Signal & Data Analysis in Neuroscience 2017
Part 2: Stochastic processes

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Overview

- Stochastic processes
- Extracellular recording
- Point processes

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Modeling our measurements

- Repetition of the same experiment will not lead to the exact same response.
- Example: The spike train of a neuron in response to stimuli is different…
- Typically we would like to know:
  - When is something unexpected?
  - What are the "normal" values?
- Thus, analyzing a sequence of measurements requires modeling of the underlying process.

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Stochastic process - definition

- **Stochastic** – (1) Involving chance or probability (2) Random (3) Non-deterministic (Merriam-Webster & Wikipedia).
- **Stochastic process** - an indexed collection of random variables $\{X_i\}$, where the index i ranges through an index set I, defined on the probability space (Ω, P). The index set may be discrete or continuous (Wikipedia).
- A stochastic process defined over the time interval domain is called a **time series**.
- A stochastic process defined over the space interval domain is called a **random field**.

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Stochastic process - examples

- Example 1: *A* continuous time series of the measured temperature in Bar-Ilan.
- Example 2: A discrete time series of whether any rain fell in Bar-Ilan during a specific day.
- Example 3: A discrete stochastic process (not a time series) of the heights of people entering the Gonda building.

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Stationary processes

- A (strictly) **stationary process** is a stochastic process in which the probability density function (pdf) of some random variable X does not change over indexes (such as time or position).
- A weak or wide-sense stationary (WSS) process only require that 1st and 2nd moments do not vary with respect to time.

$$E\big(X(t)\big) = \mu_x(t) = \mu_x(t+\tau) \qquad \forall\tau \in \mathbb{R}$$

$$E\big((X(t_1) - \mu_x(t_1)) \cdot (X(t_2) - \mu_x(t_2))\big) = Cov(X(t_1), X(t_2))$$
$$= Cov(X(t_1+\tau), X(t_2+\tau)) = Cov(X(t_1 - t_2), 0)$$

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Stationary processes - examples

- Stationary example: Sequence of L/R button presses. Each press has a 90% probability of being in the same direction as its predecessor.
  - Stationary despite strong temporal covariance.
- Non-stationary example: Amount of rainfall for each day of the year.
  - In many cases long term changes may be removed using **de-trending** techniques.

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Ergodicity

- If averaging over time and space are equal the process is **ergodic**.
- Ergodicity is usually described in terms of properties of an ensemble of objects.
- Example: Finding out how people spend their spare time. Sampling one person over 1000 days would yield the same result as sampling 1000 people once in an ergodic system.

Reading material:
http://news.softpedia.com/news/What-is-ergodicity-15686.shtml

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Ergodic & stationary processes

- In an ergodic process, the following are equal
  - Averaging across repeated trials
  - Averaging across time for a single trial
- An ergodic process is always stationary, the reverse may not be true
- A stationary process is ergodic if samples that are far enough in time are independent (asymptotic independence).

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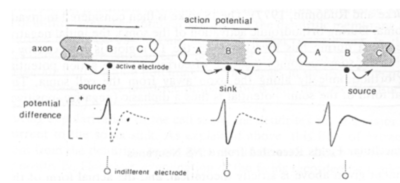
Recommended reading:
R. Lemon, Methods for neuronal recording in conscious animals, 1984, Chapter 2

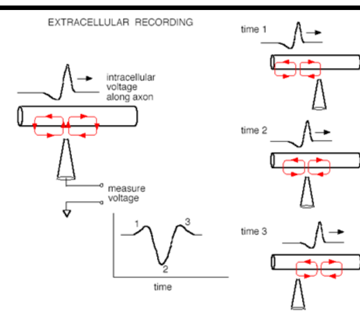
Formation of extracellular potential I

- Different membrane potentials of the neuron lead to flow of current within the neuron which is matched by an **extracellular return current**.



Sink – Active area, current flows into the neuron
Source – Inactive region, current flow out of the neuron.

