Assignment 3
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 response kernel,

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

     where α is the preferred phase, ψ the preferred orientation and a the preferred frequency. We stimulate it with the following (static) stimulus:

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

     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: $\cos(x) = (e^{ix} + e^{-ix})/2$

   - Unlike the prediction from this model, responses of cells in visual cortex saturate at high contrasts and they also adapt. 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:

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

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

where $[f]_+ = f$ if $f > 0$ and $= 0$ otherwise; $F_{1/2}$ and $G_{1/2}$ are constants, 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?

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 τ_1 and τ_2 at any point. [Assume τ_1 and τ_2 are positive.]

(d) An experimenter reports that, looking at a neuron with $\overline{\rho} = 80\text{s}^{-1}$ and $T = 0.05$s and binning spikes in 1 ms intervals, he observed the pattern (5, 50) (i.e., $\tau_1 = 5$ ms and $\tau_2 = 50$) 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 α and β. [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?