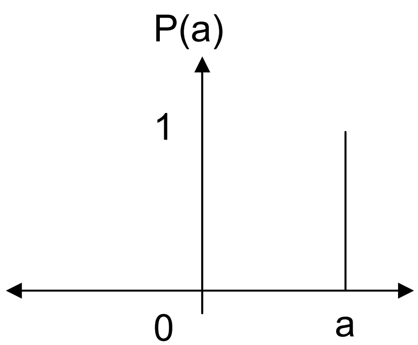
ISIH for correlated input, bipolar stochastic synaptic transmission



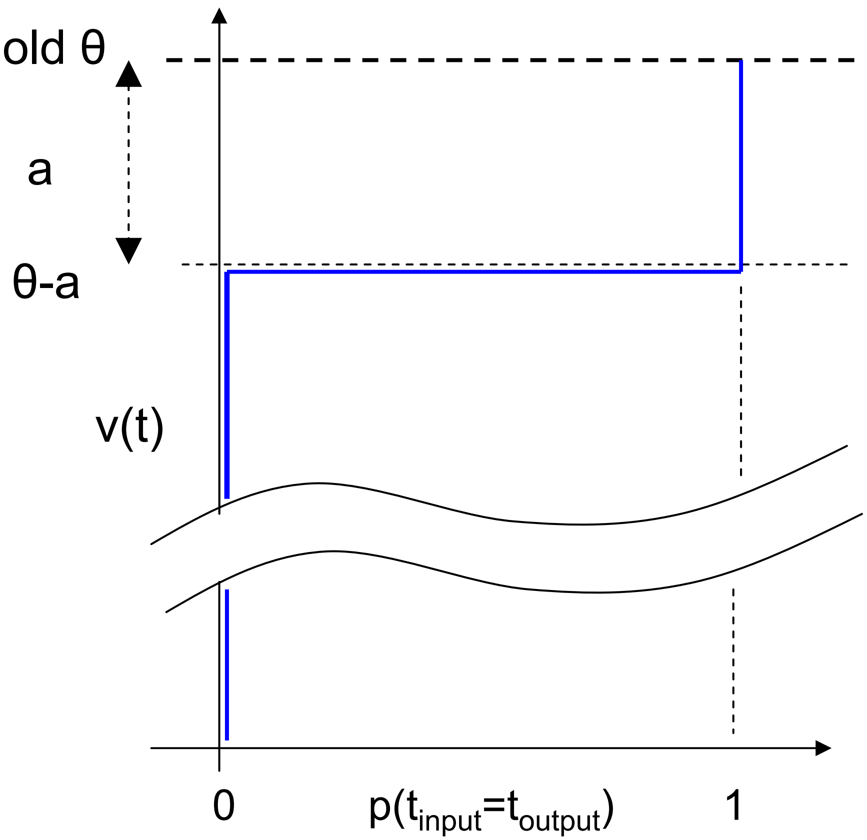
Probability of synchronization

(Synchronization: spike in, triggers immediate spike out)

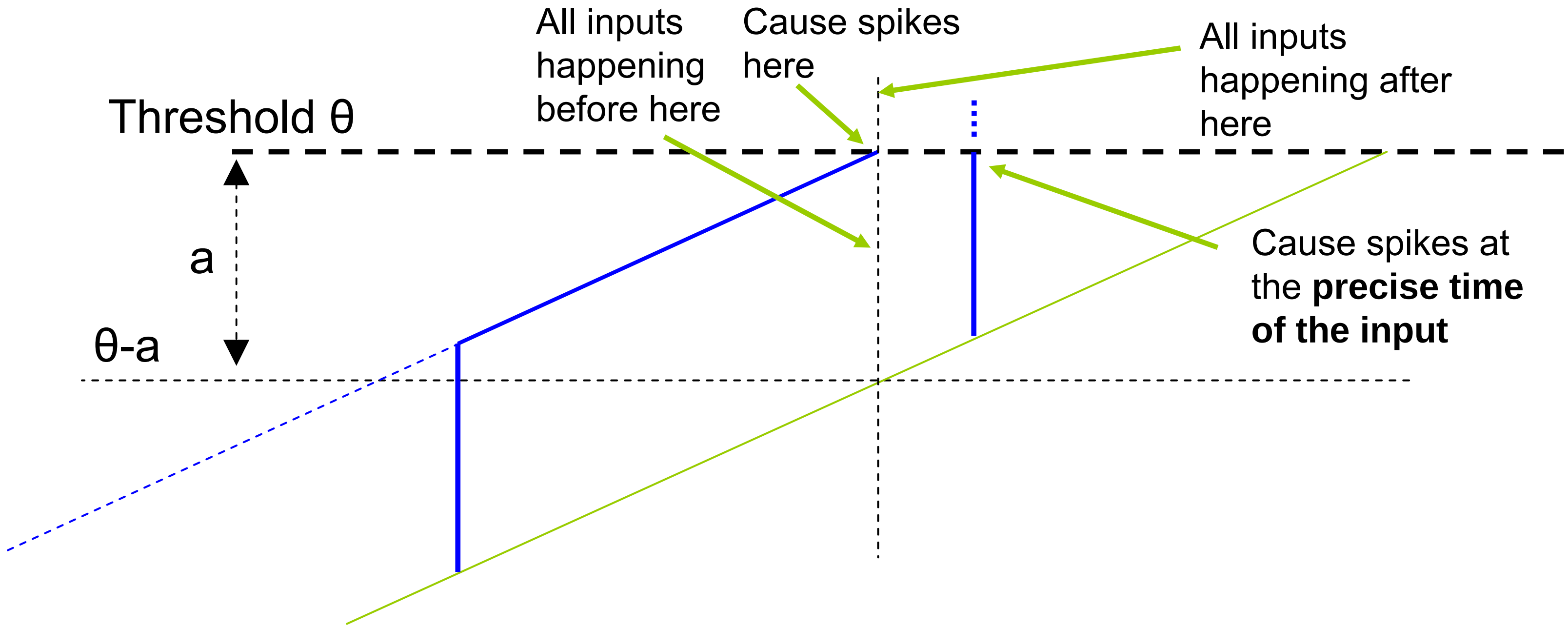
- Integrate and fire, no randomness:

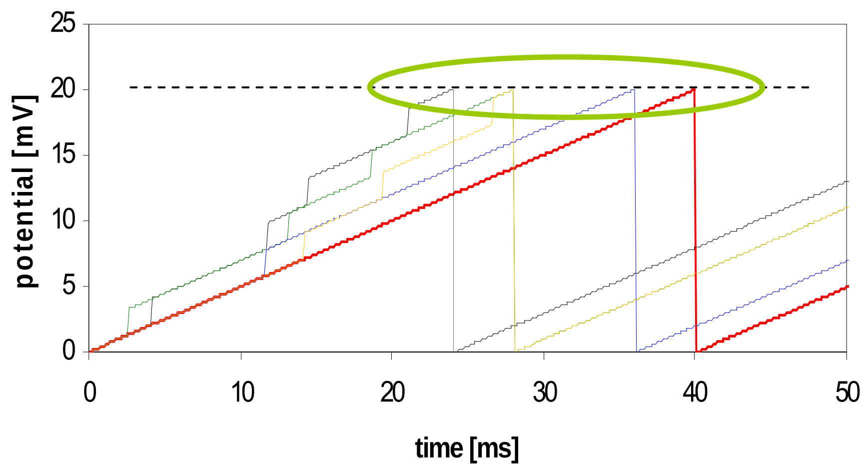


Postsynaptic input
amplitude distribution



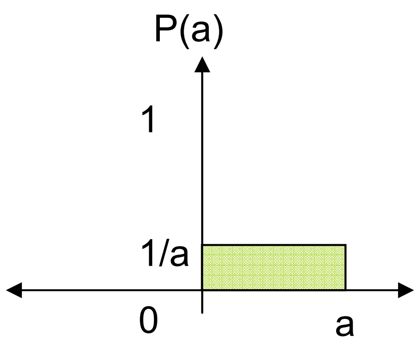
What happens near the threshold?



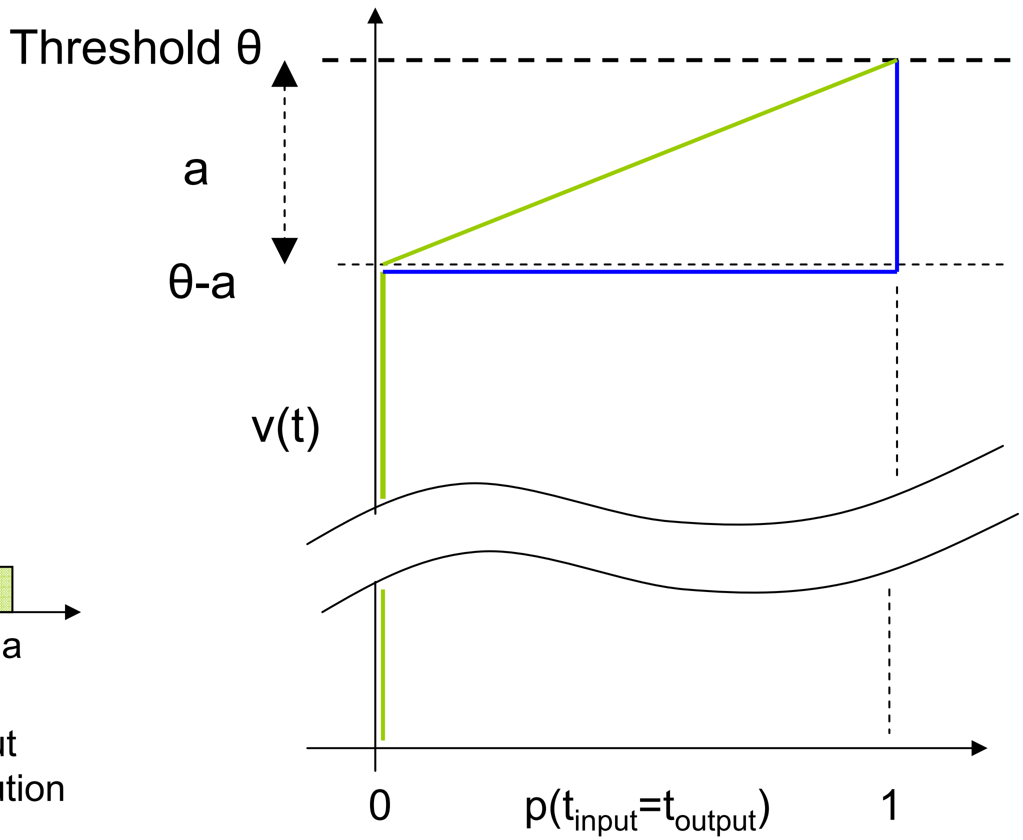


Probability of synchronization

- Integrate and fire, uniform distribution of spike amplitude:

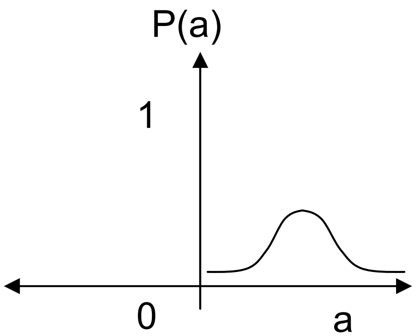


Postsynaptic input amplitude distribution

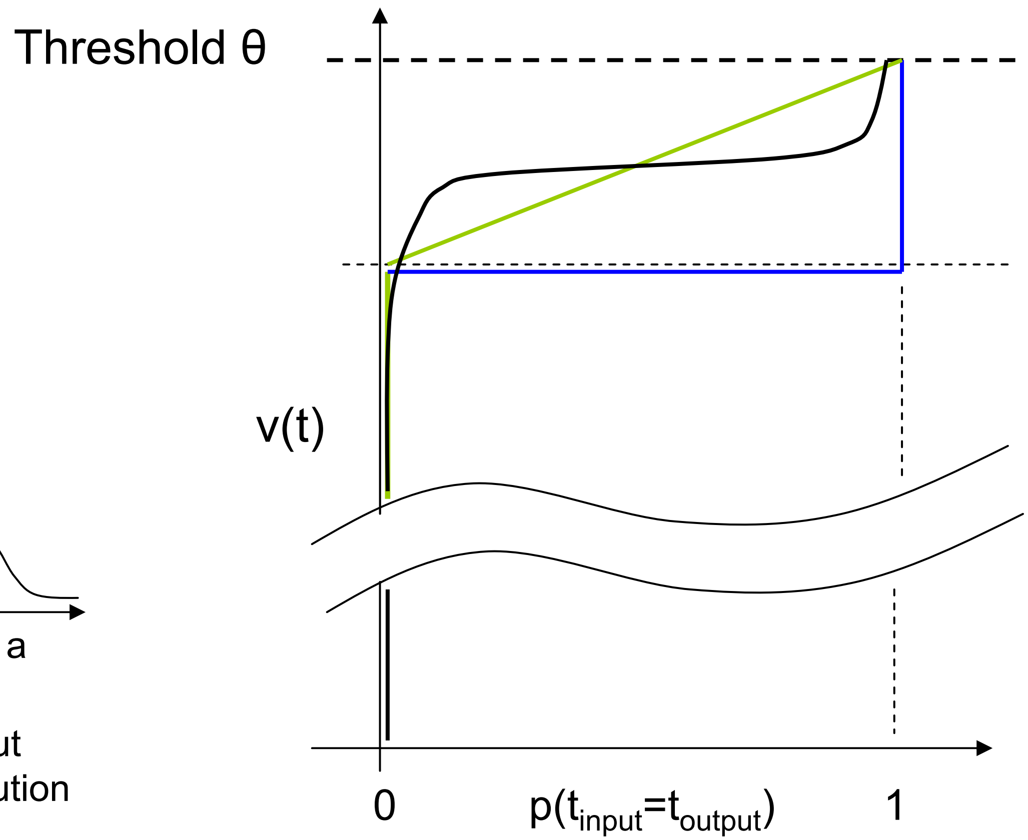


Probability of synchronization

- Integrate and fire, monopolar normal distribution of spike amplitude:

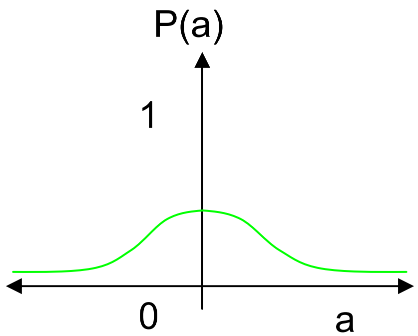


Postsynaptic input amplitude distribution

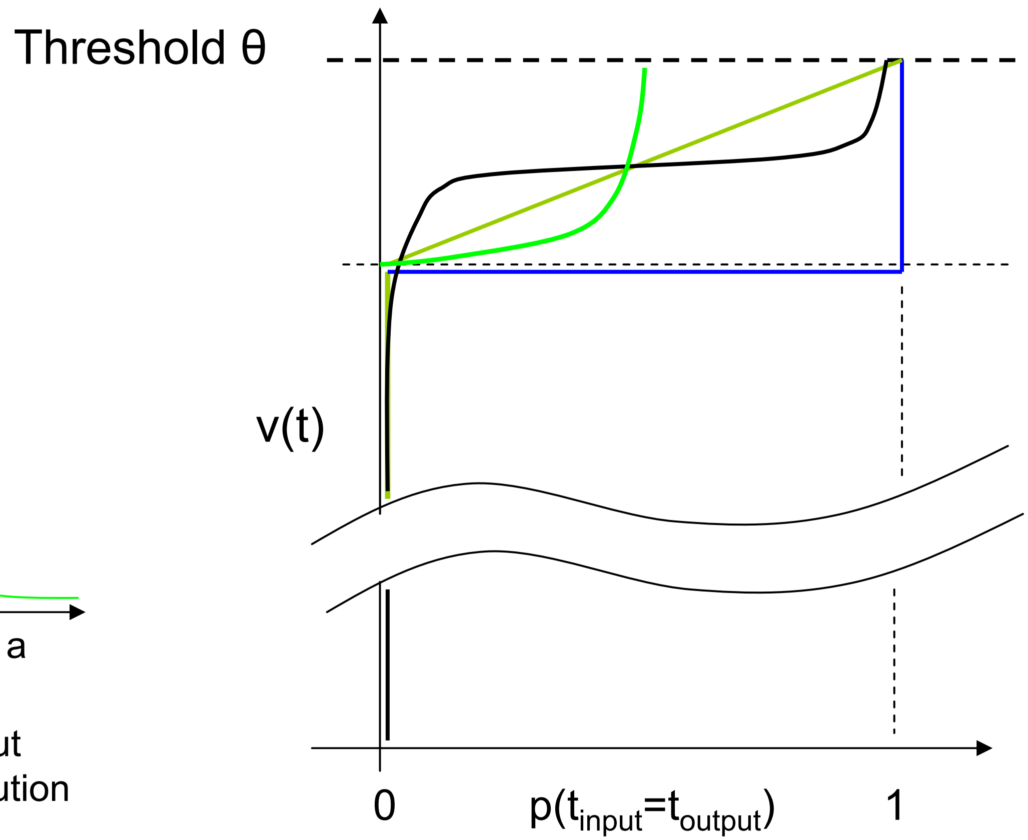


Probability of synchronization

- Integrate and fire, bipolar normal distribution of spike amplitude:

