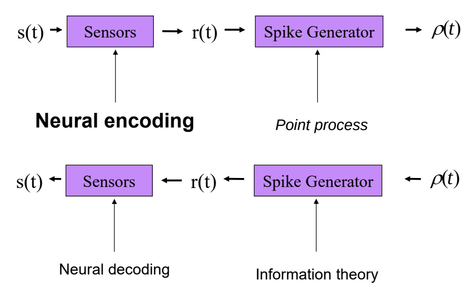
Signal & Data Analysis in Neuroscience 2016

Part 7: Neural Encoding

Izhar Bar-Gad

Room: 408 Phone: 7141 Email: izhar.bar-gad@biu.ac.il

The neuronal transformation



Outline

- Reverse correlations
- Linear filters
- Static non-linearity
- Example: V1 simple neurons

Based heavily on:
Theoretical neuroscience, *Dayan P & Abbott LF*, Chapter 2

Stimulus → Spike train

- In the event driven activity lecture we related stimulus described as a **point process** to the neuronal activity.
- This lecture will describe the general case of a **time series** representation of the stimulus (or even more generally: a stochastic process) and its relation to neuronal activity.

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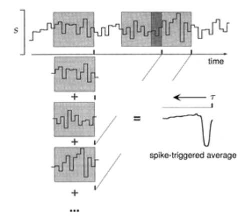
Spike triggered average

- What does the spike encode?
- What is the average stimulus preceding a spike?



Stimulus and response are defined periodically: r(t+T)=r(t), s(t+T)=s(t).

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Reverse correlation

- Average stimulus preceding the spike = Reverse correlation of the stimulus and the spike train

$$\begin{aligned} C(\tau) &= \frac{1}{n}\sum_{i=1}^{n} s(t_i - \tau) \\ &= \frac{1}{n}\int dt\rho(t)s(t-\tau) \\ \langle C(\tau)\rangle &= \frac{1}{n}\int dt r(t)s(t-\tau) \\ &= \frac{1}{r}Q_{rs}(-\tau) \end{aligned}$$

with $r = n/T$ the average spike rate and $Q_{rs} = \frac{1}{T}\int_0^T dt r(t)s(t+\tau)$ the correlation between the signals r and s.

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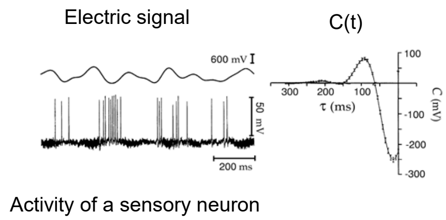
Reverse correlation - Electric fish

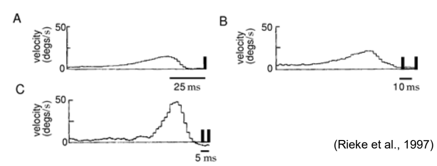


Spike triggered average - notes

- Reverse correlations assumed rate-based changes (Poissonian neuron).
- Non-Poissonian activity adds complexity to the spike triggered average.

Multi-spike triggered averages

H1 movement sensitive visual neuron of the blowfly.



A: Spike triggered average
B: Two-spike at 10±1 ms triggered average – linear sum
C: Two-spike at 5±1 ms triggered average – non linear sum

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Stimulus → Rate

- We will try to describe the rate of the neuron as a function of the stimulus at all previous time.
- We will define this function as a filter on the stimulus. Filters will be discussed in great detail in the spectral part of course…
- The general description (Volterra expansion)

$$r_{est}(t) = r_0 + \int_0^{\infty} d\tau D(\tau)s(t-\tau)) + \int_0^{\infty} d\tau_1 d\tau_2 D_2(\tau_1,\tau_2)s(t-\tau_1)s(t-\tau_2)) + ...$$

