Spiking Neurons and Noise

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Last year...

- Marginalize to eliminate primary Markov property:

\[
q_{t_{2}-t_{1}}(\tau) = \{\text{Prob that first and second spikes after } t_0 \text{ are separated by } \tau\}
\]

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

\[
= \int_{t_0}^{\infty} \rho_{LP}(t_1 + \tau|t_1) \rho_{LP}(t_1|t_0) dt_1
\]

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

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

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

\[
q_{t_{2}-t_{1}}(\tau) = \rho(\tau) + w^2 \rho(\tau) \int_{t_0}^{\infty} g(t_1 + \tau) g(t_1) dt_1
\]

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

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

\[ v(\tau) > \theta : v(\tau) \leftarrow v_{\text{reset}} \]

\[ kT = \theta - v_{\text{reset}} \]
Add a stimulus

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

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

$$v(\tau) > \theta : v(\tau) \leftarrow v_{\text{reset}}$$
Add a stimulus

- Excitatory synaptic input spikes of constant energy \( a \) at random times \( t_i \):

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

\[
v(\tau) > \theta : v(\tau) \leftarrow v_{\text{reset}}
\]
More spikes

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

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

# spikes

ISIH

\[ k\tau + na = \theta - v_{reset} \]

potential [mV]

0 5 10 15 20 25

0 10 20 30 40 50

time [ms]
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

\[ v(\tau) = \int_{t_0}^{t_0+\tau} k + b \nu + a \delta(t - t_i) \, dt \]
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
What happens near the threshold?

Threshold $\theta$
What happens near the threshold?

Threshold $\theta$

All inputs happening before here
Cause spikes here

All inputs happening after here

Cause spikes at the precise time of the input

$\theta - a$

Potential [mV] vs. time [ms]
What happens near the threshold?

Threshold $\theta$

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

nT, n integer

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
    \[ v(\tau) = \int_{t_0}^{t_0 + \tau} k + \zeta(t) + a \delta(t - t_i) \, dt \]
    Where \( \zeta \) 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:

\[ v(t) \]

Threshold \( \theta \)

\[ P(a) \]

Postsynaptic input amplitude distribution

\[ p(t_{input}=t_{output}) \]
What happens near the threshold?

Threshold $\theta$

All inputs happening before here

Cause spikes here

All inputs happening after here

Cause spikes at the precise time of the input
Probability of synchronization

- Integrate and fire, uniform distribution of spike amplitude:

\[ v(t) \]

Threshold \( \theta \)

\[ a \]

\[ \theta - a \]

Postsynaptic input amplitude distribution

\[ P(a) \]

0 1

0 1/a a

\[ p(t_{\text{input}} = t_{\text{output}}) \]

1
Probability of synchronization

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

  ![Diagram showing probability of synchronization](image)

  - Postsynaptic input amplitude distribution
  - Threshold $\theta$
  - $p(t_{\text{input}} = t_{\text{output}})$
  - $v(t)$
Probability of synchronization

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

![Diagram showing the probability distribution and the threshold for synchronization.](image)
Probability of synchronization

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

\[ v(t) \]

\[ \theta \]

\[ P(a) \]

0 \[\rightarrow\] 1

Postsynaptic input amplitude distribution

Modulated input

Threshold \( \theta \)

Modulated synchronization

\[ p(t_{\text{input}}=t_{\text{output}}) \]

0 \[\rightarrow\] 1
Input spike spread function

\[ \Delta \rho(\tau) \]

Time [ms]

membrane potential [mV]

\[ u = kt \]
Input spike spread function

\[ \Delta \rho(\tau) \]

\[ u = kt \]
Another view

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

\[ v(\tau) = \int_{t_0}^{t_0+\tau} k + \zeta + g(t) \, dt \]

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

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

input signal
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.

\[
\rho_c(\tau, \phi) = \rho_0(\tau)(1+wg(t,\phi))
\]
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

$\tau$
Multiplication by Combination of Probabilities

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

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

Probability of two spikes here and here is $\rho(\tau)\rho(\tau+t)$. 

\begin{align*}
\text{Probability of two spikes} & \quad \text{here and here is } \rho(\tau)\rho(\tau+t) \\
T & \quad t \quad T+t
\end{align*}
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

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.
First order intervals and second order intervals between spikes
Multi-Order Spike Intervals

Up to $10^{\text{th}}$ 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

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

PETER A. CARIANI AND BERTRAND DELGUTTE
Autocorrelation in the auditory nerve

- **Click train**
  - $F_0 = 160$ Hz

- **AM tone**
  - $F_m = 160$ Hz
  - $F_c = 6400$ Hz

- **AM noise**
  - $F_m = 160$ Hz
What if we combine two different neuron outputs?

\[ \rho(A \text{ and } B) = \rho(A)\rho(B) \]

Probability of two spikes here and here is \( \rho_1(\tau)\rho_2(\tau+t) \)
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 \( \theta \) at time \( \tau \) 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:

\[
\rho_{AM}(\tau | t_0) = \rho(\tau)(1 + wg(t_0 + \tau))
\]

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

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

\[
= \int_{t_0}^{\infty} \rho_{IFN1}(t_1 + \tau | t_1) \rho_{IFN2}(t_1 | t_0) \, dt_1
\]

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

\[
= \int_{t_0}^{\infty} \rho(\tau) \rho(t_1 - t_0) \, dt_1 + w \int_{t_0}^{\infty} \rho(\tau) \rho(t_1 - t_0) y(t_1 + \tau) \, dt_1
\]

\[
+ w \int_{t_0}^{\infty} \rho(\tau) \rho(t_1 - t_0) x(t_1) \, dt_1
\]

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

\[
= \rho(\tau)(1 + w^2 \bar{R}_{xy}(\tau))
\]
Physiological Plausible Implementation
Implementation on CPG chip

Fig. 3. Steady state behavior of the network ($T_{wi} = 0$)

Fowosele et al., Proc. IEEE ISCAS 2008
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

1. All satellites have clocks set to exactly the same time.
2. All satellites know their exact position from data sent to them from the system controllers.
3. Each satellite transmits its position and a time signal.
4. The signals travel to the receiver delayed by distance traveled.
5. The differences in distance traveled make each satellite appear to have a different time.
6. The receiver calculates the distance to each satellite and can then calculate its own position.

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)

\[ R_{x,y}(\tau) \]
\[ R_{x,x}(\tau) \]
\[ R_{x+y,x+y}(\tau) \]
Cross-Correlation of PN codes

Δθ = phase delay

autocorrelation

cross-correlation

IFN2

IFN1

spike count / V

time [ms]
Stochastic Cross-Correlation

- Problem of range:

\[ N_{\text{spikes}} = (\Delta t/\tau) \cdot 2^{n-1} \]
Multi-unit architecture

Tapson et al., BioCAS 2007
Variable bias values

![Graph showing variable bias values over time.](image-url)
System Cross-Correlating
System Cross-Correlating
System Cross-Correlating
System Cross-Correlating
simpler architecture

1. Record count and store (per neuron)
2. Retrieve prior count
3. Subtract (2’s comp)
4. Increment bin
A practical circuit

Mark Vismer, 2008
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 ISIIsHs 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