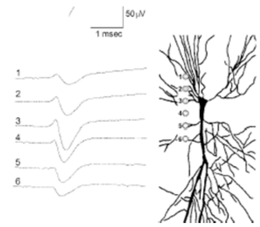
Formation of extracellular potential II



Axon – Triphasic shape (+/-/+)

Somatic extracellular spike shape

- Soma – Biphasic shape (-/+),
  - Negative due to flow from the initial segment
  - Positive due to flow to dendrite.
- Magnitude is proportional to surface area divided by the distance.



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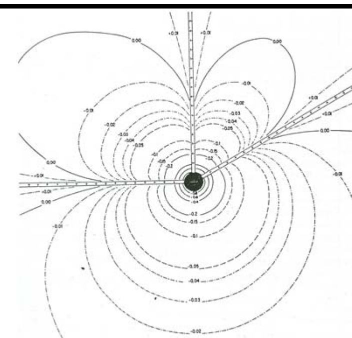
Decay of extracellular signal



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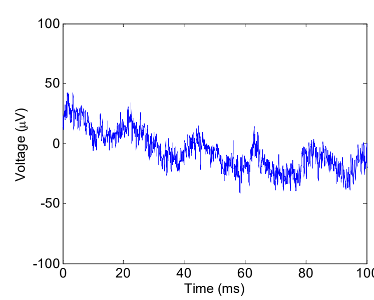
Extracellular recording I



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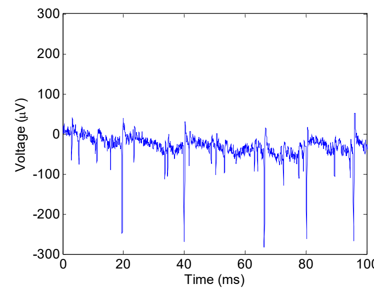
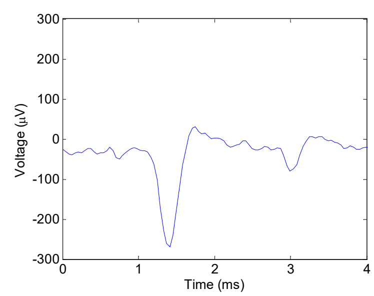
Extracellular recording II

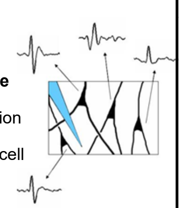


Extracellular recording III

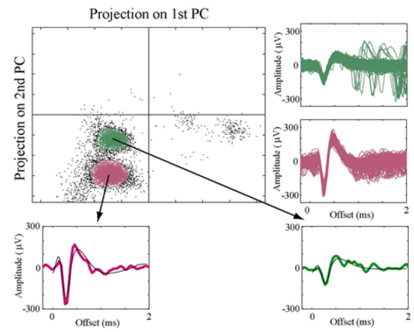


Multiple units

- The electrode detects multiple neurons (also called **units**) which are close to its tip.
- The signals differ in:
  - **Amplitude** -dependent on cell **size** and **distance**.
  - **Phase shape** - depends on direction to soma, axon & dendrites.
  - **Temporal shape** - dependent on cell type.
- Spikes from the same neuron also vary significantly due to noise, bursts, drift of electrode, etc..



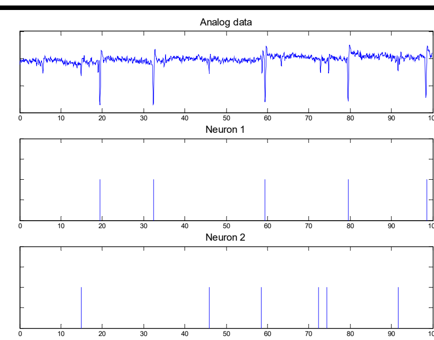
Sorting multiple units



Multiple units

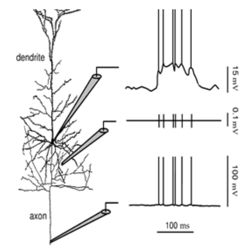
- Multiple single units
- Multi-unit activity
- Local field potential