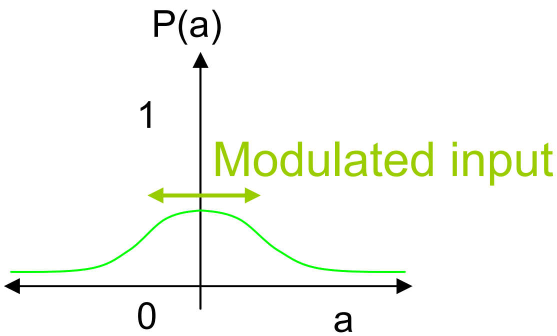


Postsynaptic input amplitude distribution

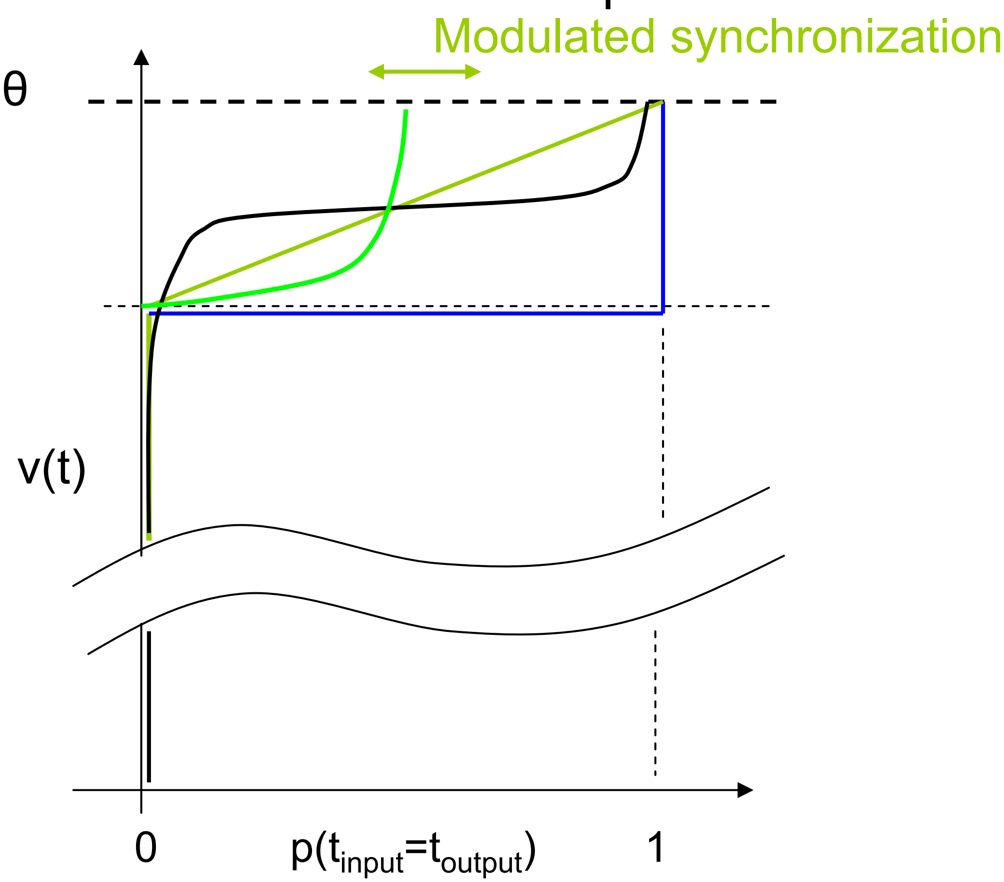


Probability of synchronization

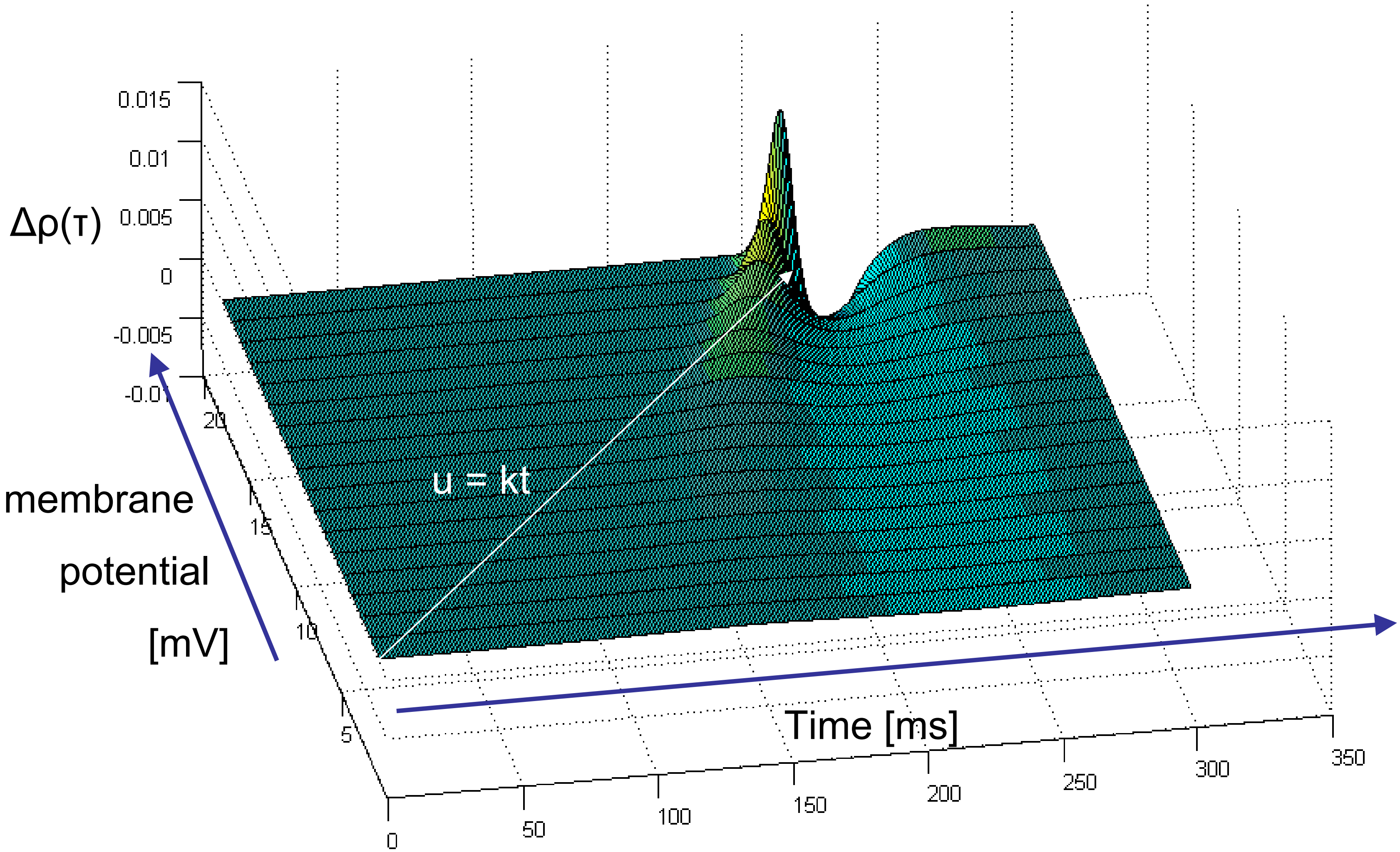
- Integrate and fire, bipolar normal distribution of spike amplitude:



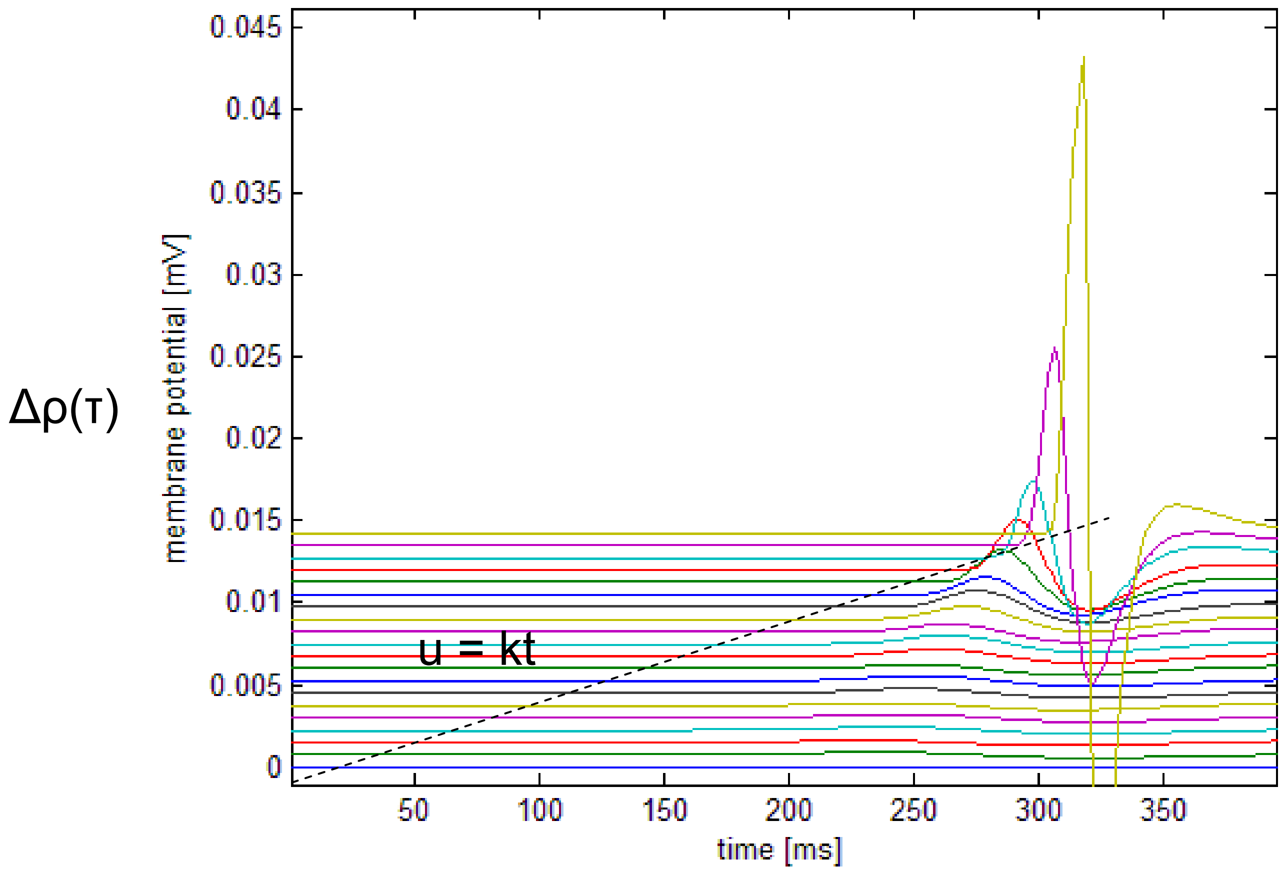
Postsynaptic input amplitude distribution



Input spike spread function



Input spike spread function



Another view

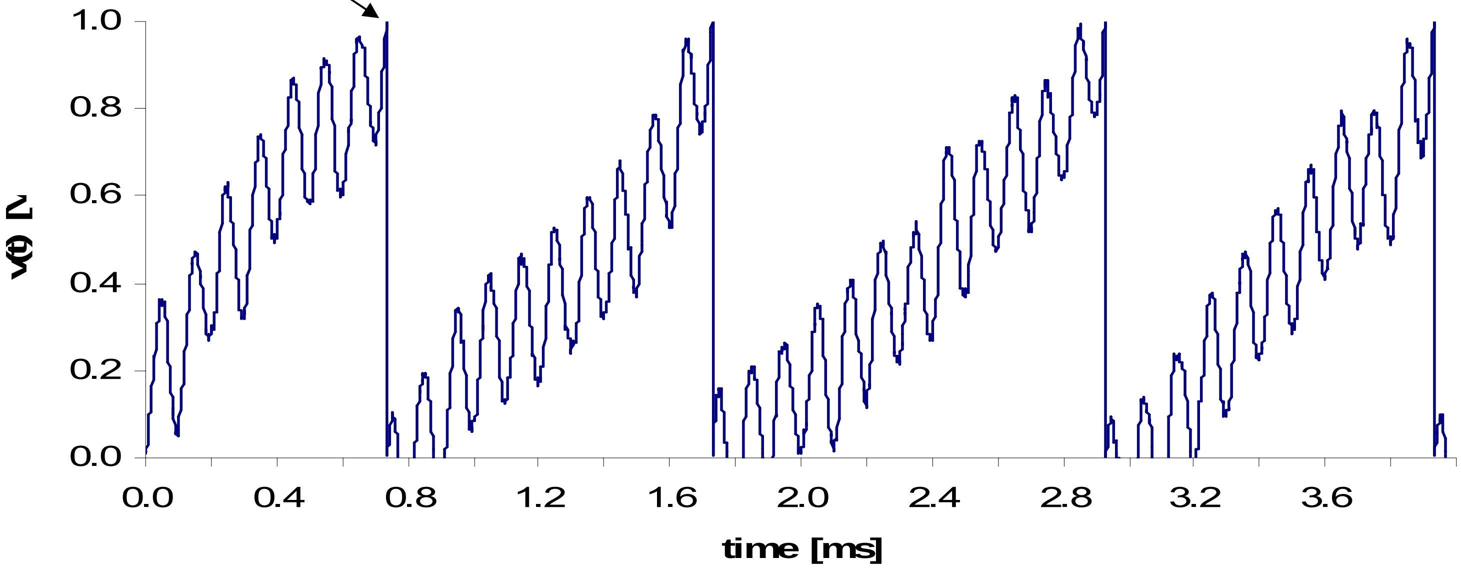
The probability of spiking depends on the local slope of the membrane potential:

$$v(\tau) = \int_{t_0}^{t_0+\tau} k + \varsigma + g(t)\, dt$$

$$\frac{dv}{dt} = k + g(t)$$

input signal

1. Probability of firing depends on slope of v(t)



The story so far…

- Inputs which occur when the membrane potential is far from threshold affect firing **rate** but not firing time; their timing is not preserved.

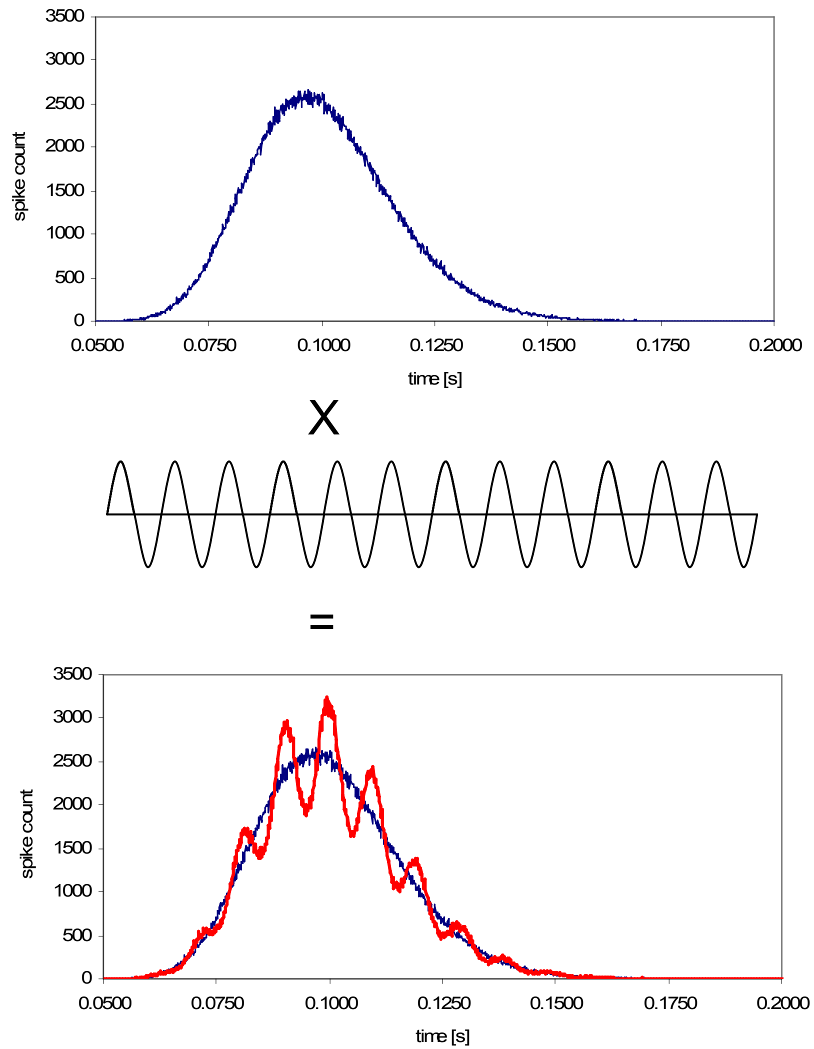
- Inputs which occur with the potential close to the threshold are more likely to produce a spike at that time; their timing may be preserved.

- Features in the spike output density are probably a result of input events which are coincident (in time) with those features…provided there is some randomization or noise in the system.

Towards a model

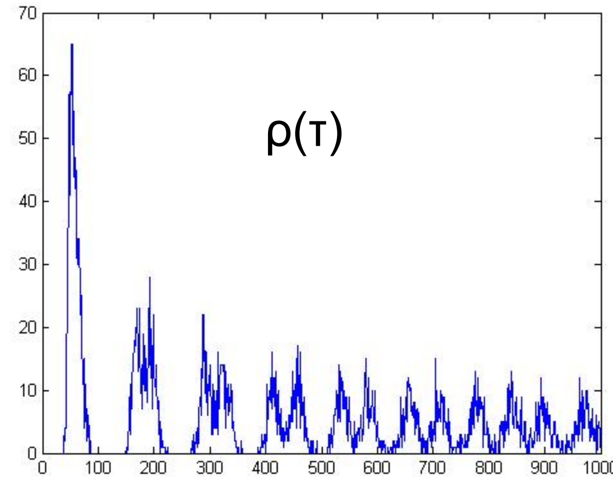
- Hypothesis:

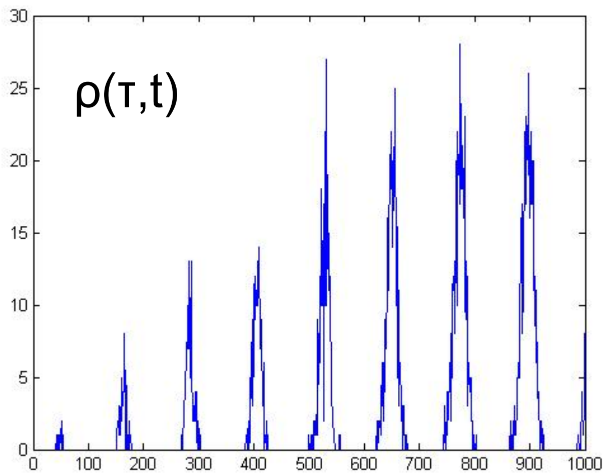
  For a noisy IF neuron with small-signal inputs, the spike interval distribution can be modeled by a product of the distribution with no input, and the input signal itself.

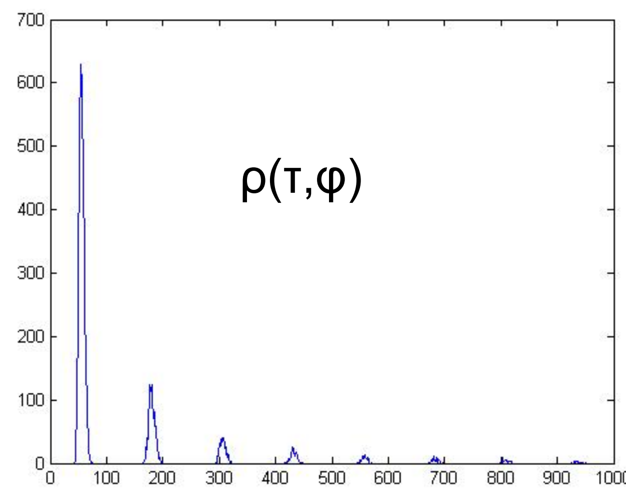


How do we specify the starting phase of the signal?

- ISIH for sine wave input with identical parameters, except…
  – Random phase start
  – Same phase start
  – Continuous (started where
  – last trial ended)







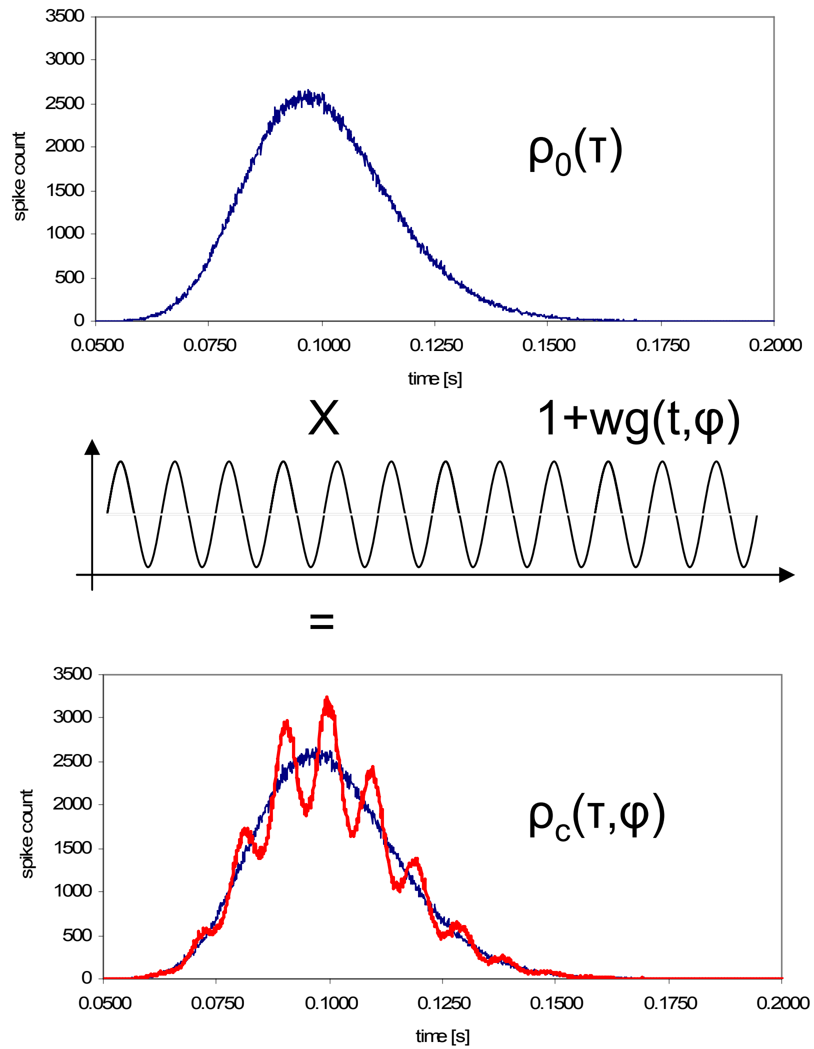
Towards a model

- Hypothesis:

  For a noisy IF neuron with a small modulating input, the first-order conditional spike interval distribution can be modeled by a product of the distribution with no input, and the input signal itself…

  …for a fixed start phase of the modulating signal.

$$\rho_c(\tau,\varphi) = \rho_0(\tau)(1+wg(t,\varphi))$$

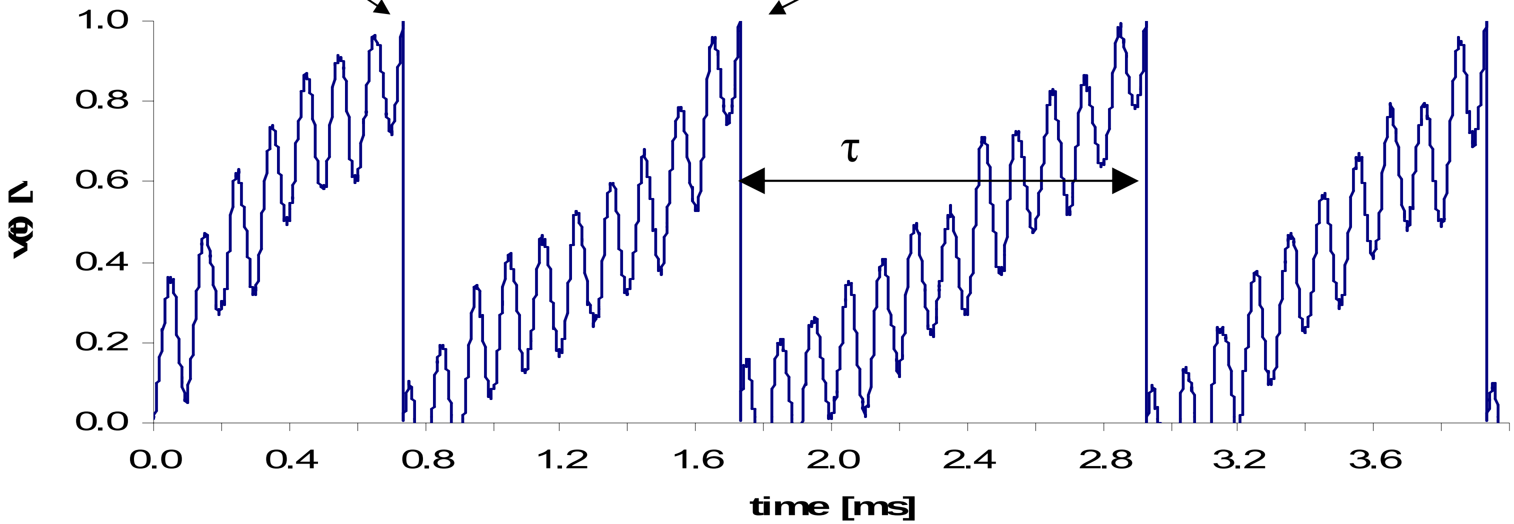


What affects the ISIH?

