# Assignment 4
# Theoretical Neuroscience

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1. **Essay: early visual and auditory processing.**

   This question will ask you to read about the mammalian visual and auditory pathways. As a first source, take a look at Kandel et al.: Principles of Neural Science; if you want further material, look at Zigmond et al.: Fundamentals of Neuroscience or ask for suggestions. Most of these questions don't actually have a right answer – just argue on the basis of what you read.

   - How many **synapses** are there between the receptors and the cortex in each system? Can the **subcortical** processing in the two pathways be compared?
   - Where does **bilateral convergence** happen? Why the difference?
   - Imagine you wanted to build **efficient** auditory and visual sensory systems. How do you think computational goals of processing in the two modalities might influence the anatomy of the system? Think in particular about the very early parts and bilateral convergence.

2. **Contrast saturation and nonspecific suppression.**

   - Assume a V1 cell has a receptive field

     $$f_{\alpha,a,\psi}(x,y) = r_{max} \exp(-\frac{x^2+y^2}{2\sigma^2}) \cos(a\cos(\psi)x - \alpha)$$

     where $\alpha$ is the preferred phase, $\psi$ the preferred orientation and $a$ the preferred frequency. We stimulate it with the following (static) stimulus:

     $$s(x,y) = B\cos(b\cos(\phi)x + b\sin(\phi)y - \beta)$$

     Plot the response

     $$L_{\alpha,a,\psi}(\phi,\beta,b) = \int dxdy f_{\alpha,a,\psi}(x,y)s(x,y)$$

     for $\alpha = \beta$ as a function of orientation for $\psi = 0$ and as a function of frequency for $a = 0$, showing that this cell is tuned to both spatial frequency and orientation. Hint: $\cos(x) = \cosh(ix)$
   - Unlike the prediction from this model, responses of cells in visual cortex saturate at high contrasts and they also adapt (figure 1). Furthermore, presentation of a grating at an orientation to which the cell shows no response prevents the cell from responding to a grating presented at its preferred stimulus orientation (nonspecific suppression). Heeger (1992) proposed a very simple modification of this model that accounts for these two effects. Let simple $SC_{\alpha,a,\psi}$ and complex cells $CC_{a,\psi}$ respond as:

     $$SC = \frac{[L]_+^2}{F_{1/2}^2 + [L]_+^2}$$

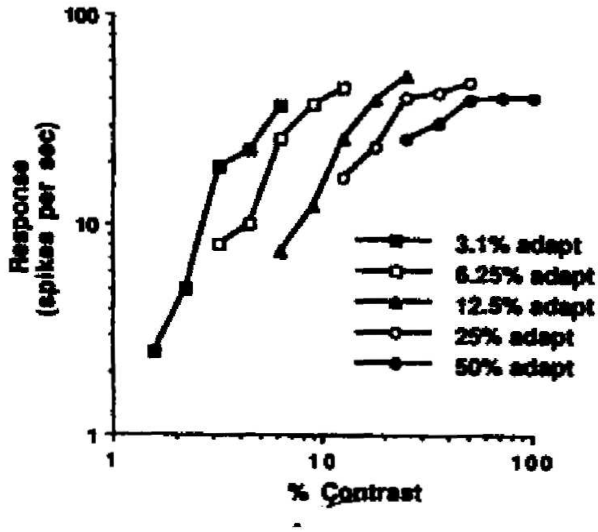


Figure 1: From Heeger (1992): The top plot shows the response of a complex cell as a function of contrast, after having adapted to various contrasts. The bottom plot shows the effect of the nonlinearity described, with $\sigma = G_{1/2}$.

$$CC = \frac{\sum_{\alpha=0,90,180,270}[L_\alpha]_+^2}{G_{1/2}^2 + \sum_{\alpha=0,90,180,270}[L_\alpha]_+^2}$$

where $[f]_+ = f$ if $f > 0$ and $= 0$ otherwise; and we have suppressed the subscripts where possible. Show analytically that this formulation leads to saturation at high stimulus contrasts $B$. How might you modify the two models to produce nonspecific suppression? What might these expressions imply about cortical architecture?

- `OPTIONAL` Suppose that natural scenes are composed of sums of Gabor functions. Assuming that the properties of V1 cells are matched to the statistics of natural scenese, what might the normalization structure implied by Heeger's model imply about those statistics?

