Problem Set 8:

Correlated Spike Trains

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In all preceding problem sets, when we have considered multiple random variables, we have understood them to be independent. In this sheet, we will look at how one can define ideas such as statistical dependence and correlation by focusing on correlated spike trains. Indeed, a neuron in a network will not receive completely uncorrelated spike trains as input, since these trains often come from the same recurrent network of neurons.

Let us consider the single interaction process (SIP) model (see Lecture 9). In this model, n individual spike trains are modelled as $x_i(t) = w_u(t) + w_i(t)$ for $i = 1, \dots, n$, where $w_u(t) = \sum_k \delta(t - t_k)$ is a single realisation of a stationary Poisson point process with rate α common to all spike trains $x_i(t)$, and $w_i(t)$ is a new independent realisation of a Poisson point process of rate β unique to that neuron. Remember that the sum of Poisson processes is also a Poisson process of rate $r = \alpha + \beta$.

Obviously, these spike trains $x_i(t)$ and measures of the trains, such as spike counts, are not independent. Let us quantify this dependence with the use of some statistical measures.

Problem 1: Covariance and correlation 4 points

We will first look at statistical measures of random variables, rather than stochastic processes which are functions of time. As an example, let N_i be the event counts of the respective spike train $x_i(t)$ during an observation of duration of length T. To look at the dependence of these random variables, let us first define **covariance** as

$$\mathbb{C}\mathrm{ov}[X, Y] = \mathbb{E}[(X - \mathbb{E}[X])(Y - \mathbb{E}[Y])] = \mathbb{E}[XY] - \mathbb{E}[X]\mathbb{E}[Y]. \tag{1}$$

For independent random variables X and Y, $\mathbb{E}[XY] = \mathbb{E}[X]\,\mathbb{E}[Y]$, such that $\mathbb{C}\mathrm{ov}[X, Y] = 0$. Note, however, that one cannot determine that two random variables are independent if their covariance vanishes.

Since the covariance is bounded by $\mathbb{C}\mathrm{ov}[X, Y]^2 \leq \mathbb{V}\mathrm{ar}[X]\,\mathbb{V}\mathrm{ar}[Y]$, the **correlation** coefficient $\mathbb{C}\mathrm{or}[X, Y]$ between two variables provides a normalised notion of covariance. It is defined as

$$\rho_{XY} \equiv \mathbb{C}\mathrm{or}[X, Y] = \frac{\mathbb{C}\mathrm{ov}[X, Y]}{\sqrt{\mathbb{V}\mathrm{ar}[X]\,\mathbb{V}\mathrm{ar}[Y]}}, \tag{2}$$

which is always falls in the interval $[-1, 1]$.

Problem 1.1: The covariance of counts N_i 4 points

Calculate the covariance between the counts N_i and N_j of two processes $x_i(t)$ and $x_j(t)$ $(i \neq j)$ from the SIP model over some time interval of length T. Use this to calculate the correlation coefficient between the counts. What are the bounds of the correlation?

Solution.

Let W_u and W_i be the counts of the processes $w_u(t)$ and each $w_i(t)$ during the same interval of length T. Thus, the random variable is $N_i = W_u + W_i$. Covariance is a bilinear operator such that: $\mathbb{C}\text{ov}[X+Y, Z+K] = \mathbb{C}\text{ov}[X,Z] + \mathbb{C}\text{ov}[Y,Z] + \mathbb{C}\text{ov}[X,K] + \mathbb{C}\text{ov}[Y,K]$. Also, different counts W_i are independent, and independent to W_u, such that $\mathbb{E}[W_i W_j] = \mathbb{E}[W_i]\,\mathbb{E}[W_j]$ for $i \neq j$ and $\mathbb{E}[W_i W_u] = \mathbb{E}[W_i]\,\mathbb{E}[W_u]$. Thus, $\mathbb{C}\text{ov}[W_i, W_j] = \mathbb{C}\text{ov}[W_u, W_j] = 0$. Putting this all together:

$$\begin{aligned}
\mathbb{C}\text{ov}[N_i, N_j] &= \mathbb{C}\text{ov}[W_u + W_i, W_u + W_j] \\
&= \mathbb{C}\text{ov}[W_u, W_u] + \mathbb{C}\text{ov}[W_u, W_j] + \mathbb{C}\text{ov}[W_i, W_u] + \mathbb{C}\text{ov}[W_i, W_j] \\
&= \mathbb{C}\text{ov}[W_u, W_u] \\
&= \mathbb{E}[W_u W_u] - \mathbb{E}[W_u]\,\mathbb{E}[W_u] \\
&= \mathbb{V}\text{ar}[W_u] \\
&= \alpha T,
\end{aligned}$$

since $w_u(t)$ is a Poisson process with rate α, such that $\mathbb{E}[W_u] = \mathbb{V}\text{ar}[W_u] = \alpha T$ for an interval of length T.

