Assignment 4
Theoretical Neuroscience

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31 October 2008

1. **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?

2. **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, λ 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_τ instead? The third spike?

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

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

(d) 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.

3. **Encoding Models**

(a) Prove Bussgang's Theorem. That is, show that if we have samples $\{\mathbf{x}_i, y_i\}$, where y_i is a random variable whose expectation is given by $E[y_i|\mathbf{x}_i] = f(\mathbf{w}\cdot\mathbf{x}_i)$, then the cross-correlation $\sum_i y_i \mathbf{x}_i$ (i.e. the "spike-triggered average" if y_i is binary) provides an unbiased estimate of $\alpha\mathbf{w}$ (i.e. $\mathbf{w}$ times an unknown constant α) if:

i. $P(\mathbf{x})$ is spherically symmetric, where we define spherical symmetry to mean that,

$$\forall\, \mathbf{x}_1, \mathbf{x}_2 \in \mathbb{R}^n, \|\mathbf{x}_1\| = \|\mathbf{x}_2\| \Rightarrow P(\mathbf{x}_1) = P(\mathbf{x}_2).$$

ii. $E[y\mathbf{x}] \neq \mathbf{0}$ (i.e. the expected spike-triggered average is not zero).

(b) Simulate the response of an LNP (Linear-Nonlinear-Poisson) model to a temporal stimulus. Let $\mathbf{w}$ be a 20-tap filter (sampled in 10-msec bins) with biphasic temporal structure (i.e. a short, large-amplitude peak and a longer, smaller-amplitude trough). Choose the nonlinear response function f to be a sigmoid that saturates at 200 spikes/sec. Recall that the instantaneous rate for an LNP neuron is given by

$$r_i = f(\mathbf{w} \cdot \mathbf{x}_i)$$

and that Poisson spikes can be generated by flipping a biased coin in each (suitably small) time bin with the probability of "heads" equal to $(\Delta t) r_i$.

i. Simulate the neuron with a 1-sec Gaussian white noise stimulus sampled at a framerate of 100-Hz. Generate 200 responses of the neuron to this stimulus. Compute the PSTH of these responses, and show that it matches the rate prediction given by convolving the stimulus with $\mathbf{w}$ and passing the output through f.

ii. Simulate the response to a long Gaussian white noise stimulus, and compute the STA (spike-triggered average). Plot the STA rescaled as a unit vector, and show that it provides a reasonable match to $\mathbf{w}/\|\mathbf{w}\|$.

iii. Reconstruct the nonlinearity of the cell: begin by filtering the raw stimulus with the STA. Make a histogram of the filtered stimulus values, and make another histogram of the spike-triggered filtered stimulus values, using in the same binning. Divide the latter histogram by the former and multiply by the inverse of the bin size. Plot this estimate of the nonlinearity against the true f.

iv. Stimulate the model cell with correlated Gaussian white noise: take the original (Gaussian white noise) stimulus and filter it with a Gaussian whose standard deviation is 20ms). Rescale if necessary to ensure that the standard deviation of the new stimulus is the same as the old. Now simulate the neuron and compute the STA, and compare it to $\mathbf{w}$. Compute the decorrelated STA (obtained by "whitening" with the inverse of the stimulus covariance matrix), and compare with $\mathbf{w}$. If necessary, regularize by adding a small constant to the diagonal of the stimulus covariance matrix (this corresponds to doing "ridge regression"), and examine how this affects the estimate.

v. Change f to be a symmetric function, such as $f(\xi) = \alpha\xi^2$. Simulate the new model neuron with Gaussian white noise, and compute the STA and largest eigenvector of the spike-triggered covariance (STC) matrix. Compare with $\mathbf{w}$. Reconstruct the nonlinearity using both filters, and compare with the true f.