1. Probability of firing depends on slope of v(t)

2. Probability of firing at this interval depends on probability of firing here…

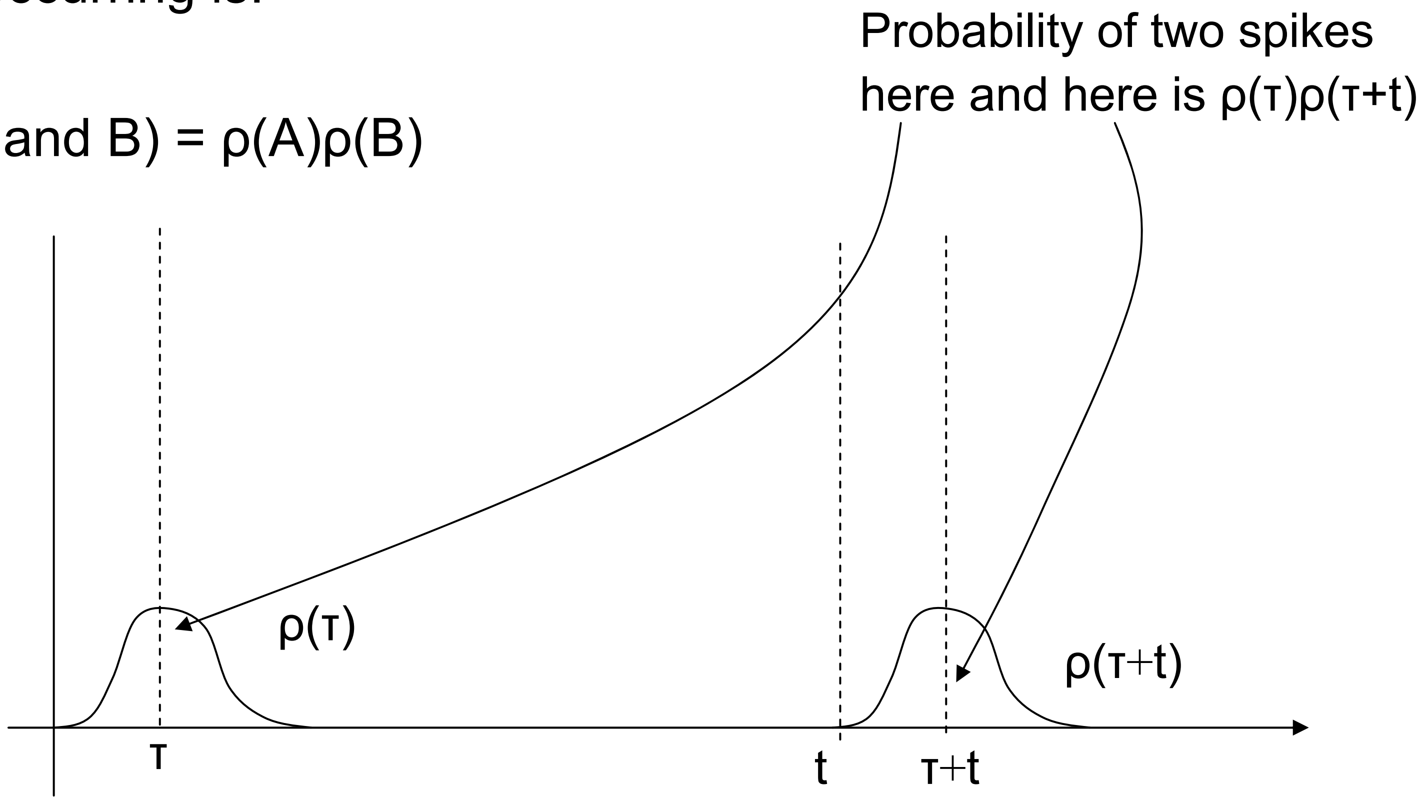
…and probability of firing here



Multiplication by Combination of Probabilities

If we have two independent events A and B with probabilities ρ(A) and ρ(B) then the probability of both A and B occurring is:

ρ(A and B) = ρ(A)ρ(B)



Mathematical Correlation

- Autocorrelation function of a signal f(t):

$$R_{ff}(\tau) = \lim_{T \to \infty} \frac{1}{2T} \int_{-T}^{T} f(t) f(t+\tau) dt$$

- Cross-Correlation
  - Periodic

$$R_{fg}(\tau) = \frac{1}{T} \int_{0}^{T} f(t) g(t+\tau) dt$$

  - Non-periodic

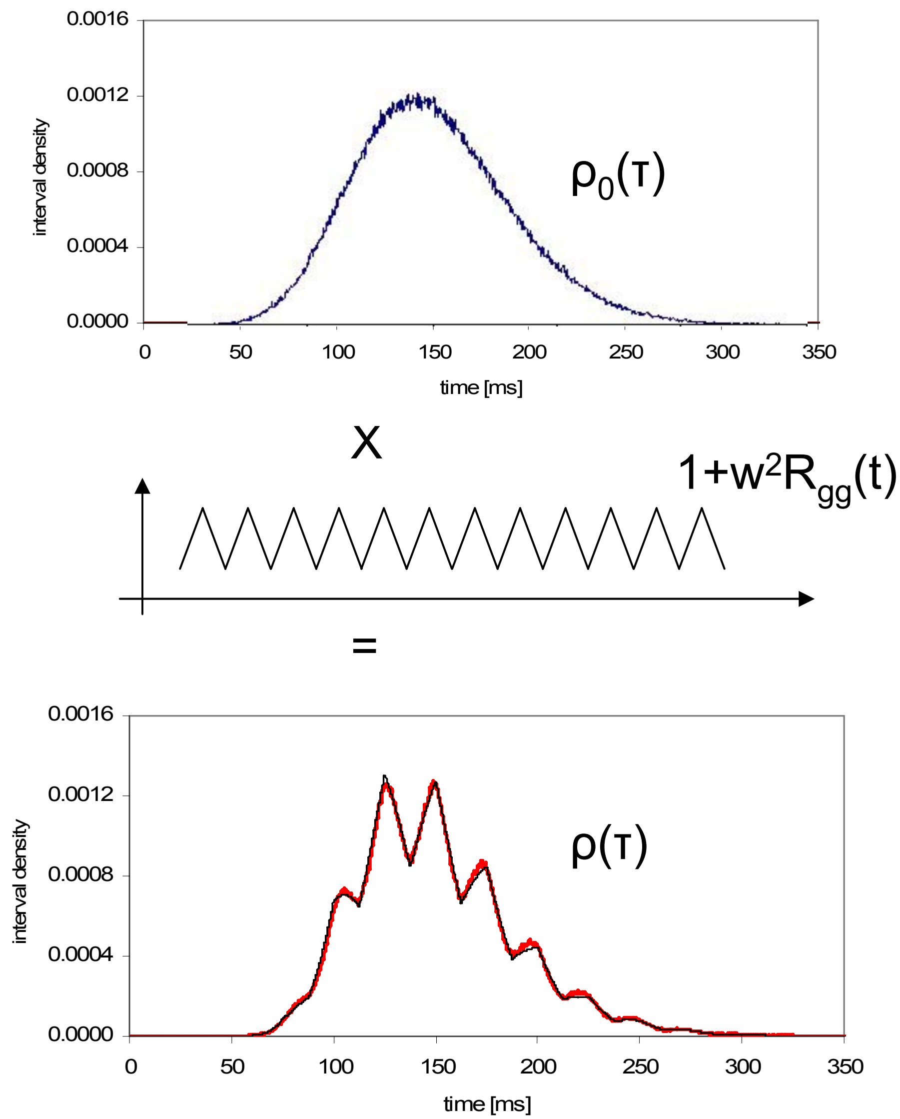
$$R_{fg}(\tau) = \lim_{T \to \infty} \frac{1}{2T} \int_{-T}^{T} f(t) g(t+\tau) dt$$

A model for the continuous spike density

- Another hypothesis:

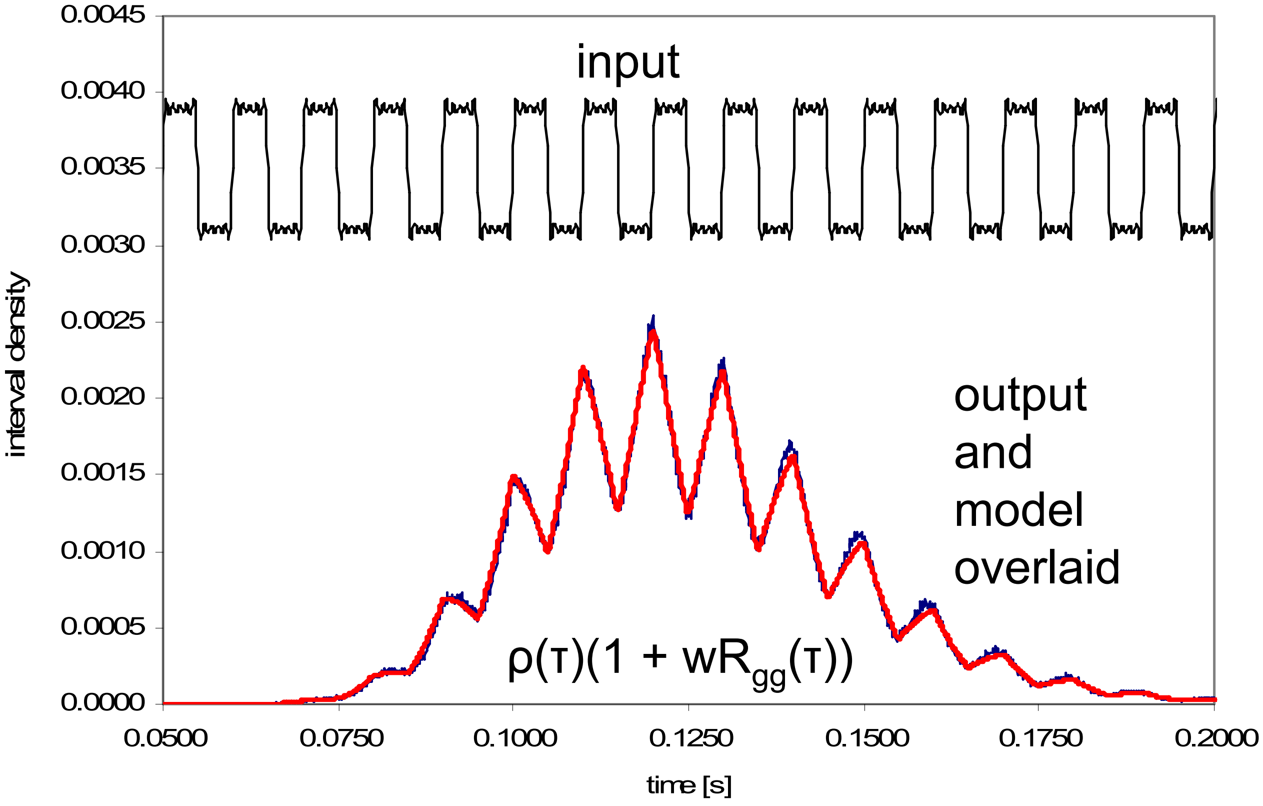
  For a noisy IF neuron with a small modulating input, the first-order spike interval distribution under continuous stimulation can be constructed as a product of the unstimulated neuron's distribution, and the autocorrelation function of the input stimulus.

$$\rho(\tau) = \rho_0(\tau)(1+w^2R_{gg}(t))$$



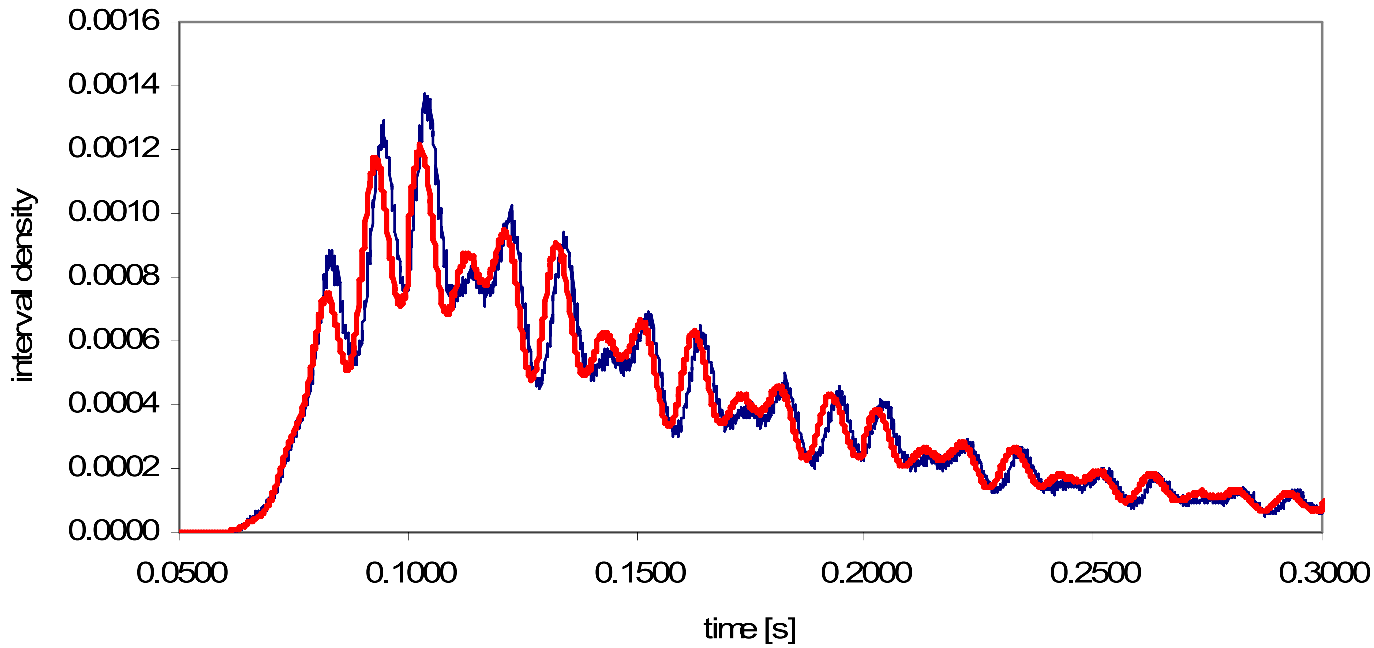
Stochastic autocorrelation

- Autocorrelation output:



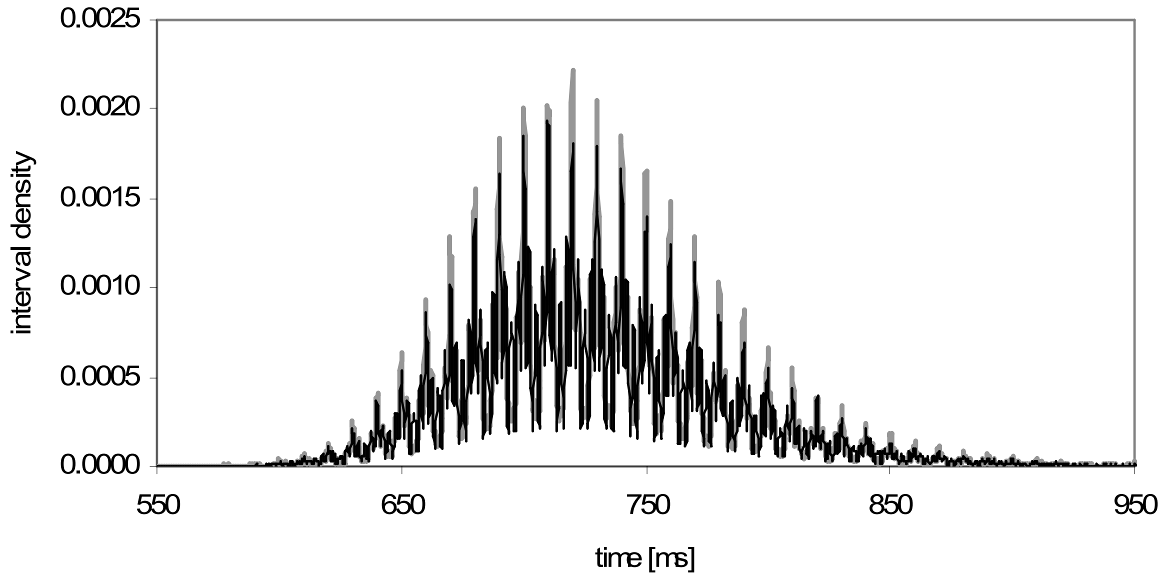
Further examples of stochastic autocorrelation (N > 15000 available)

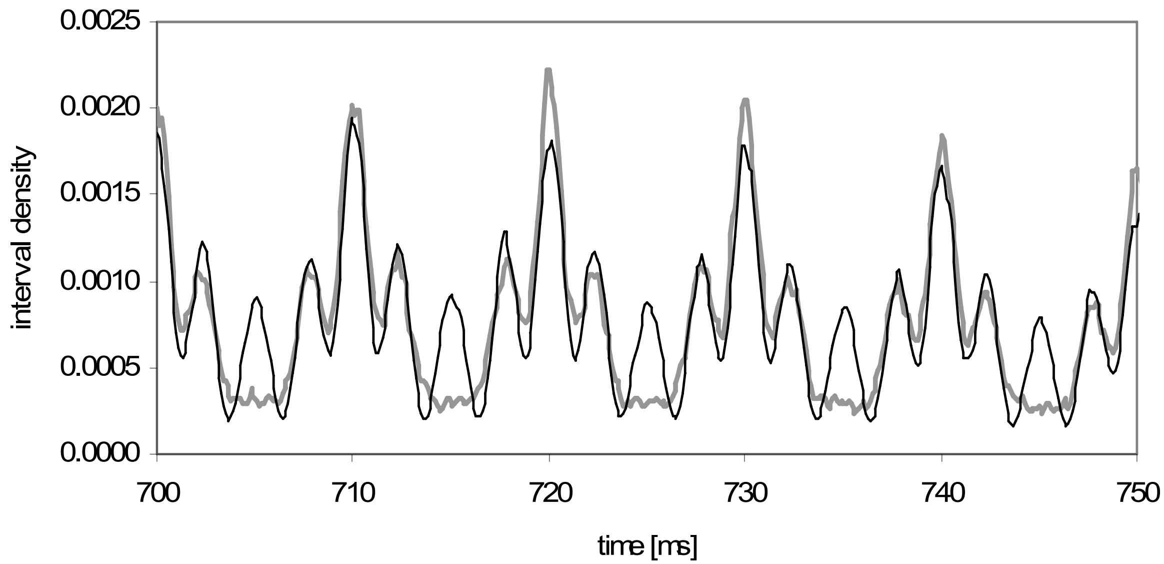
- Random periodic signal, neuron with refractory period and quadratic leakage



Tapson, Jin, Van Schaik and Etienne-Cummings, Neural Computation, in press, (2008)