3. **Doubly stochastic Poisson processes and spike patterns.**

   In the 1980s Abeles suggested that the integrative properties of neurons coupled with the density of connections between them would lead to self-supporting synchronous volleys of firing that could propagate between different constellations of neurons with extremely high temporal precision (a phenomenon called a "synfire chain"). This prompted an experimental search for the precisely timed spike patterns that might be a signature of such a phenomenon. A single neuron might participate in more than one synchronous volley of a synfire chain. Thus, in part because of technological limitations, many experiments looked for patterns in the spike train of a single cell. Here, we will look at one such hypothetical experiment.

   Suppose the mean response rate of a neuron to a stimulus flashed shortly before time 0, is given by the function
   $$\overline{\lambda}(t) = \Theta(t)\overline{\rho}e^{-t/T}$$
   where $\Theta(t)$ is the Heaviside function (0 if $t < 0$ and 1 if $t \geq 0$) and $\overline{\rho}$ and $T$ are constants. We begin by making the common assumption that the firing of the neuron is described by an inhomogeneous Poisson process with intensity $\overline{\lambda}(t)$.

(a) On average, how many spikes will the cell emit in response to the stimulus (assume the experimental counting interval is $\gg T$).

(b) Under the inhomogeneous Poisson model, what is the intensity with which we would observe spikes within small intervals around three specific times $t, t + \tau_1$ and $t + \tau_2$ all greater than 0. [We want the marginal probability of those 3 times – don't assume anything about what the cell is doing at any other time].

(c) Integrate your expression with respect to $t$ to find $\sigma(\tau_1, \tau_2)$, the intensity of observing a pattern with intervals $\tau_1$ and $\tau_2$ at any point. [Assume $\tau_1$ and $\tau_2$ are positive.]

(d) An experimenter reports that, looking at a neuron with $\overline{\rho} = 80\text{s}^{-1}$ and $T = 0.05\text{s}$ and binning spikes in 1 ms intervals, he observed the pattern (5 ms, 50 ms) 8 times in 1000 trials. Given your result above, is this surprising? Assume that he looked only for the (5,50) ms pattern. [`OPTIONAL` Why should that matter to your answer?]

Looking more closely at his data, you note that the Fano Factor of the spike count is about 2. This leads you to consider a doubly stochastic Poisson process model instead, with an intensity

$$\lambda(t) = \Theta(t)\rho e^{-t/T}$$

which depends on a random variable $\rho \sim \text{Gamma}(\alpha, \beta)$.

(e) Use moment matching to estimate values of the parameters $\alpha$ and $\beta$. [Hint: find an expression for the variance of a Poisson distribution with random mean parameter.]

(f) Repeat the calculation for the expected number of (5,50) ms patterns. [Hint: you'll need the third moment of the Gamma distribution]. Is the experimental result surprising now?

4. **The expected autocorrelation function of a renewal process.**

In class, we analysed the autocorrelation function of a point process in terms of its intensity function $\lambda(t, \ldots)$. For a self-exciting point process, $\lambda$ depends on the past history of spiking, and so computing the expected value of the correlation in this way can be quite difficult. Fortunately, for the special case of a renewal process (i.e. a point process with iid inter-event intervals), there is an alternative way to compute the autocorrelation function.

Consider a neuron whose firing can be described by a renewal process with inter-spike interval probability density function $p(\tau)$.

(a) Given an event at time $t$, the probability that the next spike arrives in the interval $I_\tau = [t + \tau, t + \tau + d\tau)$ is $p(\tau)d\tau$. What is the probability that the *second* spike after the one at $t$ arrives in $I_\tau$ instead? The third spike?

(b) What is the probability that, given a spike at $t$, there is a spike in $I_\tau$, regardless of the number of intervening spikes?

(c) Your answer to the previous question has given you the right half of the autocorrelation function. What does the left half look like? What happens at $\tau = 0$?

(d) `OPTIONAL` Show that for a Gamma process with ISI density

$$p(\tau) = \beta^2 \tau e^{-\beta\tau},$$

the Laplace transform of (the right half of) the expected autocorrelation function is

$$\mathcal{L}[Q(\tau)](s) = \frac{\beta^2}{(\beta + s)^2 - \beta^2}.$$

[Hint: Recall that $\mathcal{L}[f](s) = \int_0^\infty dx \ f(x)e^{-sx}$. Apply the Laplace convolution theorem, after setting $p(\tau) = 0$ for $\tau < 0$. Finally, use the fact that for $|x| < 1$, $(1-x)^{-1} = 1 + x + x^2 + x^3 + ...$]

Find the expected power spectrum (i.e. the Fourier transform of the expected autocorrelation function) for this process.