Linear filter model

- The basic model that we will use is of the neuron as a linear filter on the stimulus

$$r_{est}(t) = r_0 + \int_0^{\infty} D(\tau)s(t-\tau)d\tau$$

r_0 – baseline firing rate *D - response kernel*
r(t) – firing rate a time t *s(t) – stimulus at time t*

- Rate → Convolution of the stimulus & response kernel.
- **What is the best rate estimation $r_{est}(t)$? Or in other words what is the best kernel $D_{opt}(t)$?**
- To do that we'll first define white noise…

White noise stimulus

- White noise is random (non-restricted values), uncorrelated stochastic process - s(t):

$$\langle s(t)\cdot s(t+\tau)\rangle = \sigma_s{}^2 \cdot \delta(\tau)$$

- The stimulus autocorrelation function - Q:

$$Q_{s,s}(\tau) = \frac{1}{T}\cdot\int_0^T s(t)\cdot s(t+\tau)dt$$

- Thus, the autocorrelation of white noise – Q:

$$Q_{s,s}(\tau) = \sigma_s^2 \cdot \delta(t)$$

- Assuming an ergodic signal we traded ensemble average for time average.

Optimal kernel I

- The best rate estimator is defined by the difference from the actual rate function.

$$E = \frac{1}{T}\cdot\int_0^T (r_{est}(t) - r(t))^2 dt$$

- The best estimator minimizes the difference

$$\begin{aligned}\frac{dE}{dD(\tau)} &= \frac{2}{T}\int_0^T dt(r_{\text{est}}(t) - r(t))s(t-\tau)\\ &= \frac{2}{T}\int_0^T dt\left(r_0 + \int_0^\infty d\tau' D(\tau')s(t-\tau') - r(t)\right)s(t-\tau)\\ &= 2\int_0^\infty d\tau' D(\tau')Q_{ss}(\tau-\tau')d\tau' - Q_{rs}(-\tau)\end{aligned}$$

$$Q_{s,s}(\tau) = \frac{1}{T}\cdot\int_0^T s(t)\cdot s(t+\tau)dt \qquad Q_{r,s}(\tau) = \frac{1}{T}\cdot\int_0^T r(t)\cdot s(t+\tau)dt$$

Optimal kernel II

- The best estimation is achieved:

$$\int_0^\infty d\tau' Q_{ss}(\tau-\tau')D(\tau') = Q_{rs}(-\tau)$$

For white-noise stimuli $Q_{ss}(\tau) = \sigma_s^2\delta(\tau)$, so

$$\sigma_s^2\int_0^\infty \delta(\tau-\tau')D(\tau')d\tau' = \sigma_s^2\cdot D(\tau) = Q_{r,s}(-\tau)$$

$$\boxed{D(\tau) = \frac{Q_{rs}(-\tau)}{\sigma_s^2} = \frac{\langle r\rangle C(\tau)}{\sigma_s^2}}$$

Optimal kernel calculation

- Create white noise stimulus (no correlations).
- Calculate spike triggered average response to the stimulating white noise.
- Normalize the spike triggered average by the rate to get the optimal kernel.

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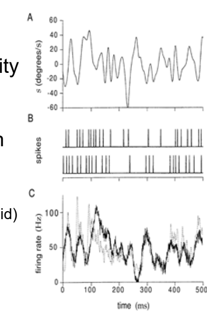
H1 neuron in visual system of blowfly

- Stimulus – image velocity
- Response of H1 neuron
- Estimated rate $r_{est}(t)$ (solid) assuming linear kernel
- Neural rate r(t) (dashed) averaged spike trains



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Optimal kernel without white noise input

- Solving the equation: $\int_0^\infty d\tau' Q_{ss}(\tau-\tau')D(\tau') = Q_{rs}(-\tau)$
- When the input is not white, a Fourier transform of the correlation functions enables finding the optimal kernel

$$\tilde{D}(\omega) = \frac{\tilde{Q}_{r,s}(-\omega)}{\tilde{Q}_{s,s}(\omega)}$$

$$D(\tau) = \frac{1}{2\pi} \cdot \int_{-\infty}^{\infty} \frac{\tilde{Q}_{r,s}(-\omega)}{\tilde{Q}_{s,s}(\omega)} \cdot e^{-i\omega\tau} d\omega$$