Now that we have the covariance, and knowing that $\mathbb{V}\text{ar}[N_i] = (\alpha+\beta)T$, the correlation is:

$$\begin{aligned}
\mathbb{C}\text{or}[N_i, N_j] &= \frac{\mathbb{C}\text{ov}[N_i, N_j]}{\sqrt{\mathbb{V}\text{ar}[N_i]\,\mathbb{V}\text{ar}[N_j]}} \\
&= \frac{\alpha T}{\sqrt{(\alpha+\beta)T \cdot (\alpha+\beta)T}} \\
&= \frac{\alpha}{(\alpha+\beta)}.
\end{aligned}$$

From this, the bounds are $\rho_{N_i N_j} = 0$ for vanishing rate $\alpha \to 0$ of the shared process $x_u(t)$ (or $\beta \gg \alpha$), and $\rho_{N_i N_j} = 1$ for vanishing rate $\beta \to 0$ of the individual processes $x_i(t)$ (or $\beta \ll \alpha$). Negative correlation coefficients are not possible. Note that the correlation coefficient is also independent of the time interval length T, while the covariance increases with interval length.

Problem 2: Cross- and autocorrelation 8 points

Let us now turn to the random processes themselves. The **crosscorrelation** of two *real* stochastic processes $R(s)$ and $S(t)$ is defined as

$$\rho_{RS}(s,t) = \mathbb{E}[R(s)S(t)], \tag{3}$$

providing a measure of similarity of two processes as a function of their evolutions in time t and s.

If both processes are *jointly stationary*, such that their joint distribution remains unchanged under time shifts (that is, it doesn't suffice that the individual processes are stationary, but their dependence must also be unchanging in time), the crosscorrelation is then just a function of the displacement $\Delta = s - t$ of one process relative to the other:

$$\rho_{RS}(\Delta) = \mathbb{E}[R(t+\Delta)S(t)]. \tag{4}$$

Comparing a process to itself, one obtains the **autocorrelation**

$$\rho_{SS}(s,t) = \mathbb{E}[S(s)S(t)], \qquad \text{or} \qquad \rho_{SS}(\Delta) = \mathbb{E}[S(t+\Delta)S(t)], \tag{5}$$

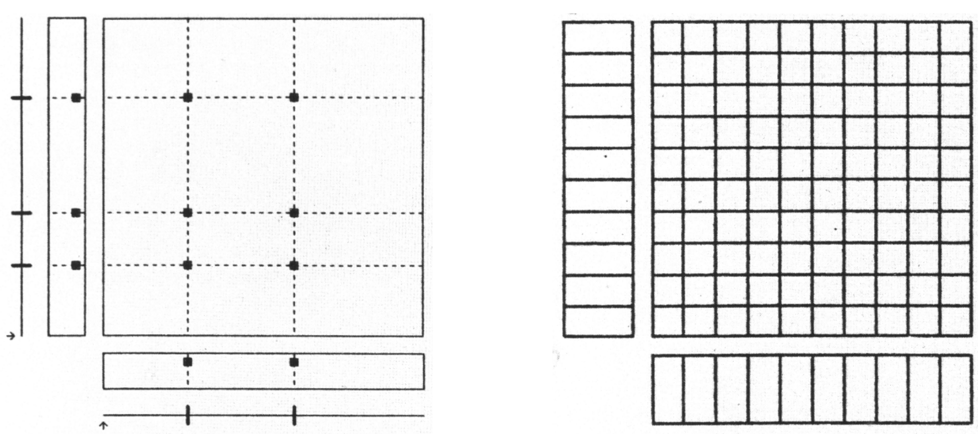
where again the second equality holds if the autocorrelation is simply a function of the displacement Δ rather than absolute time t, s.