Hodgkin-Huxley Neuron

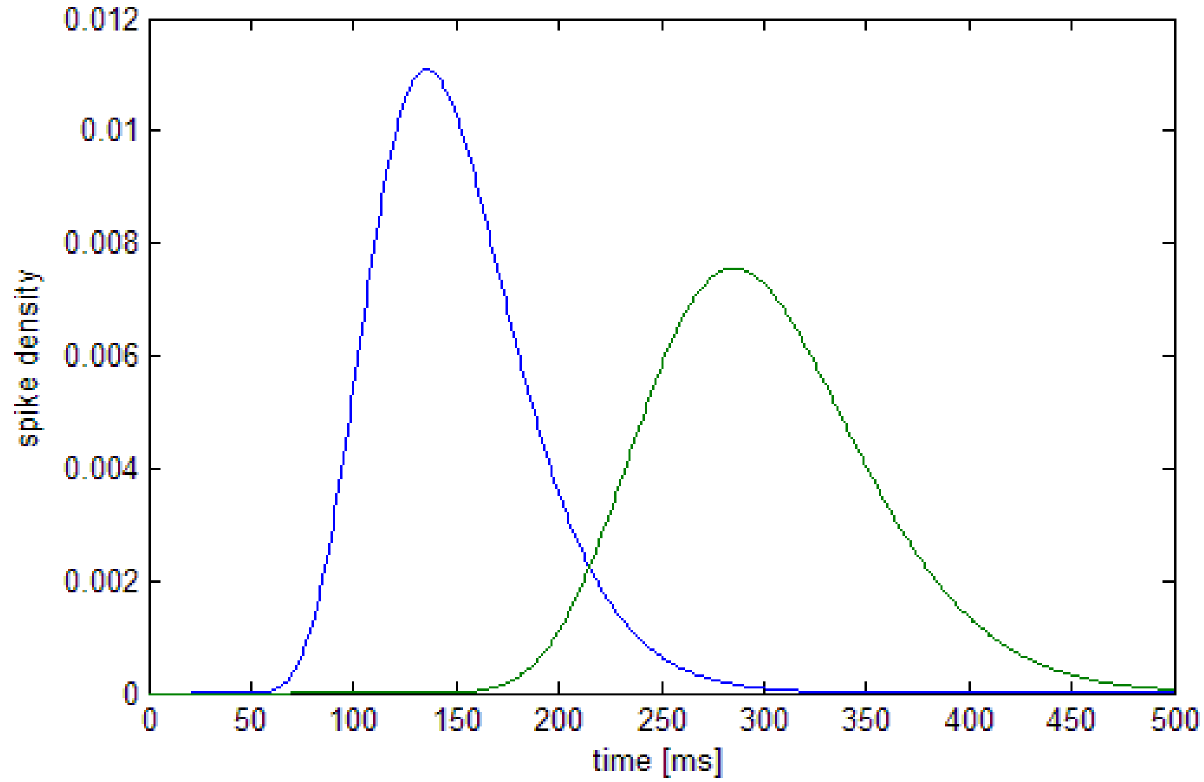




So…

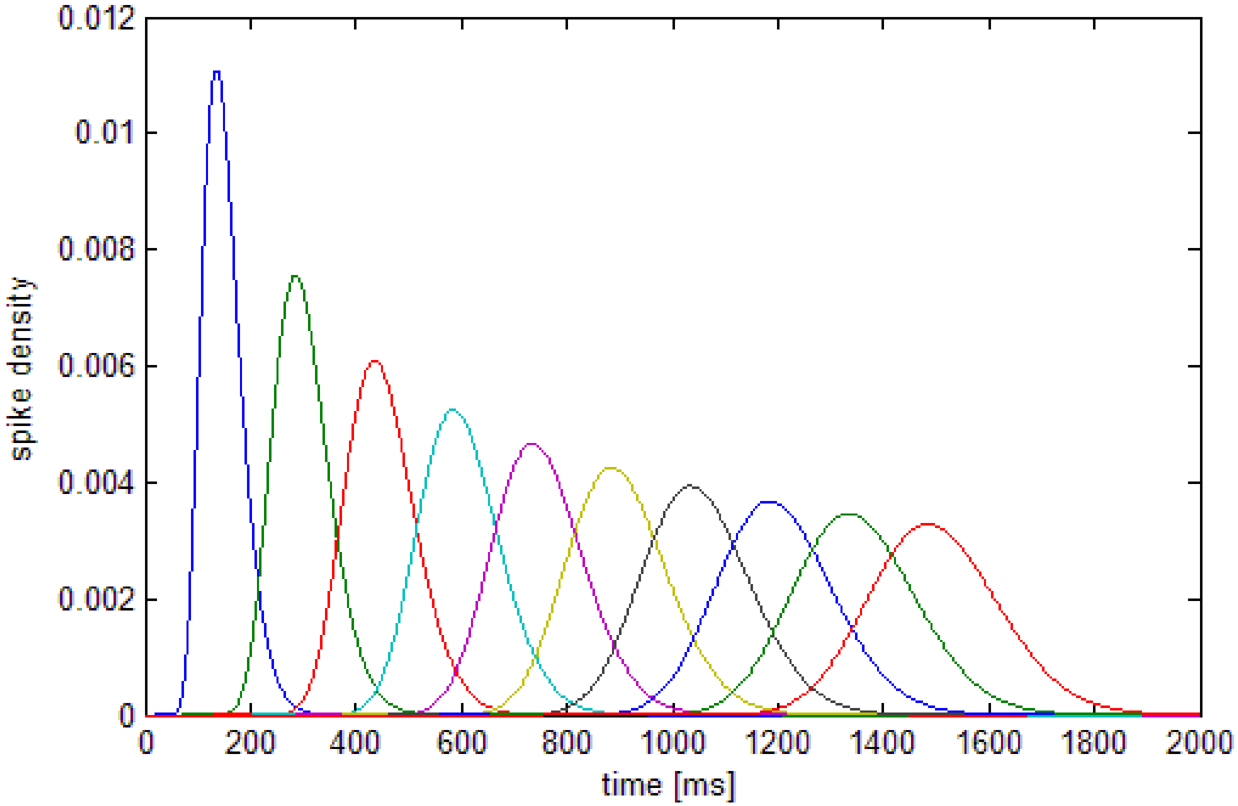
- When a spiking neuron with broad-sense I&F behavior is stimulated by a small continuous signal (and noise), the first order interspike-interval density will reflect the autocorrelation function of the input signal.

Multi-Order Spike Intervals



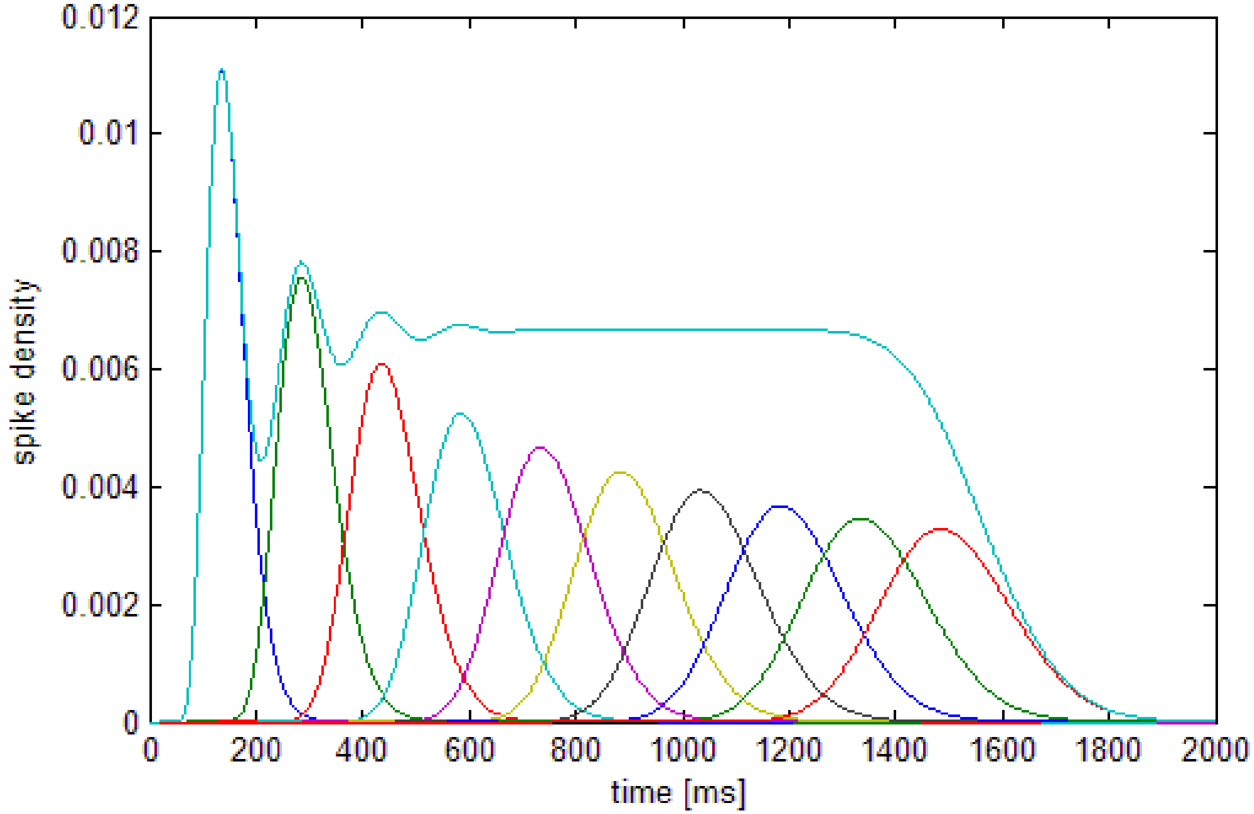
First order intervals and second order intervals between spikes

Multi-Order Spike Intervals



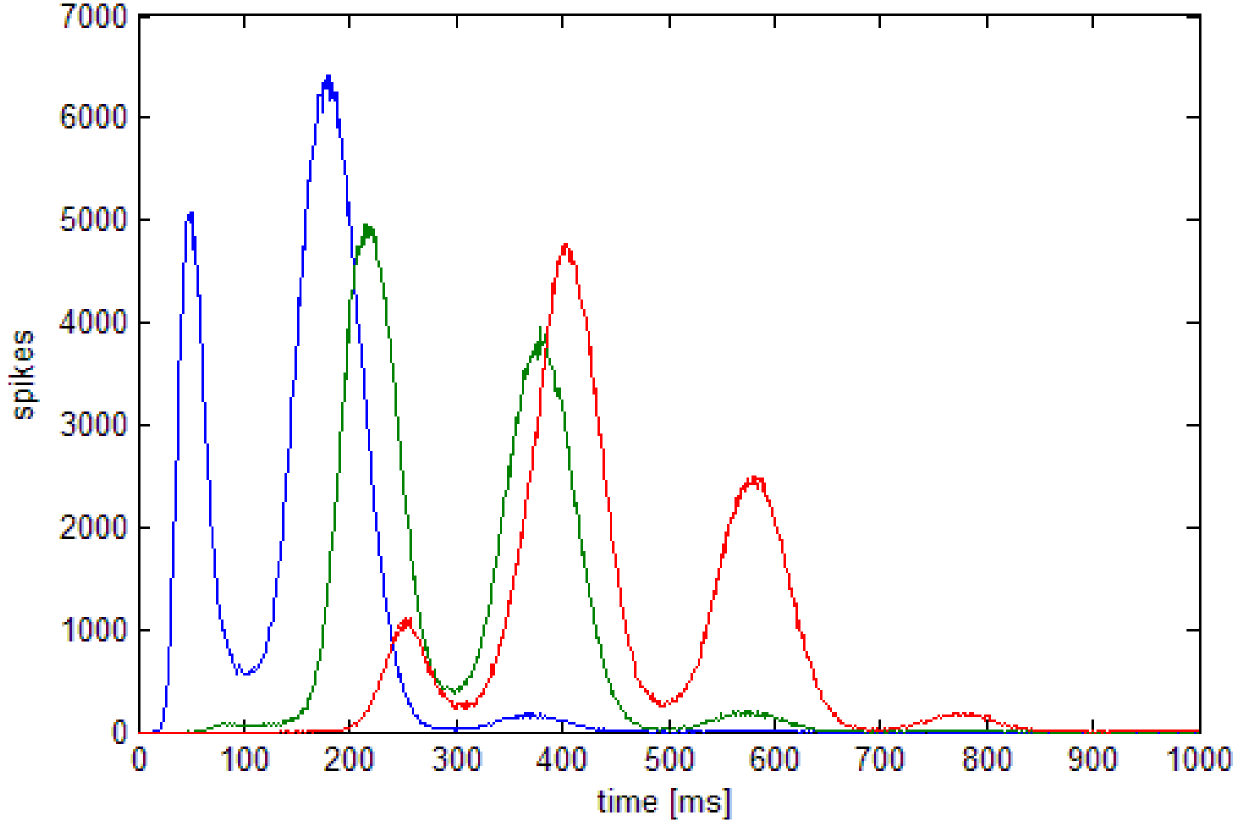
Up to 10^{th} order…

Multi-Order Spike Intervals



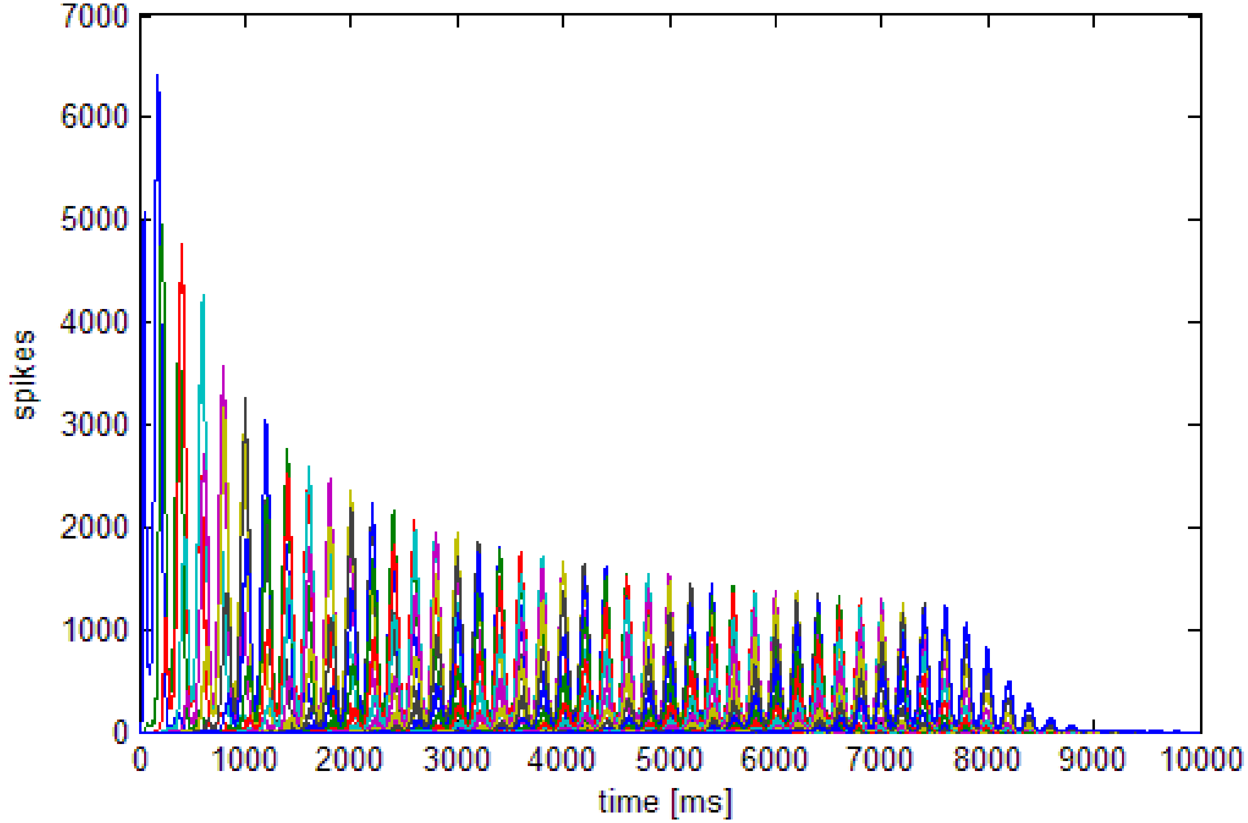
All order spike density emerges

Multi-Order Spike Intervals – Stimulated Neuron



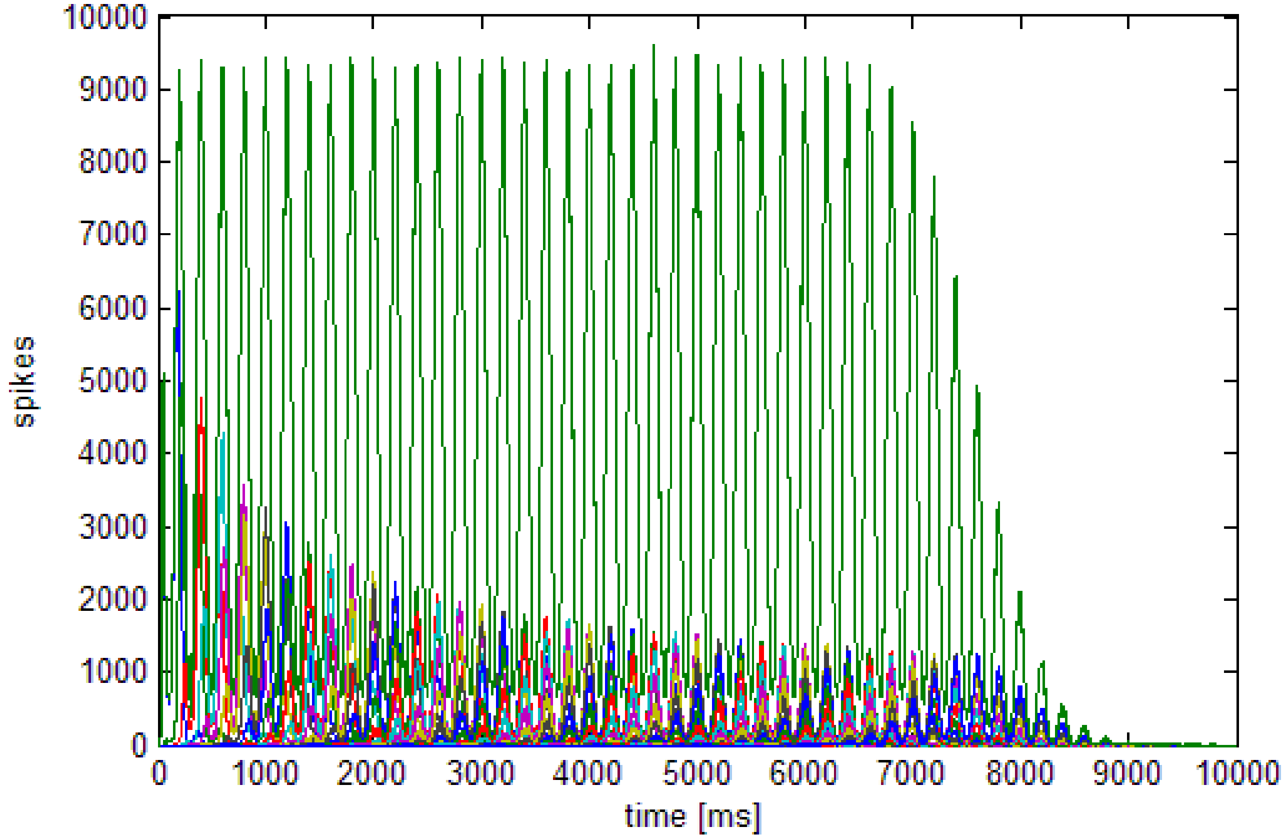
First three order intervals of square-wave driven neuron

Multi-Order Spike Intervals – Stimulated Neuron



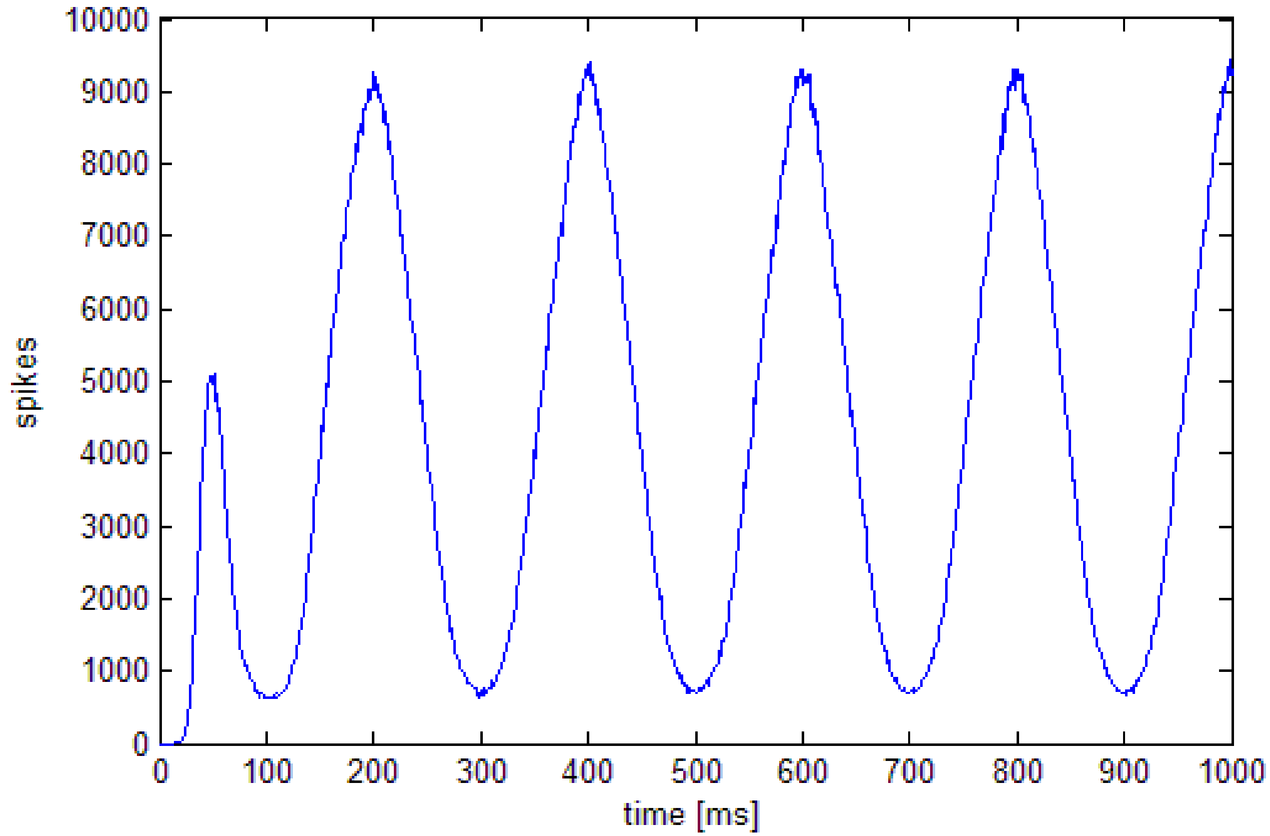
First fifty order intervals of square-wave driven neuron