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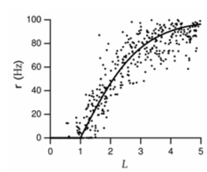
Deviation from linearity

- Typically neurons deviate from the linear relationship: $r_{est}(t) = r_0 + \int_0^{\infty} D(\tau)s(t-\tau)d\tau = r_0 + L(t)$
- The most common deviations are **saturation** and **threshold**.



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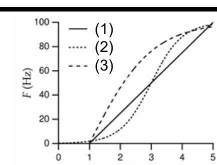
Static non-linearity I



$$(1)\ F(L) = G \cdot [L-1]_+$$

$$(2)\ F(L) = \frac{r_{max}}{1+e^{2(L_{1/2}-L)}}$$

$$(3)\ F(L) = r_{max} \cdot [\tanh(0.5(L-L_0))]_+ \qquad \tanh(x) = \frac{\sinh(x)}{\cosh(x)} = \frac{e^x - e^{-x}}{e^x + e^{-x}}$$

$G = 25$ Hz, $L_0 = 1$, $L_{1/2} = 3$, $r_{max} = 100$ Hz, $g_1 = 2$, and $g_2 = 1/2$

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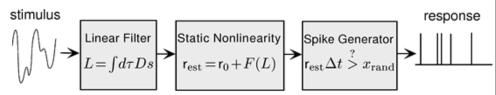
Static non-linearity II



The rate estimate is

$$r_{est}(t) = r_0 + F(L(t))$$

with F the non-linear function and L estimated using the linear theory.

A two-step approach: first estimate the optimal linear filter, then fit the best non-linearity.

Suboptimal: No inclusion of (non-linear interactions of) higher order moments
Linear filter is optimized ignoring the non-linearity.

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Non-linearity – other options

- The optimization method is non optimal even for static non linearity. However, *Bussgang* theorem demonstrates that it is close to optimal for Gaussian white noise.
- The other options are:
  - Optimize a non-linear function

$$r_{est}(t) = r_0 + \int_0^\infty D(\tau) f(s(t-\tau)) d\tau$$

  - Use more terms in the Volterra or Wiener expansion

$$r_{est}(t) = r_0 + \int_0^\infty d\tau D(\tau) s(t-\tau)) + \int_0^\infty d\tau_1 d\tau_2 D_2(\tau_1,\tau_2) s(t-\tau_1) s(t-\tau_2)) + ...$$

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Visual stimuli

Sinusoidal grating

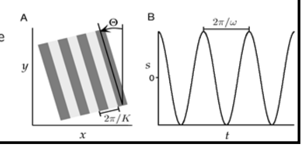
$$s(x,y,t) = A\cos(Kx\cos\Theta + Ky\sin\Theta - \Phi)cos(\omega t)$$

K, ω spatial, temporal frequency. Θ is orientation.

White-noise stimulus

$$\left\langle s(x,y,t)s(x',y',t')\right\rangle = \sigma^2\delta(t-t')\delta(x-x')\delta(y-y')$$

$\langle s\rangle = 0$ to avoid dependence on overall illumination.



Spatial receptive fields

We generalize previous concepts to 2-d visual stimuli $s(x,y,t)$:

Spike-triggered average	$C(x,y,\tau) = \frac{1}{n}\left\langle \sum_{i=1}^{n} s(x,y,t_i-\tau)\right\rangle$
Correlation function	$Q_{rs}(x,y,\tau) = \frac{1}{T}\int_0^T dt r(t)s(x,y,t+\tau)$
	$C(x,y,\tau) = \frac{Q_{rs}(x,y,-\tau)}{\langle r\rangle}$
Linear filter	$L(t) = \int_0^\infty d\tau \int dx dy D(x,y,\tau)s(x,y,t-\tau)$
For white-noise	$D(x,y,\tau) = \frac{Q_{rs}(x,y,-\tau)}{\sigma_s^2}$
Separable kernel	$D(x,y,\tau) = D_s(x,y)D_t(\tau)$
	$D_s(x,y) \propto \int d\tau D(x,y,\tau)$

V1 spatial receptive fields

$D(x,y)$ from spike triggered average of two different cat visual cortex area 17 simple cells.