Continuous signal → spike trains I



Continuous signal → spike trains II

- Intracellular soma
- Extracellular
- Intracellular axon



Spike trains

- Transformation from a continuous recording to a series of discrete **timestamps**.
- Is all the information contained in the **timing** of the spikes?
- What are we losing?
  - Spike shapes
  - Non spiking activity
  - Sub-threshold activity

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Time series & Point processes

- Continuous time series
  - Electroencephalogram (EEG)
  - Electromyogram (EMG)
  - Intracellular potential
  - …

(Note: “Continuous” is the common term but is misleading since it applies to both discrete and continuous in time)

- Stochastic point processes
  - Neural action potentials
  - Heart beats
  - Behavioral events
  - …

Delta functions (reminder)

- Dirac’s delta function

$$\delta(x-\tau)=0 \qquad x \neq \tau$$

$$\int_{-\infty}^{\infty} \delta(x-\tau)dx = 1$$

- Kronecker’s delta function

$$\delta(n-k)=\begin{cases}1 & n=k \\ 0 & n \neq k\end{cases} \qquad \sum_{n=-\infty}^{\infty} \delta(n)=1$$

Point process

- The spike train is represented by the sum of Dirac’s delta functions at its firing times (t_i)

$$\rho(t)=\sum_{i=1}^{n} \delta(t-t_i)$$

- Point processes are unitary events in time. The actual values in time are meaningless.

Properties of a single spike train

- Firing rate
- Response to events
- Firing pattern
- Exact timing
- Entropy
- …

The neural transformation

x(t) → Sensors → r(t) → Spike Generator → $\rho(t)$

x(t) = external signal

r(t) = spike rate

$\rho(t)$ = actual spikes

We observe $\rho(t)$, and we need to estimate r(t)

(eventually we will use this to estimate x(t))

Firing rate definition

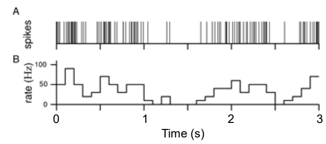
- There are actually quite a few definitions to firing rate
  - r – rate over the whole period T also called *spike count rate*
  - <r> - rate averaged over all the trials, also called *average firing rate*
  - *r(t)* – trial average rate over a short period ($\Delta t \rightarrow 0$)

and they are constantly mixed…

Firing rates – number of spikes

Firing rate: $r = \frac{n}{T} = \frac{1}{T}\int_0^T \rho(\tau)d\tau.$

Δt = 100 ms



From: Theoretical neuroscience / Dayan & Abbott

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Convolution

- Convolution is an **operator** which takes two functions *f* and *g* and produces a third function that represents the overlap between *f* and a reversed version of *g*.
- Continuous: $(f * g)(t) = \int f(\tau)g(t-\tau)\,d\tau$
- Discrete: $(f * g)(m) = \sum_n f(n)g(m-n)$

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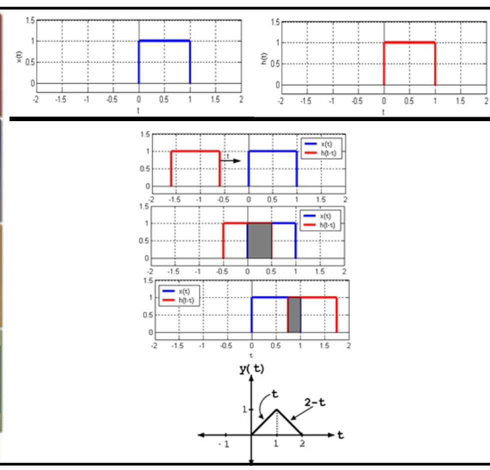

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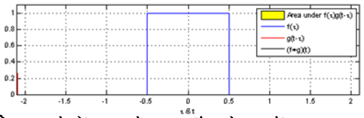
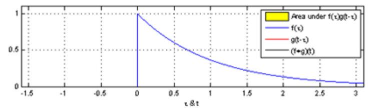
Convolution examples

- Convolution of a box function



- Convolution of a spiky function



(From: www.wikipedia.org, Brian Amberg)

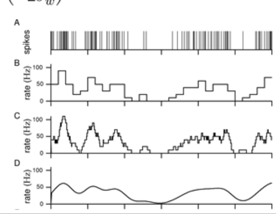
Convolution & Moving average

- A convolution is a general **moving average** when the averaging function integral is 1.
- In that case it functions as a **smoothing** function.
- When the averaging function is square it will function as regular mean using **overlapping bins**.
- Non-square functions enable **emphasis** of parts of the window.