Multi-Order Spike Intervals – Stimulated Neuron



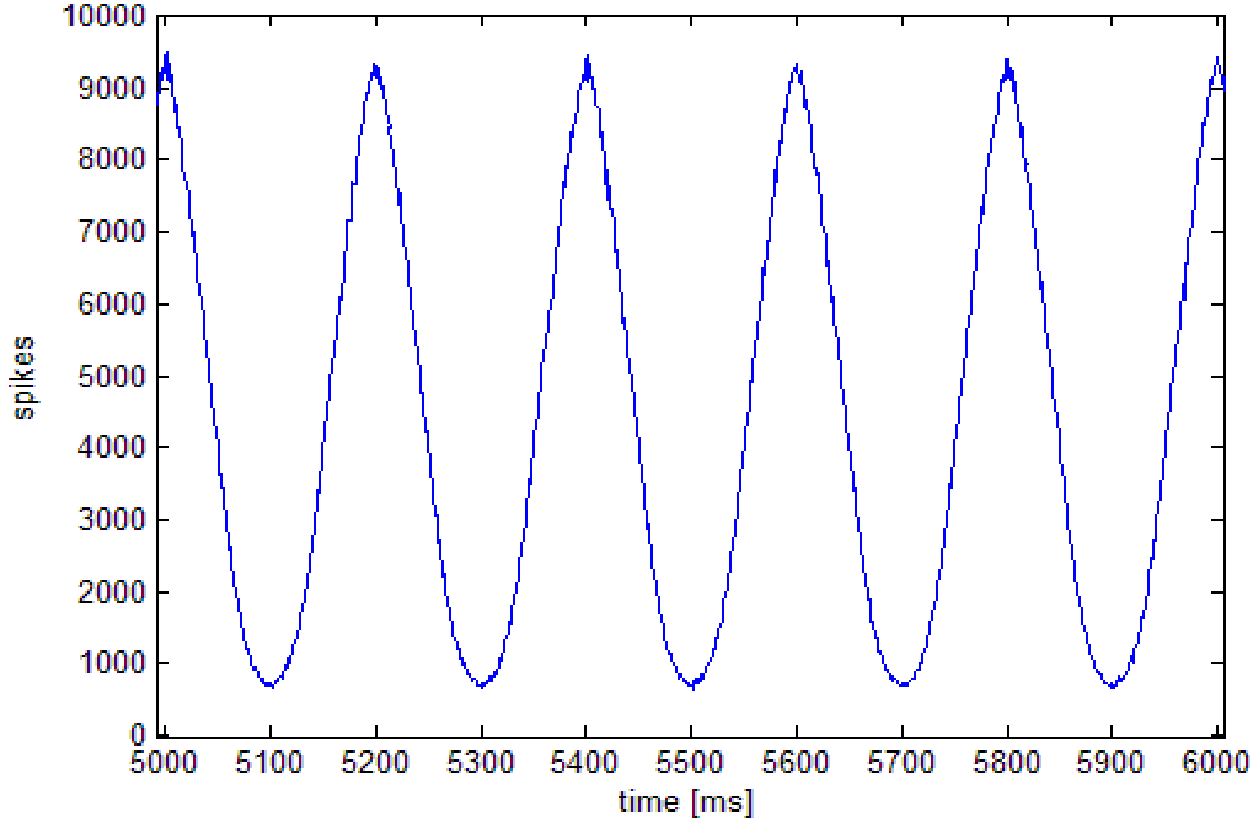
All-order intervals of square-wave driven neuron

Multi-Order Spike Intervals – Stimulated Neuron



All-order interval distribution for spikes within one second

Multi-Order Spike Intervals – Stimulated Neuron



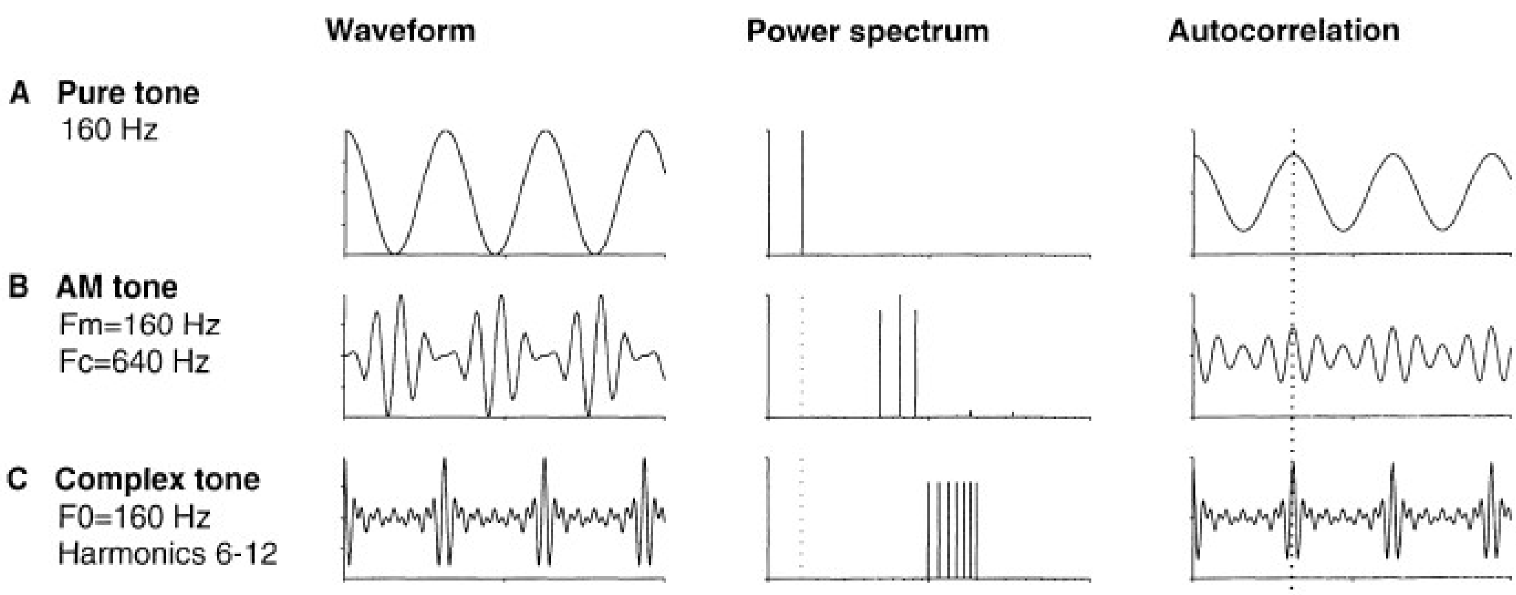
All-order interval distribution for spikes with 5-6 seconds separation

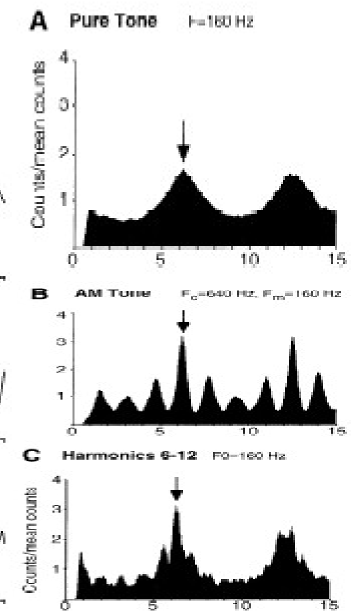
Autocorrelation in the auditory nerve

JOURNAL OF NEUROPHYSIOLOGY
Vol. 76, No. 3, September 1996. *Printed in U.S.A.*

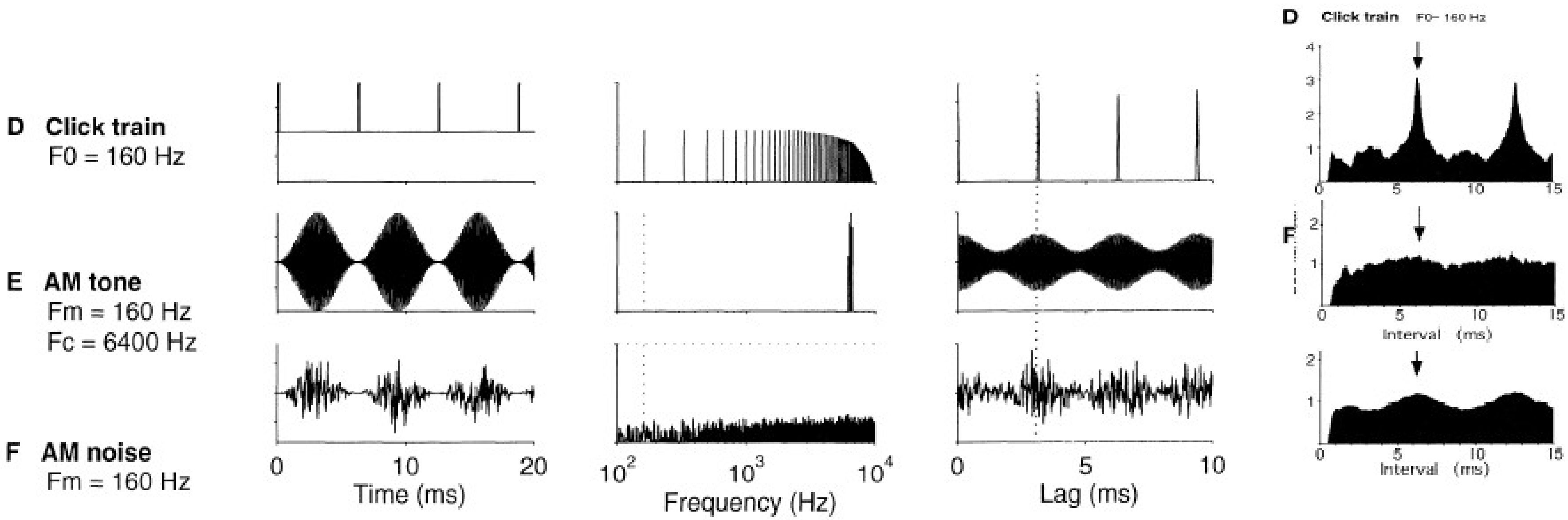
Neural Correlates of the Pitch of Complex Tones. I. Pitch and Pitch Saliencc

PETER A. CARIANI AND BERTRAND DELGUTTE



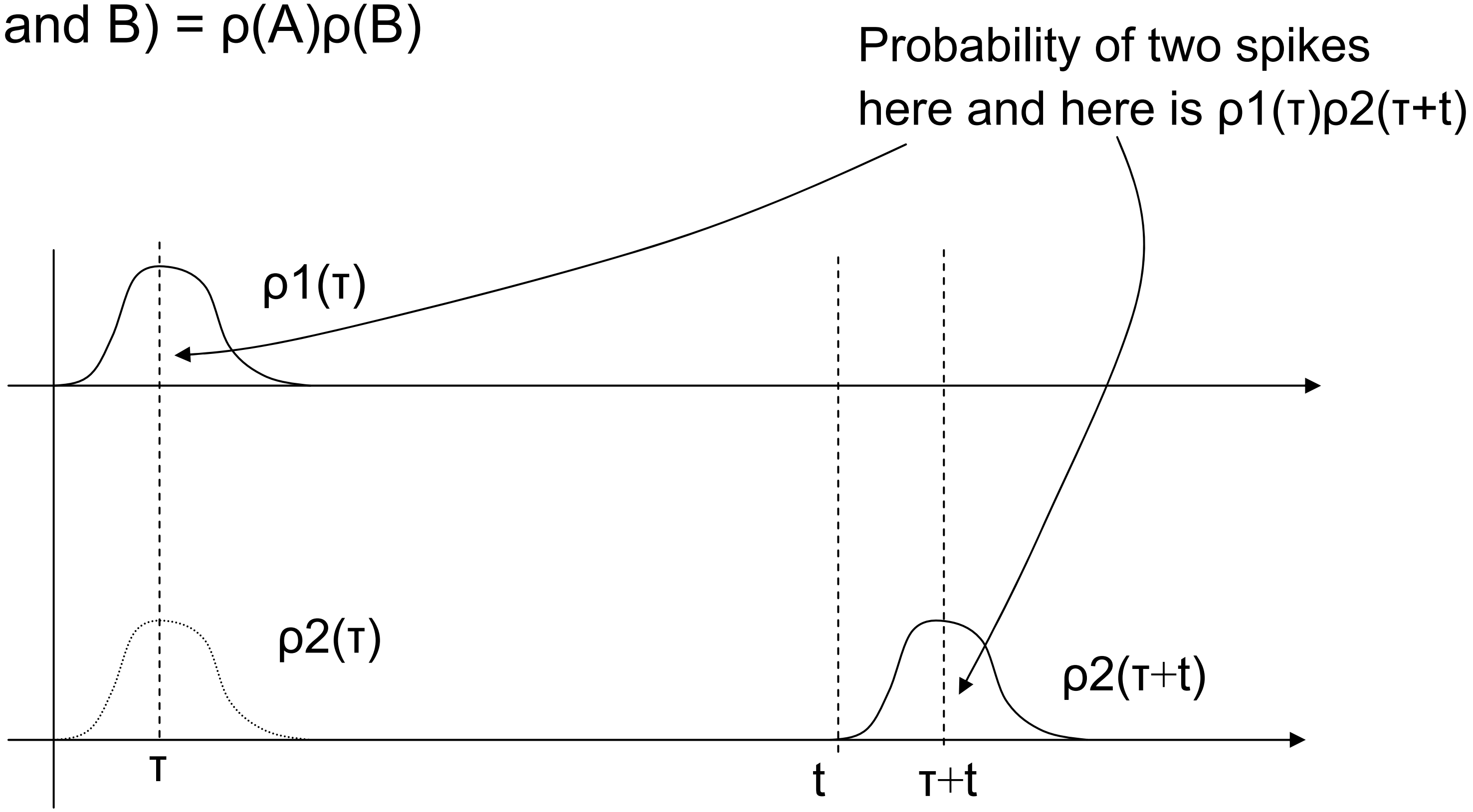


Autocorrelation in the auditory nerve



What if we combine two different neuron outputs?

$\rho(A \text{ and } B) = \rho(A)\rho(B)$



Mathematical Correlation

- Autocorrelation function of a signal f(t):

$$R_{ff}(\tau) = \lim_{T\to\infty} \frac{1}{2T} \int_{-T}^{T} f(t) f(t+\tau) dt$$

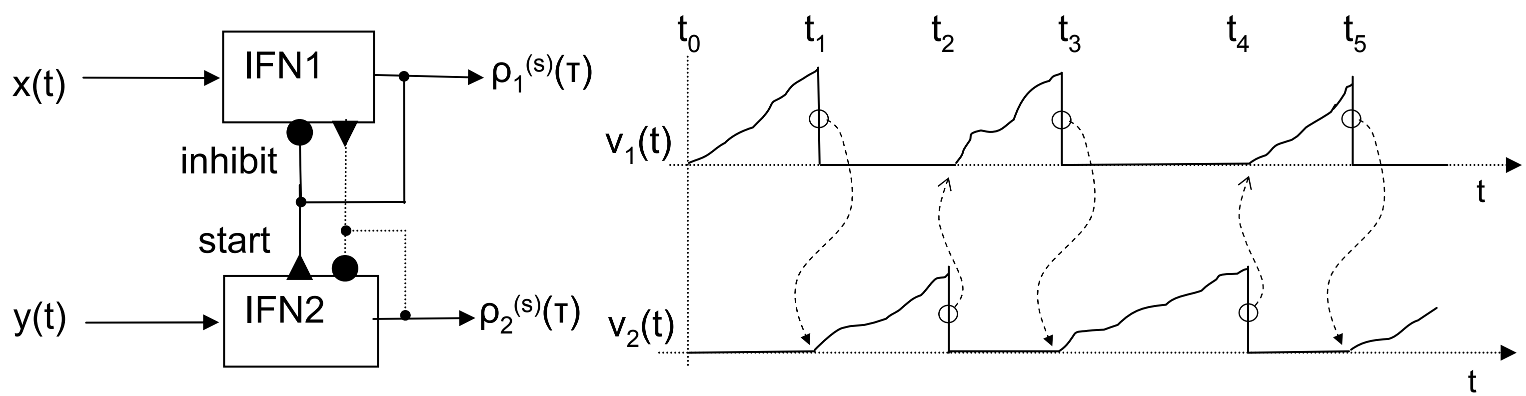
- Cross-Correlation
  - Periodic

$$R_{fg}(\tau) = \frac{1}{T} \int_{0}^{T} f(t) g(t+\tau) dt$$

  - Non-periodic

$$R_{fg}(\tau) = \lim_{T\to\infty} \frac{1}{2T} \int_{-T}^{T} f(t) g(t+\tau) dt$$

The Alternating-Neuron Circuit



Theoretical Foundation

If we have an integrate and fire neuron with input g(t) described by:

$$v(\tau) = \int_{t_0}^{t_0+\tau} f(v,t,\sigma) + kg(t)dt$$

Then its differential is:

$$\frac{dv(\tau)}{dt} = \frac{d}{d\tau}\int_{t_0}^{t_0+\tau} f(v,t,\sigma) + g(t)dt$$

And if it approaches threshold θ at time τ this becomes:

$$\left.\frac{dv(\tau)}{dt}\right|_{v\to\theta} = f(v,t_0+\tau,\sigma) + g(t_0+\tau)$$

Which suggests that the effect of the signal g(t) on the firing times will be:

$$\rho_{AM}\left(\tau \middle| t_0\right) = \rho(\tau)\left(1 + wg\left(t_0+\tau\right)\right)$$

If we model the alternate neuron circuit distribution of firing times:

$$q_{2(IFN2),1(IFN1)}(\tau, t_{0(}(\text{IFN1})) = \{\text{Prob that in sequence}\,[t_0(\text{IFN2}), t_1(\text{IFN1}), t_1\ (\text{IFN2})],\ t_1 \text{ and } t_2 \text{ are separated by } \tau\}$$

