

7 January 2009

### Questions

These questions are all pretty straight-forward if you have the patience to read through their lengthy statement.

1. The spike triggered average is

$$\bar{A}(t) = \left\langle \sum_{t_i} s(t_i - t) \right\rangle \quad (1)$$

where  $s(t)$  is the stimulus, the  $t_i$  are the spike times and the angle brackets denote the average over trials. For convenience let us write the spike triggered average of a single trial as

$$A(t) = \sum_{t_i} s(t_i - t) \quad (2)$$

so  $\bar{A} = \langle A \rangle$ . If we represent the spike train as

$$\rho(t) = \sum_{t_i} \delta(t - t_i) \quad (3)$$

then

$$\bar{A}(t) = \left\langle \int dt' s(t' - t) \rho(t) \right\rangle = \int dt' s(t' - t) r(t) \quad (4)$$

where the firing rate is

$$r(t) = \langle \rho(t) \rangle \quad (5)$$

If there is only a smooth number of trials, so that the rate is smoothed with a kernel

$$r(t) = \left\langle \int d\tau \rho(t - \tau) k(\tau) \right\rangle \quad (6)$$

what is  $\bar{A}(t)$  in terms of  $k(\tau)$  and  $A(t)$ ? What about  $Q_{rs}(\tau)$  which is used in the linear rate model? These comments are intended to show that kernel smoothing, something that is always done, might be useful when presenting a rate function, but is not necessarily useful in applications of the firing rate where some other integral might provide some smoothing.

*Solution:* The point being made here is that the spike rate is a smoothing of the spike train and this isn't always needed, since the spike train is smoothed anyway:

$$Q_{rs}(\tau) = \int d\tau' s(\tau') s(\tau - \tau') \quad (7)$$

and so

$$Q_{rs}(\tau) = \left\langle \int dt \rho(\tau' - t) k(t) s(\tau - \tau') \right\rangle = \int dt k(t) \int dt \langle \rho(\tau' - t) \rangle s(\tau - \tau') \quad (8)$$

so if

$$q_{rs}(\tau) = \int dt \langle \rho(\tau') \rangle s(\tau - \tau') \quad (9)$$

then

$$Q_{rs}(\tau) = \int dt k(t) q_{rs}(\tau - t) \quad (10)$$

and so the original smoothing kernel applied to spike trains acts as a smoothing kernel on the stimulus-response correlation function, something that might not need smoothing since the stimulus will smooth it anyway.

2. For the linear rate model the integral equation for the kernel was calculated using functional differentiation, that equation was then solved by discretizing time and solving the corresponding matrix equation. Show that you get the same answer if you discretize earlier; that is, discretize the linear model

$$\tilde{r} = r_0 + \int d\tau h(\tau) s(t - \tau) \quad (11)$$

so, for example  $H_i = h(i\delta t)$  and then differentiate the error with respect to  $H_i$ .

*Solution:* So this is just a question of following the instruction to discretize the functional integral:

$$\begin{aligned} H_i &= h(i\delta t) \\ R_i \delta t &= r(i\delta t) \\ \tilde{R}_i &= \tilde{r}(i\delta t) \\ S_{ij} &= s(i\delta t - j\delta t) \end{aligned} \quad (12)$$

$S_{ij}$  has a special structure, from its definition  $S_{i-k, j-k} = S_{ij}$  for many values of  $i$ , and  $k$ . A matrix like this is called a *Toeplitz*; suprisingly this property of  $S_{ij}$  plays no rôle in what follows. The factor of  $1/\delta t$  is added for convenience

Discretizing the linear model gives

$$\tilde{R}_i = \bar{R} + \sum_k S_{ik} H_k \quad (13)$$

where  $\bar{R} = r_0 \delta t$ , the extra factors of  $\delta t$  are for convenience and mean that  $R_i$  is the probability of a spike in the small interval labelled by  $i$ . The error we need to minimize is

$$\epsilon = \sum_i (R_i - \tilde{R}_i)^2 = \sum_i \left( R_i R_i - 2R_i \tilde{R}_i + \tilde{R}_i^2 \right) \quad (14)$$

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To minimize with respect to  $H_i$  we take the derivative

$$\frac{\partial \epsilon}{\partial H_j} = \sum_i (\tilde{R}_i - R_i) \frac{\partial \tilde{R}_i}{\partial H_j} \quad (15)$$

and

$$\frac{\partial \tilde{R}_i}{\partial H_j} = S_{ij} \quad (16)$$

This means the minimum is at

$$\sum_i \left( r_0 + \sum_k S_{ik} H_k - R_i \right) S_{ij} = 0 \quad (17)$$

and so

$$\sum_k Q_{jk}^{\text{ss}} H_k = Q_j^{\text{rs}} \quad (18)$$

where the stimulus-stimulus correlation is

$$Q_{jk}^{\text{ss}} = \sum_i S_{ij} S_{ik} \quad (19)$$

and the stimulus-response correlation is

$$Q_j^{\text{rs}} = \sum_i (R_i - \bar{R}) S_{ij} \quad (20)$$

3. The convolution theorem for the Fourier transform states that

$$\mathcal{F}(f * g) = 2\pi \mathcal{F}(f) \mathcal{F}(g) \quad (21)$$

where as usual

$$\mathcal{F}(f) = \frac{1}{2\pi} \int dt f(t) e^{-ikt} \quad (22)$$

and the convolution is given by

$$f * g(t) = \int d\tau f(t) g(t - \tau) \quad (23)$$

Hence

$$\begin{aligned} \mathcal{F}(f * g) &= \frac{1}{2\pi} \int dt \int d\tau f(t) g(t - \tau) e^{-ikt} \\ &= \int dt \int d\tau f(\tau) g(t - \tau) e^{-ik(t-\tau)} e^{-ik\tau} \\ &= \int dt \int dt' f(t) g(t') e^{-ikt'} e^{-ikt} \end{aligned}$$

$$= 2\pi \frac{1}{2\pi} \int dt f(t) e^{-ikt} \frac{1}{2\pi} \int dt g(t) e^{-ikt} \quad (24)$$

as required. You should note that in proving the convolution theorem we have assumed all the integrals run over  $t \in (-\infty, \infty)$ . Ignoring the finite integration limits use the convolution theorem to solve the equation for the kernel

$$\int d\tau' Q_{\text{ss}}(\tau - \tau') h(\tau') = Q_{\text{rs}}(-\tau). \quad (25)$$

*Solution:* Well this follows fairly directly if we write the equation for the kernel as convolution

$$Q_{\text{ss}} * h(\tau) = Q_{\text{rs}}(-\tau). \quad (26)$$

Now, take the Fourier transform of both sides

$$2\pi \mathcal{F}(Q_{\text{ss}})(k) \mathcal{F}(h)(k) = \mathcal{F}(Q_{\text{rs}})(-k) \quad (27)$$

Hence

$$h(\tau) = \frac{1}{2\pi} \mathcal{F}^{-1} \left( \frac{\mathcal{F}(Q_{\text{ss}})(k)}{\mathcal{F}(Q_{\text{rs}})(-k)} \right) \quad (28)$$