Firing rates – sliding windows

Other definitions of firing rate use a sliding window: $r(t) = \int_{-\infty}^{\infty} d\tau w(\tau)\rho(t-\tau)$, with

$$w(t) = \frac{1}{\Delta t}, \quad -\Delta t/2 \leq t \leq \Delta t/2$$
$$w(t) = \frac{1}{\sqrt{2\pi}\sigma_w} \exp\left(-\frac{t^2}{2\sigma_w^2}\right)$$

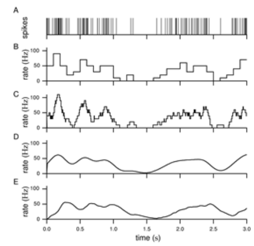


Sliding rectangular window
Δt = 100 ms

Sliding Gaussian window
σ_t = 100 ms

Firing rates - causal windows

Temporal averaging with windows is non-causal. A causal alternative is $w(t)=[\alpha^2\, t\, e^{-\alpha t}]_+$



Sliding causal window
$1/\alpha$ = 100 ms

Smoothing & Convolution

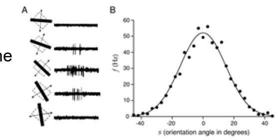
- Smoothing and convolution pitfalls
  - Introduces spurious correlations over time
  - Hidden assumption about smoothness of the external sensory or motor data
  - Edge effects: what happens at the start and end of the data?
  - Phase lag: peaks of smoothed data may occur later than the peaks in the original data. True for non-symmetric kernels and all causal filters

Tuning curves

- r() can be a function of something other than time. e.g. r(angle) if the rate varies with direction of hand movement
- r(x) will still be time-varying if the argument x changes with time as x(t). It can also change dependence on x, if r = r(x,t).
- Describes the "tuning" of the neuron. x can be a scalar, vector, or function (pattern)
- A tuning curve is a model for the neuron's behavior, and is always an approximation since neurons are likely to have multiple inputs and respond to multiple internal and external variables.

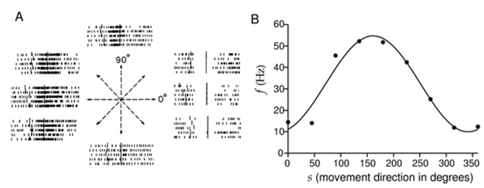
Sensory tuning curves

- For sensory neurons, the firing rate depends on the stimulus s
- Extra cellular recording V1 monkey
- Response depends on angle of moving light bar
- Average over trials is fitted with a Gaussian



$$r(s) = r_{\max} \cdot e^{-\frac{(s-s_{\max})^2}{2\cdot\sigma^2}}$$

Motor tuning curves



Extra cellular recording of monkey primary motor cortex M1 in arm-reaching task. Average firing rate is fitted with $r(s) = r_0 + (r_{\max} - r_0) \cdot \cos(s - s_{\max})$

Spike count variability

- Tuning curves model average behavior.
- Deviations of individual trials are given by a noise model.
  - Additive noise is independent of stimulus
    r(s) = f(s) + ξ
  - Multiplicative noise is proportional to stimulus
    r(s) = f(s) + g(s)·ξ

Definitions

- **Probability density function** - a function that represents a probability distribution in terms of integrals.
- **Moment** - $\mu_n = \int_{-\infty}^{\infty} (x-c)^n f(x)dx$
- **Central moment** - $\mu_n = E((X-\mu)^n)$

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