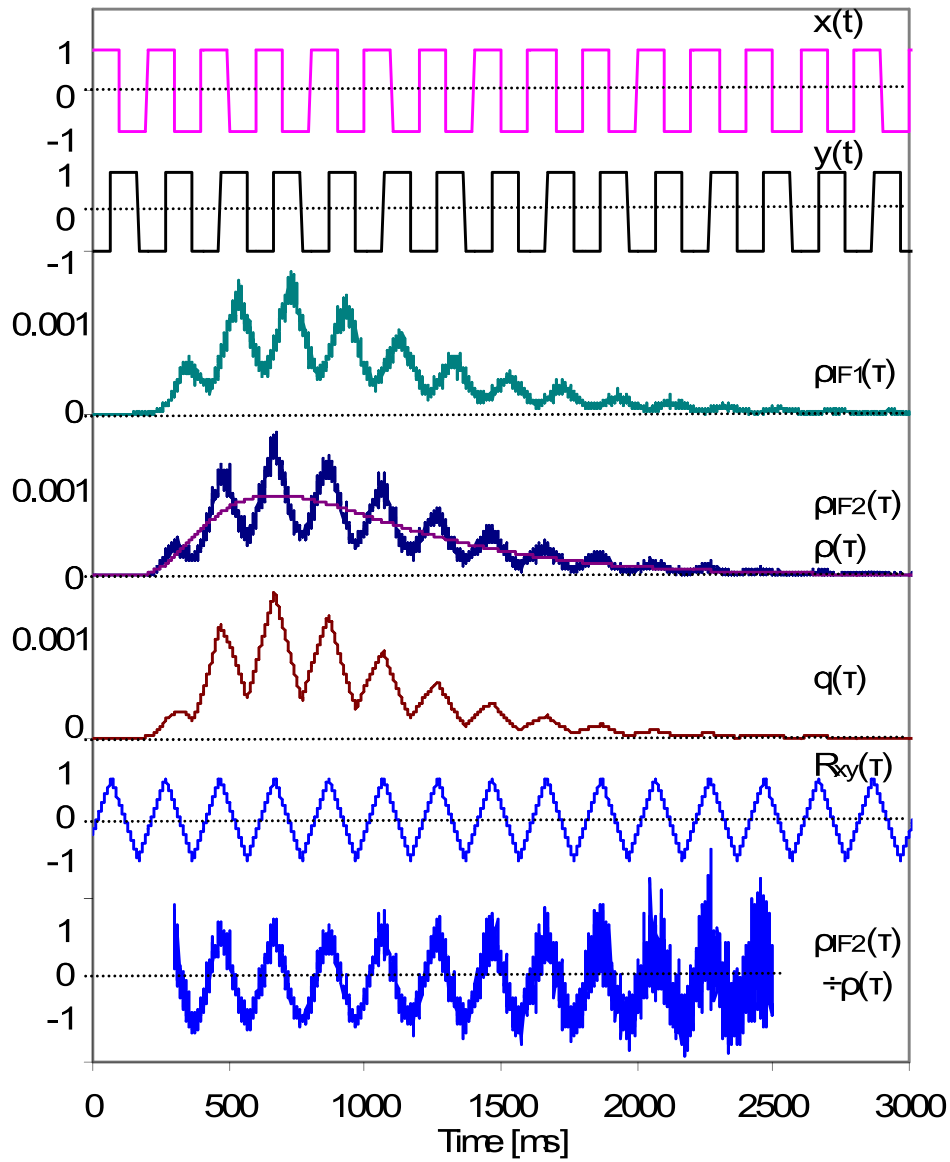
$$= \int_{t_0}^{\infty} \rho_{IFN1}\left(t_1+\tau \middle| t_1\right)\rho_{IFN2}\left(t_1 \middle| t_0\right)dt_1$$

$$= \int_{t_0}^{\infty} \rho(\tau)\rho(t_1-t_0)(1+wy(t_1+\tau))(1+wx(t_1))dt_1$$

$$= \int_{t_0}^{\infty} \rho(\tau)\rho(t_1-t_0)dt_1 + w\int_{t_0}^{\infty} \rho(\tau)\rho(t_1-t_0)y(t_1+\tau)dt_1$$
$$+ w\int_{t_0}^{\infty} \rho(\tau)\rho(t_1-t_0)x(t_1)dt_1$$
$$+ w^2\int_{t_0}^{\infty} \rho(\tau)\rho(t_1-t_0)y(t_1+\tau)x(t_1)dt_1$$

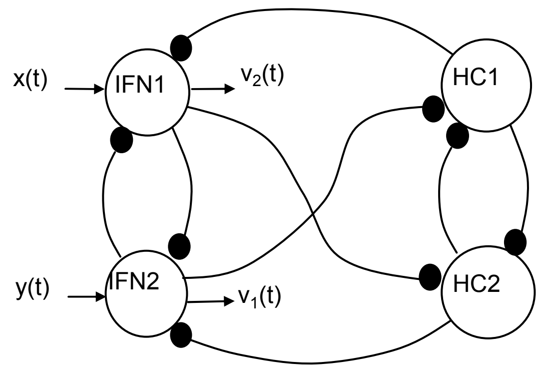
$$\approx \rho(\tau) + w^2\rho(\tau)\int_{t_0}^{\infty} y(t_1+\tau)x(t_1)dt_1$$

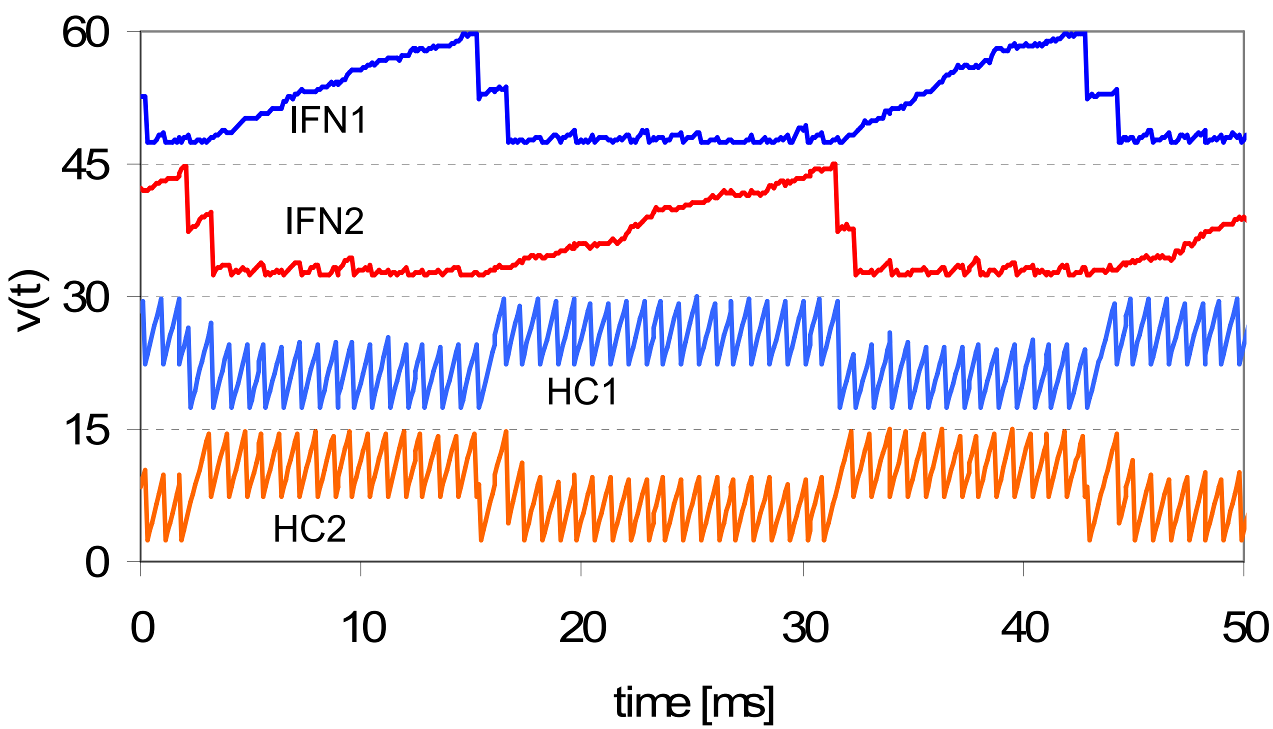
$$= \rho(\tau)\left(1 + w^2 R_{xy}(\tau)\right)$$



x(t)
y(t)
ρIF1(τ)
ρIF2(τ)
ρ(τ)
q(τ)
Rxy(τ)
ρIF2(τ)
÷ρ(τ)
1
0
-1
0.001
0
0 500 1000 1500 2000 2500 3000
Time [ms]

Physiological Plausible Implementation





Implementation on CPG chip

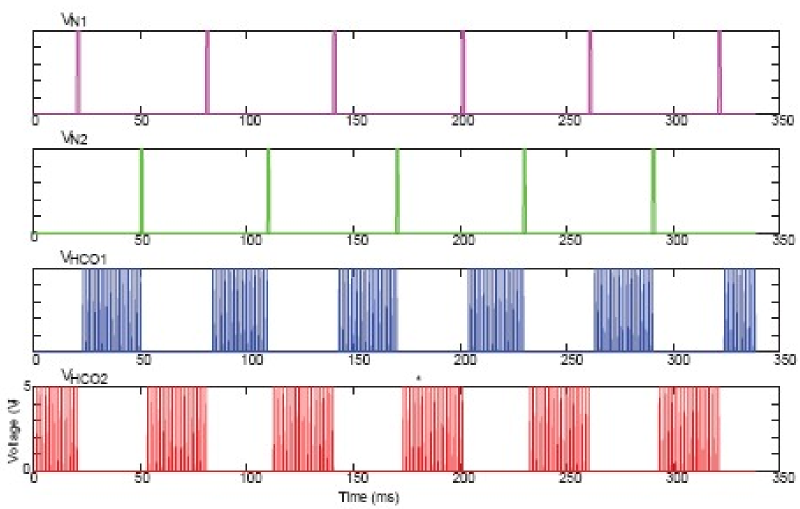
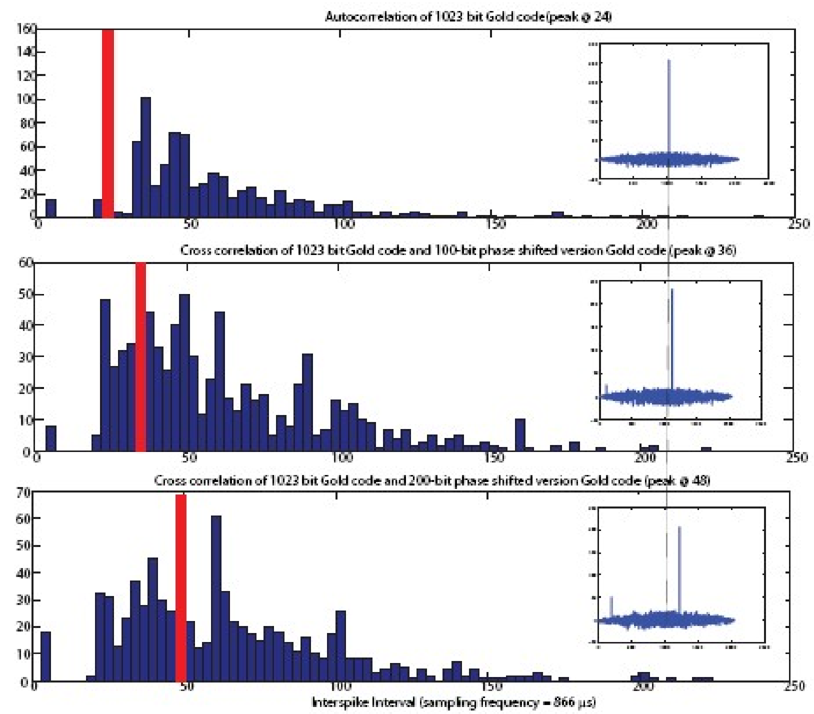
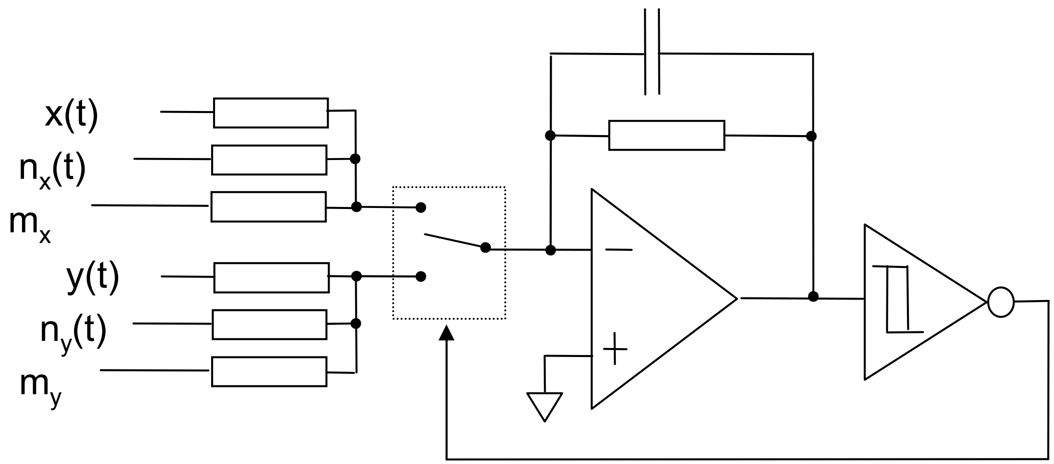


Fig. 3. Steady state behavior of the network ($T_w = 0$)



Folowosele et al., Proc. IEEE ISCAS 2008

Simple Circuit Unit



Leaky integrator which switches input source at hysteretic comparator thresholds

Two sources: each composed of the sum of

- One of the signals to be correlated
- A DC bias
- Noise (AWGN)

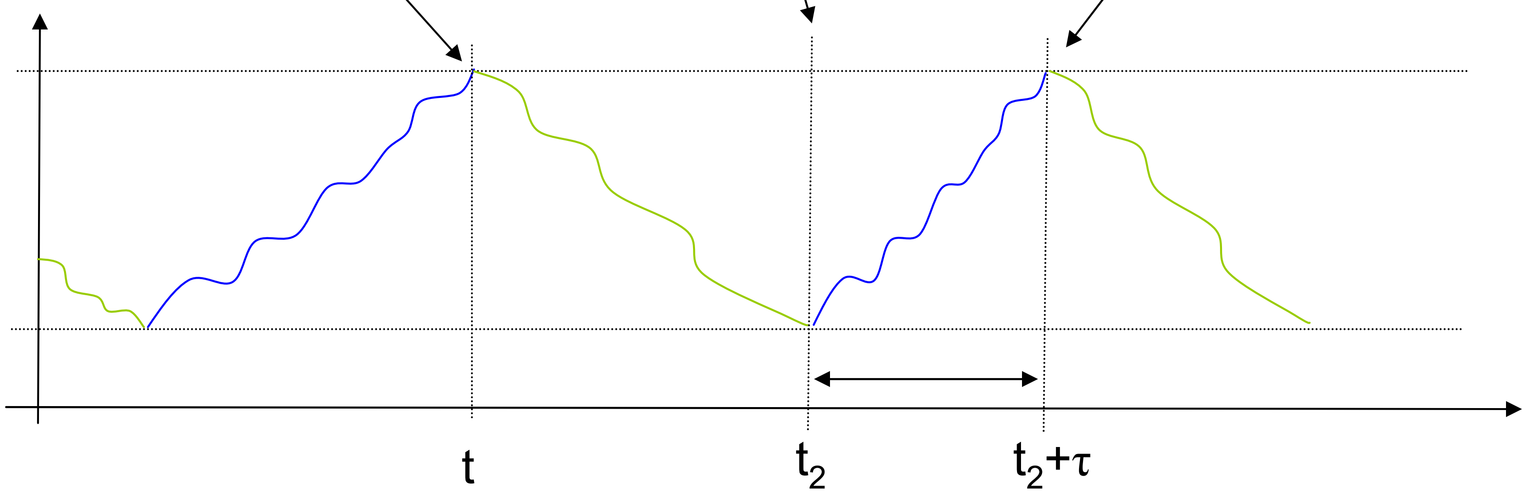
Same topology as asynchronous Δ-Σ converter by Wei, Garg, Harris (ISCAS 2006), except for alternating input signals

What affects the spike interval?

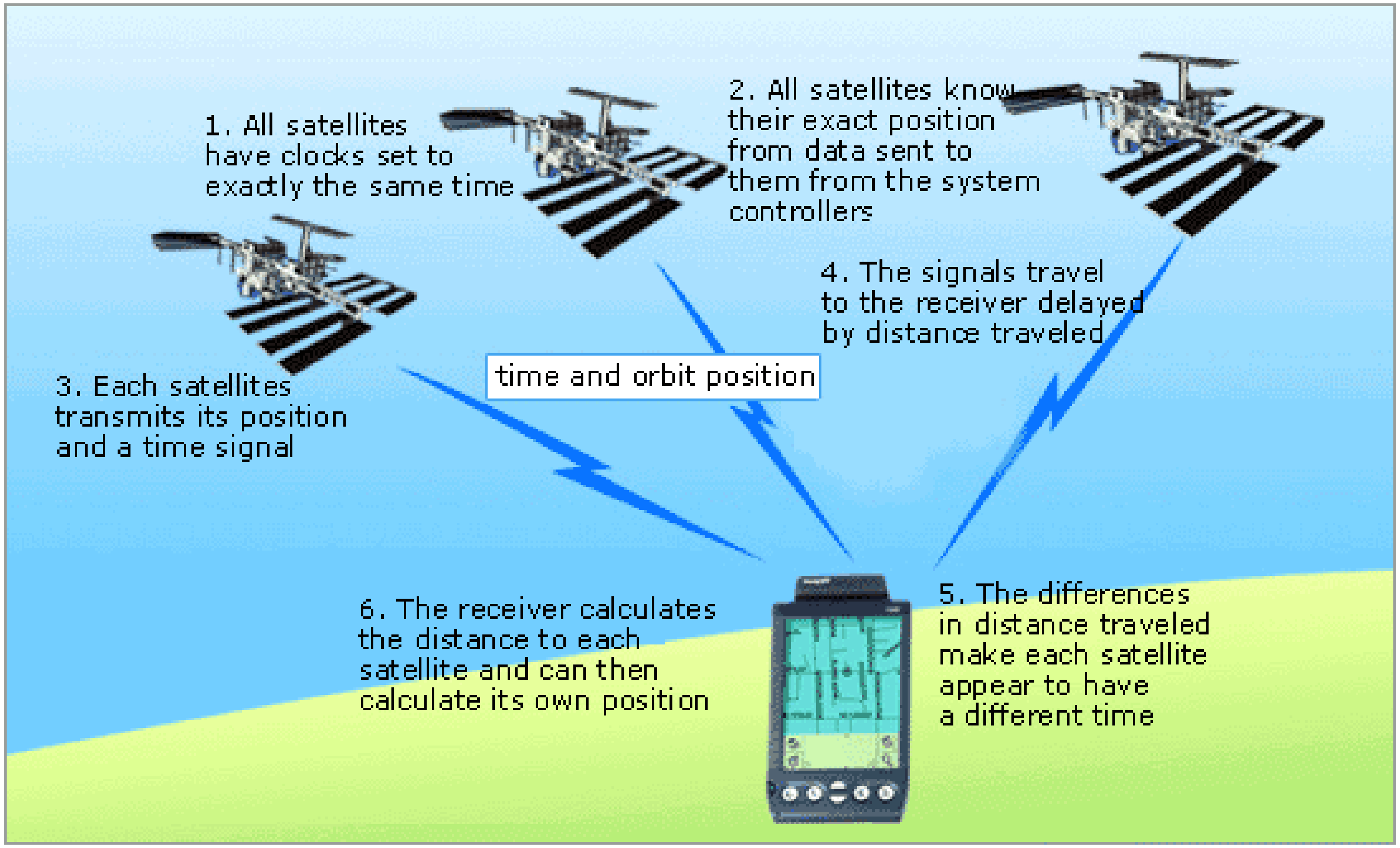
1. Probability of firing depends on slope of $x(t)$

2. Probability of firing at this interval depends on probability of firing here i.e. on $x(t_2)$…

…and probability of firing here, i.e. on $y(t_2+\tau)$



Application: the Global Positioning System



Source: www.navicom.co.kr

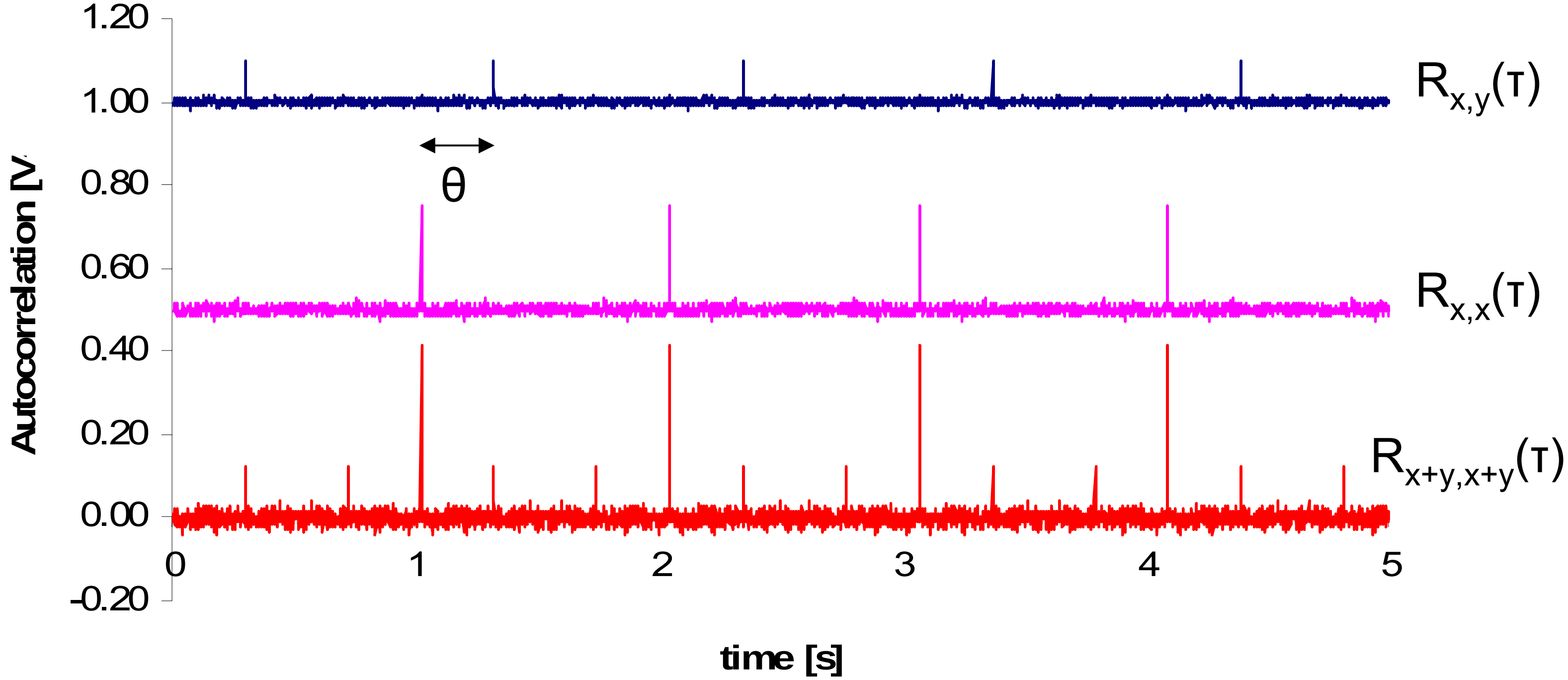
GPS Signals: Pseudorandom codes

- Binary serial codes
- Designed to have noise-like character:
  - Sharp autocorrelation peaks
  - Near orthogonality between codes
- Usually created with linear feedback shift registers
- Many types
  - maximum length sequences
  - Gold codes
  - Kasami codes
  - Welch codes
- Gold codes – 1023 bits, used in GPS C/A mode