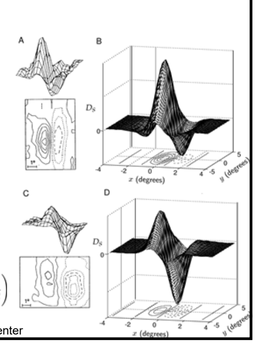
Stimulus is averaged 50-100 msec prior to action potential.

$D(x,y)$ shows separate ON and OFF region.

Simple cells with up to 5 regions are found.

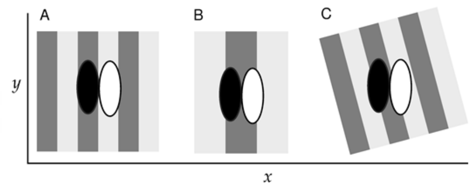
Gabor function

$$D(x,y) = \frac{\cos(kx-\phi)}{2\pi\sigma_x\sigma_y}\exp\left(-\frac{x^2}{2\sigma_x^2} - \frac{x^2}{2\sigma_y^2}\right)$$



(Border parallel to y axis i.e. Θ=0, origin at center

Response to grating



- Grating stimuli superimposed on spatial receptive fields.
- Dark oval – OFF area $D_s<0$, White oval – ON area $D_s>0$
- Optimal response when both spatial frequency and orientation of stimulus and filter match (such as in figure A)

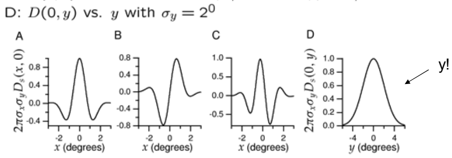
Gabor functions

Examples of other shapes of Gabor functions:

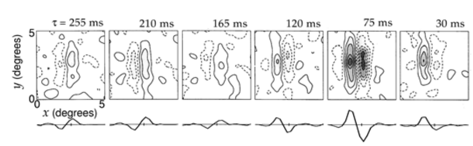
$$D_s(x,y) = \frac{1}{2\pi\sigma_x\sigma_y}\exp\left(-\frac{x^2}{2\sigma_x^2}-\frac{y^2}{2\sigma_y^2}\right)\cos(kx-\phi)$$

Preferred orientation of light bars is parallel to the y direction.

A: $D(x,0)$ vs. x with $\sigma_x = 1^0, 1/k = 0.5^0, \phi = 0$
B: $D(x,0)$ vs. x with $\sigma_x = 1^0, 1/k = 0.5^0, \phi = \pi/2$
C: $D(x,0)$ vs. x with $\sigma_x = 1^0, 1/k = 0.33^0, \phi = \pi/4$
D: $D(0,y)$ vs. y with $\sigma_y = 2^0$

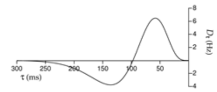


Temporal receptive fields I



- Space-time evolution of V1 cat receptive field
- ON/OFF boundary changes to OFF/ON boundary over time.
- Spatial response locations do not change with time: separable kernel.

Temporal receptive fields II



We estimate $D(\tau) = \int dx dy D(x, y, \tau)$. The result is well fitted with the difference of two Gamma functions:

$$D_t(\tau) = \alpha \exp(-\alpha\tau)\left(\frac{(\alpha\tau)^5}{5!} - \frac{(\alpha\tau)^7}{7!}\right)$$