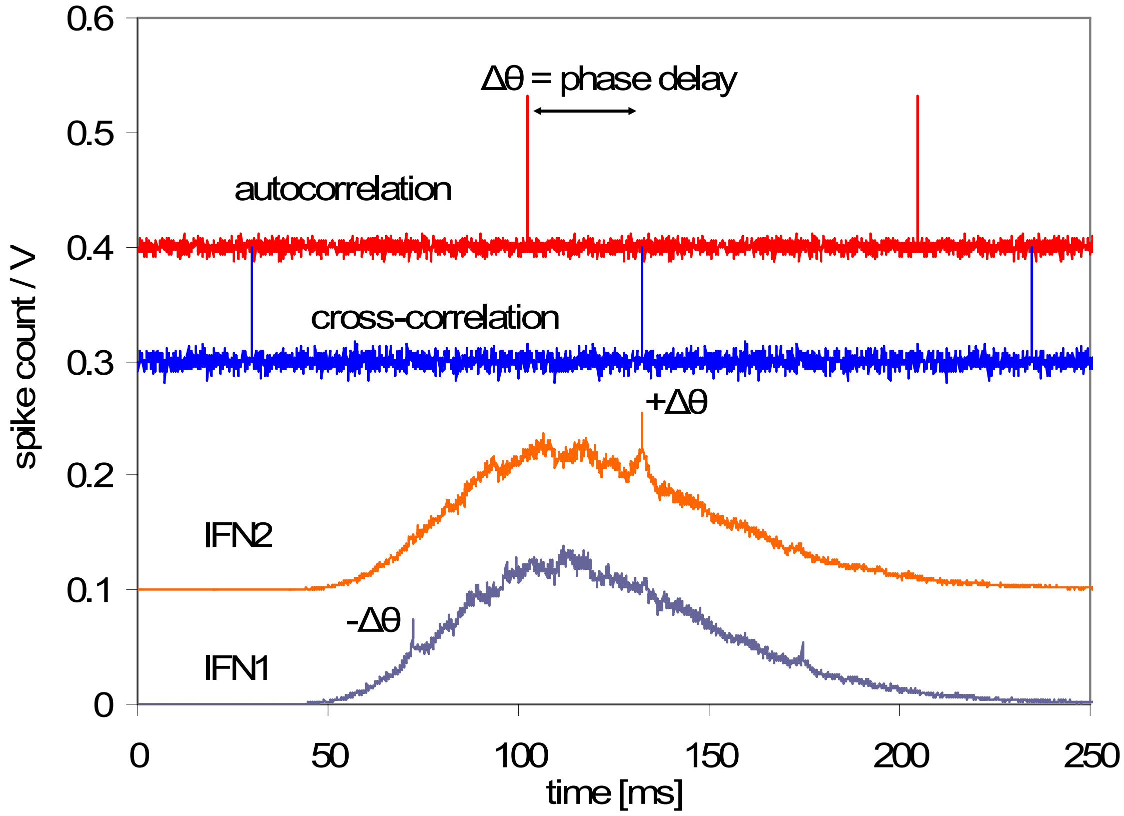
Cross-correlation functions of Gold codes

$X = G_1(t)$ (local copy)

$Y = G_1(t+\theta) + G_2(t)$ (received signal)

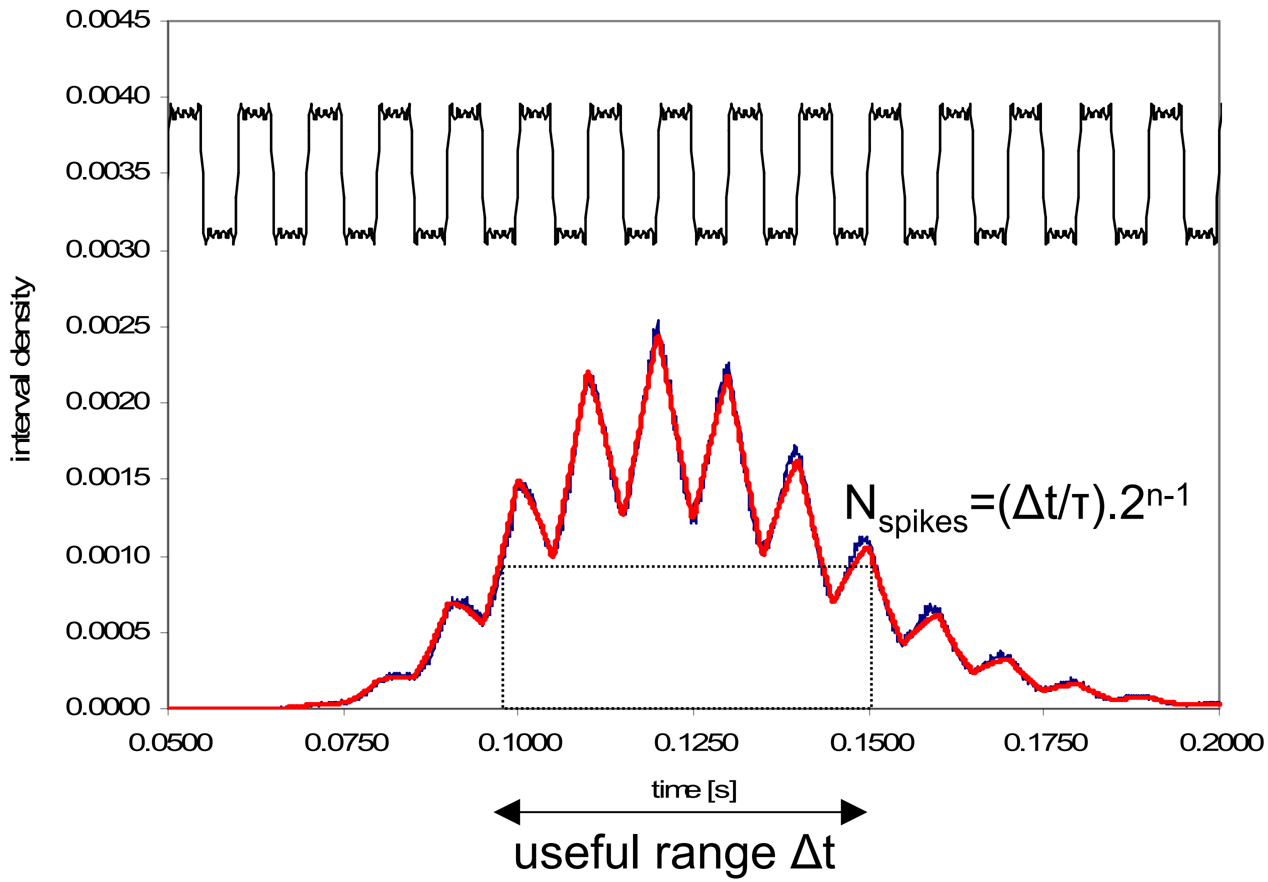


Cross-Correlation of PN codes

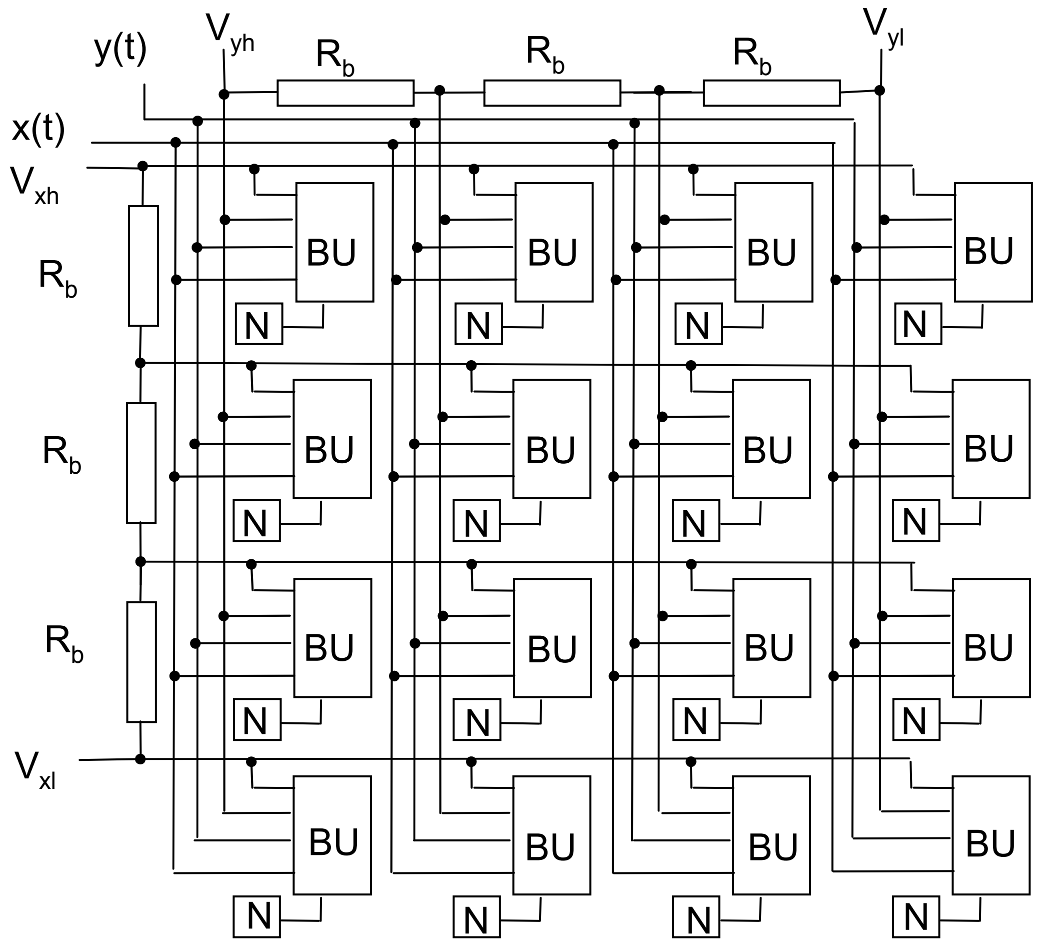


Stochastic Cross-Correlation

- Problem of range:

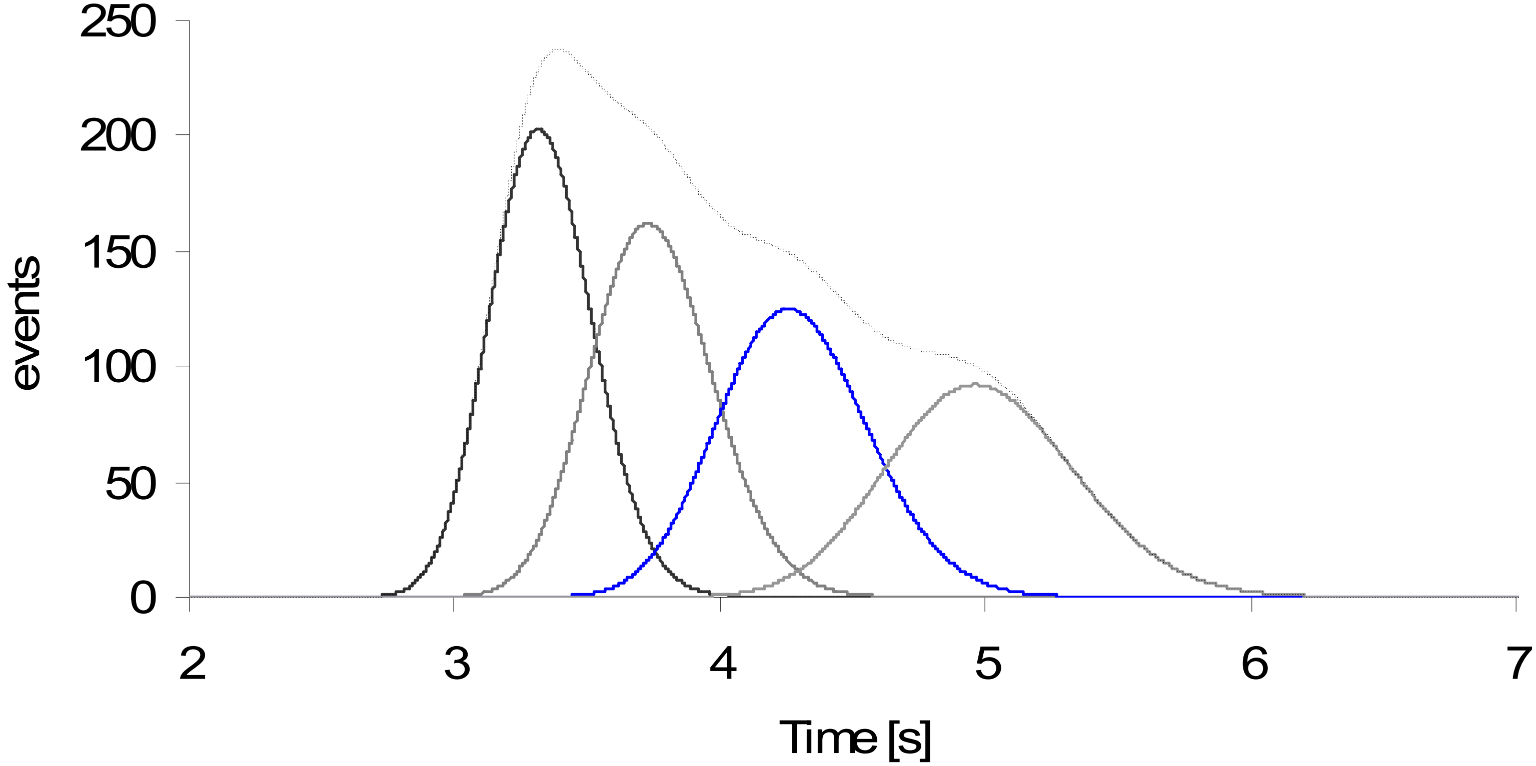


Multi-unit architecture

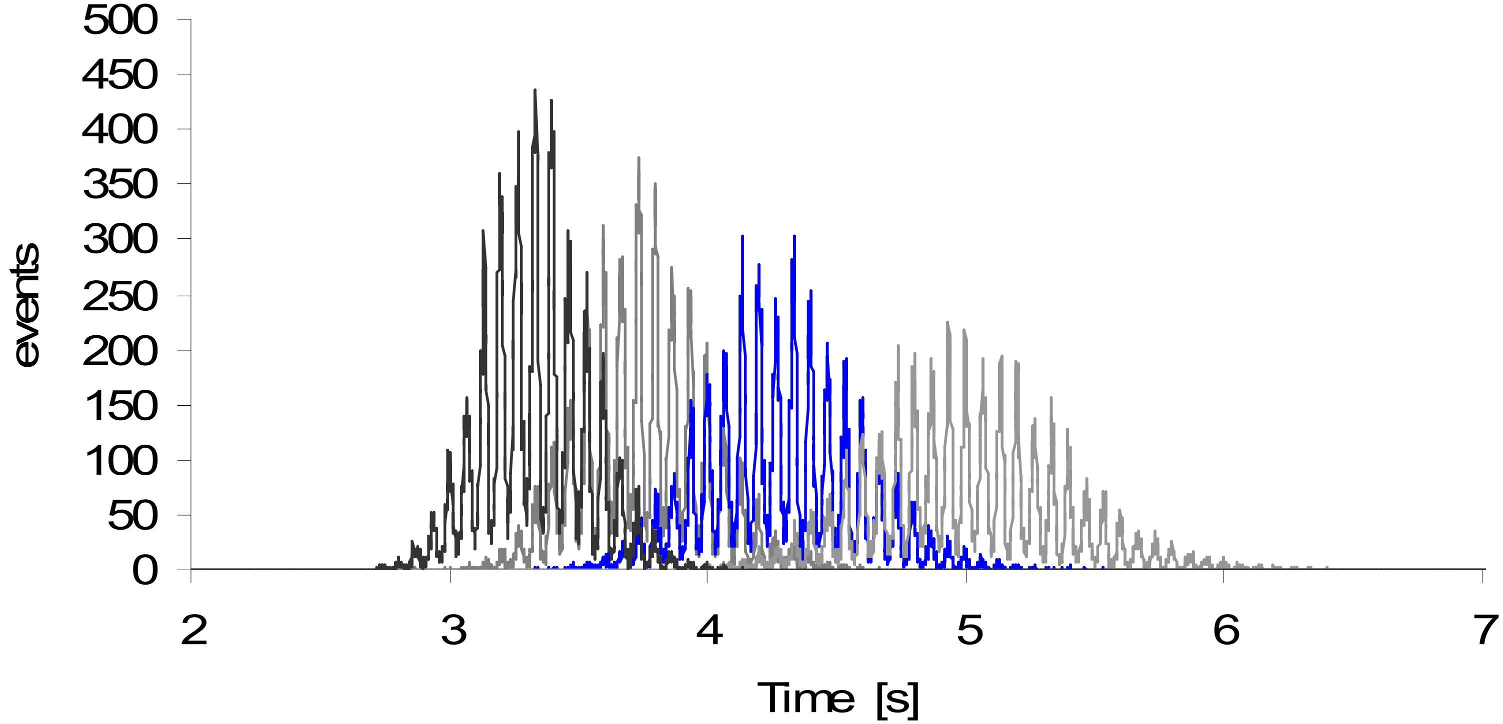


Tapson et al., BioCAS 2007

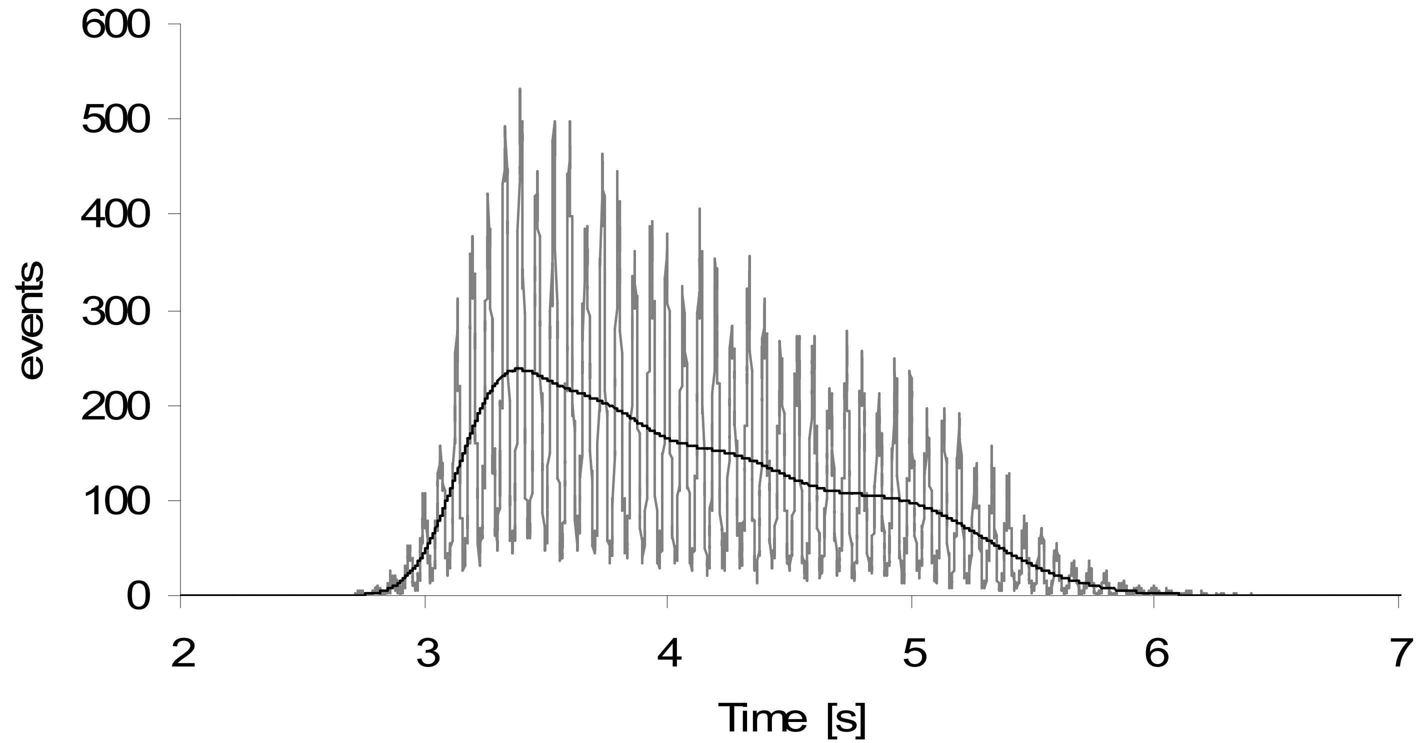
Variable bias values



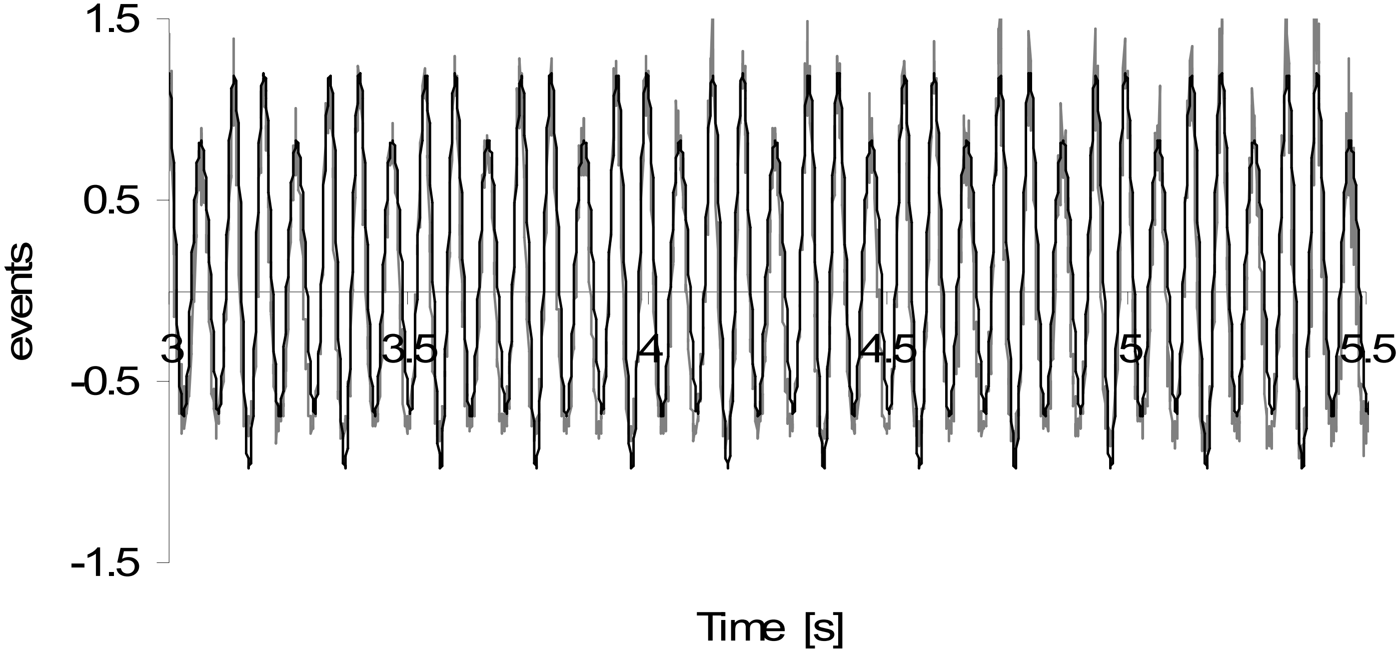
System Cross-Correlating



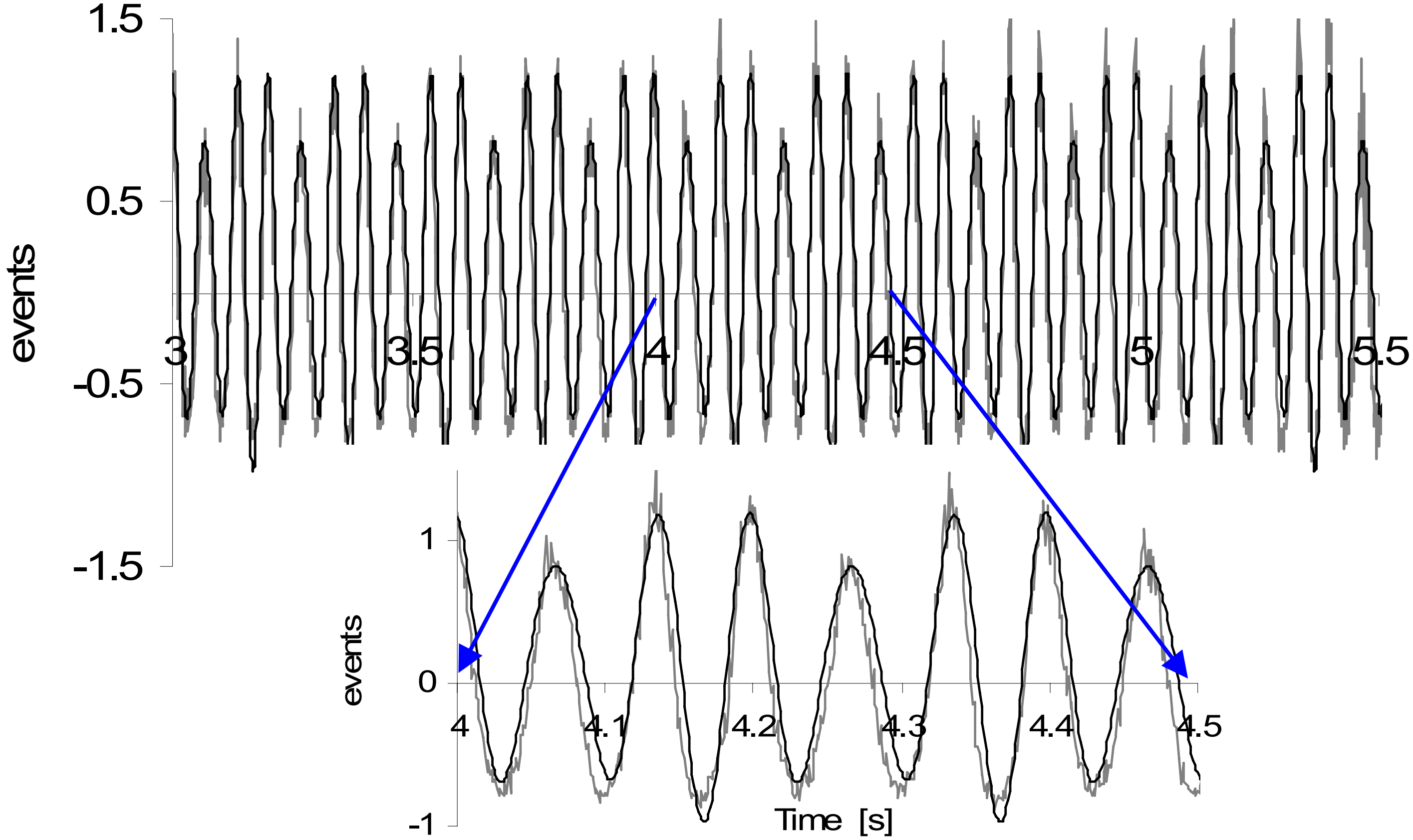
System Cross-Correlating



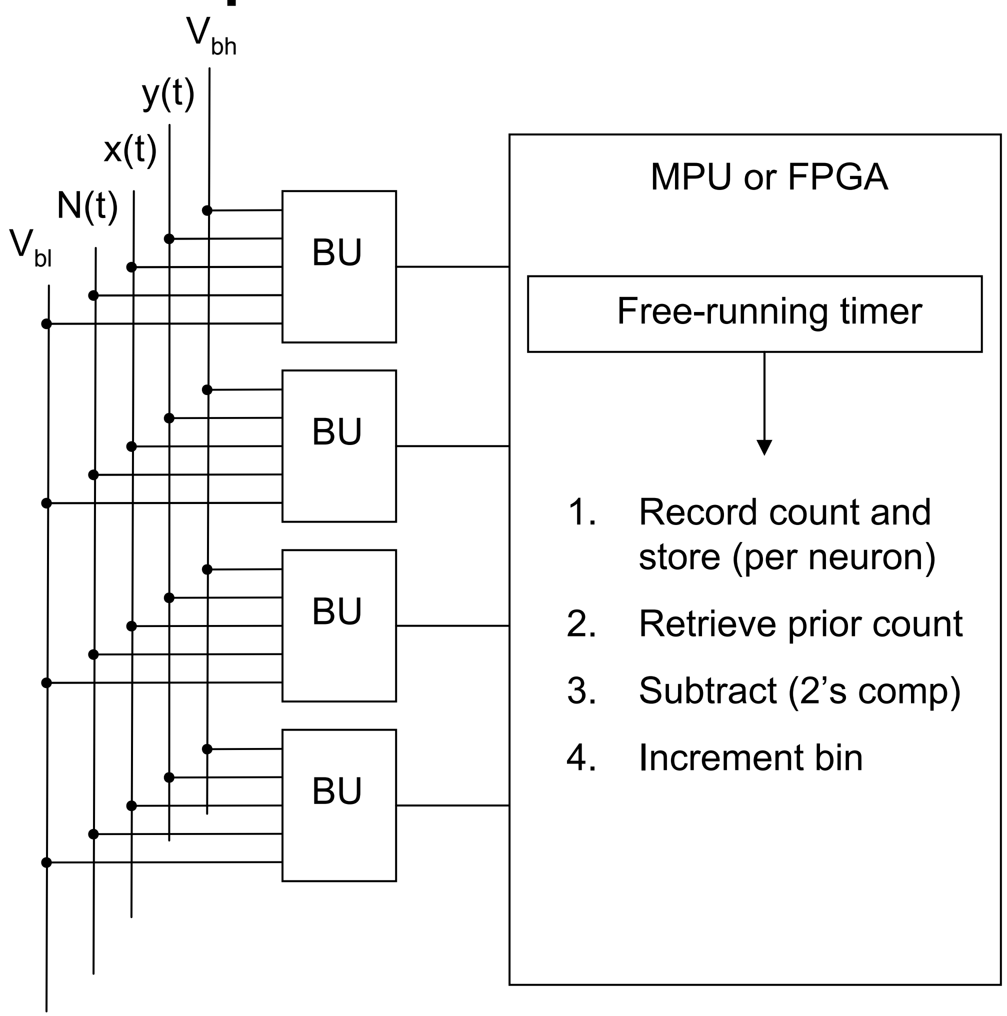
System Cross-Correlating



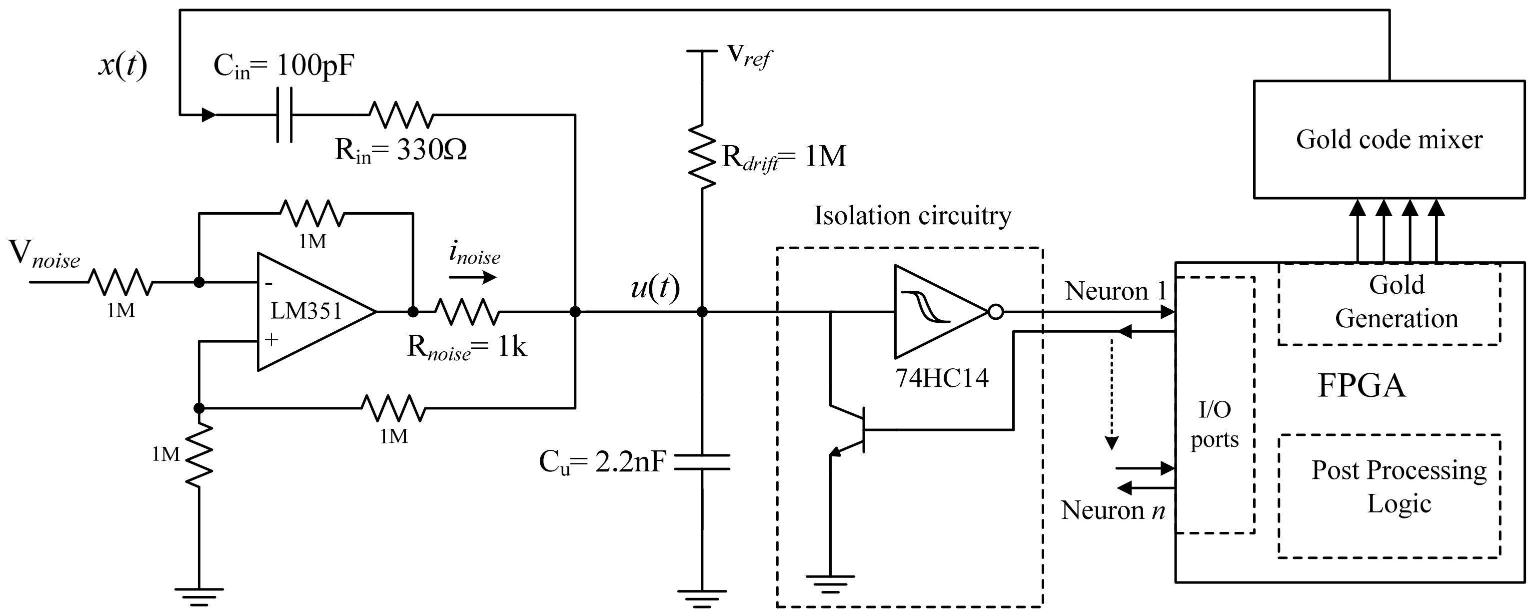
System Cross-Correlating



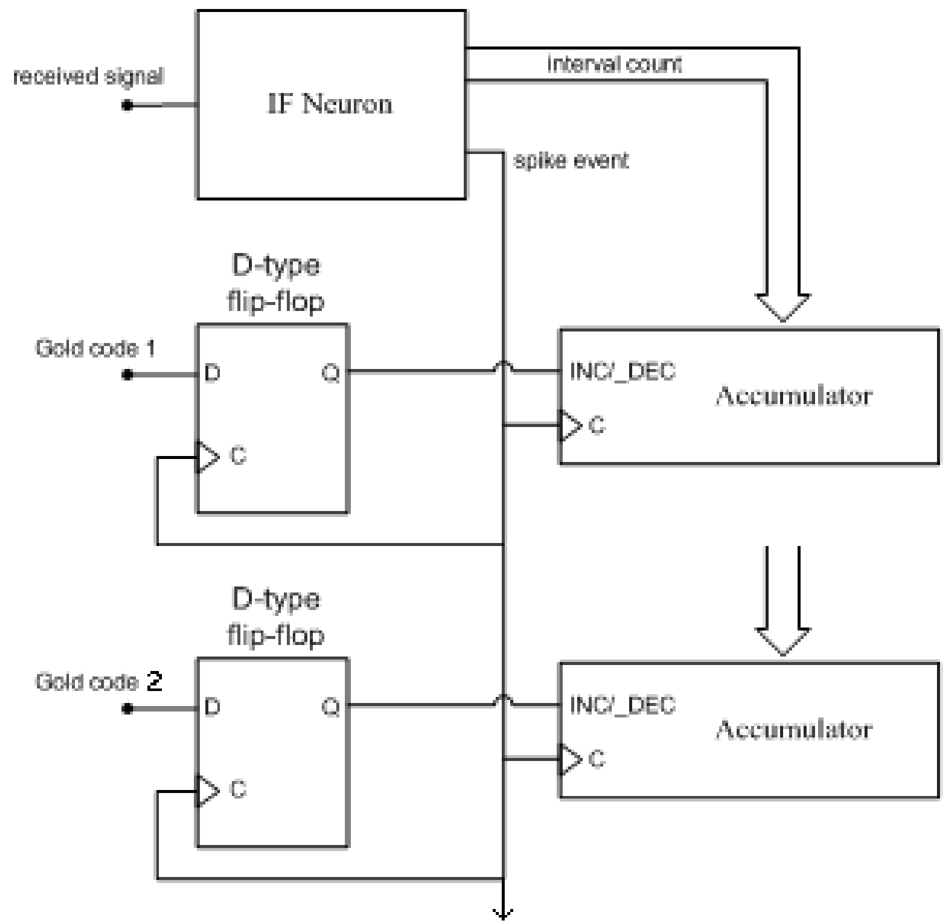
simpler architecture

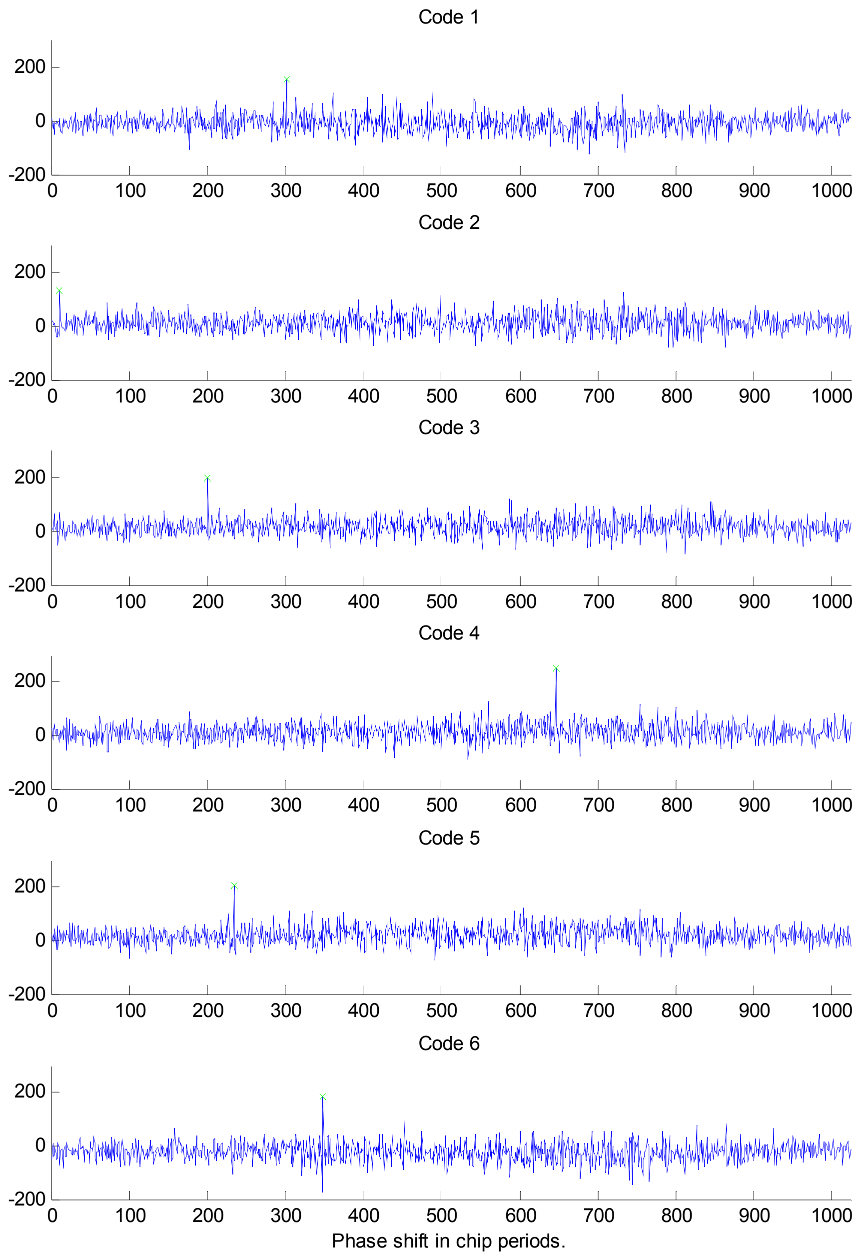


A practical circuit



Mark Vismer, 2008


received signal
IF Neuron
interval count
spike event
D-type
flip-flop
Gold code 1
D
Q
C
INC/_DEC
C
Accumulator
D-type
flip-flop
Gold code 2
D
Q
C
INC/_DEC
C
Accumulator



Code 1
Code 2
Code 3
Code 4
Code 5
Code 6
200
0
-200
0
100
200
300
400
500
600
700
800
900
1000
Phase shift in chip periods.

Conclusions

- Even very simple neurons have complex behavior in terms of transfer of spike rate and spike timing.
- Not all input spikes are equal in their effect; input spikes which occur near threshold have a disproportionate effect on output spike timing.
- The result of this is that the spike interval distribution encodes the input signal in a predictable way (if the neuron is operating in the right regime).
- Correlations in the first and all-order ISIHs arise as a natural result of this process.
- We can build spike-based circuits which take advantage of this fact to perform cross-correlations in real-world systems like GPS and CDMA.

The End