Problem 2.1: Product spike trains **6 points**

We can now obtain the auto- and crosscorrelation functions for the Poisson point process as shown in slides 15-17 of Lecture 9. To do so, we define the 2-dimensional (2D) signal given by the product of spikes trains $R(s)$ and $S(t)$ as

$$R(s)S(t) = \Big[\sum_j \delta(s-s_j)\Big]\Big[\sum_k \delta(t-t_k)\Big] = \sum_{jk} \delta(s-s_j)\delta(t-t_k), \tag{6}$$

where the signal only has spikes are points $(s,t) = (s_j, t_k)$ (see Figure 1 (left)). Make a note of how many spikes are in the 2D signal in the area of h^2, given the number of spikes in both 1D signals in their intervals of length of h. We can thus make reference to the counts of the 2D signal $N_{RS}\big((s, s+h] \times (t, t+h]\big)$, which gives the counts of $R(s)S(t)$ in the "area" (as opposed to interval for the 1D signal) defined by the limits $s : (s, s+h]$ and $t : (t, t+h]$. This is thus the 2D equivalent of $N(t)$.



Aertsen, Gerstein, Habib, Palm, 1989

Figure 1: *(Left) The 2D signal arising from the product of two 1D signals. (Right) Bins of width h, thus area h^2, covering the 2D signal space.*

The **crosscorrelation** of two point processes can then be defined as a function of $N_{RS}(s \times t)$ as:

$$\rho_{RS}(s,t) = \mathbb{E}[R(s)S(t)] = \lim_{h\to 0} \frac{1}{h^2}\, \mathbb{E}\left[N_{RS}\big((s,s+h] \times (t,t+h]\big)\right], \tag{7}$$

where h is the width of bins that one uses to count the spikes in the 2D signal (see Figure 1 (right)). Taking the limit ($\lim_{h\to 0}$) of the expected count $\mathbb{E}[N_{RS}]$ divided by the bin area h^2 amounts to finding the expected density of spikes in the 2D signal at time pair (s,t), rather than the count itself $N_{RS}(s,t)$.

Use this definition to obtain the crosscorrelation of two independent spike trains $\rho_{w_i w_j}(s,t)$ and generalise the reasoning to obtain the autocorrelation $\rho_{w_i w_i}(t)$.

Solution.

In Figure 1 (left), we see that for two *realisations* of 1D stochastic processes, the number of spikes in an interval $(s, s+h] \times (t, t+h]$ of the 2D signal is simply the product of the number spikes in either 1D signal in the respective intervals: $N_{RS}\big((s,s+h]\times(t,t+h]\big) = N_R(s, s+h) \cdot N_S(t, t+h)$. That is, in the figure the 2D signal has a total of $6 = 2 \times 3$ spikes in the area.

For stochastic point processes, we need to work with expectations instead. We thus get $\mathbb{E}[N_{RS}\big((s,s+h] \times (t,t+h]\big)] = \mathbb{E}[N_R(s,s+h) \cdot N_S(t,t+h)]$. Importantly, if the two processes are independent, we get $\mathbb{E}[N_{RS}\big((s,s+h] \times (t,t+h]\big)] = \mathbb{E}[N_R(s,s+h)] \cdot \mathbb{E}[N_S(t,t+h)]$.

We know that for a stationary Poisson process $E[N(t)] = \lambda t$. Thus, for two independent Poisson processes with rates λ and ξ, the **crosscorrelation** is

$$\begin{aligned}
\rho_{w_\lambda w_\xi}((s,s+h),(t,t+h)) &= \lim_{h\to 0} \frac{1}{h^2}\, \mathbb{E}[N_{w_\lambda w_\xi}\big((s,s+h] \times (t,t+h]\big)] \\
&= \lim_{h\to 0} \frac{1}{h^2}\, \mathbb{E}[N_{w_\lambda}(s,s+h)]\, \mathbb{E}[N_{w_\xi}(t,t+h)] \\
&= \lim_{h\to 0} \frac{1}{h^2} \lambda h \cdot \xi h \\
&= \lambda\xi.
\end{aligned}$$

For both processes having rates β, we get $\rho_{w_i w_j}(\Delta) = \beta^2$. Note, this makes sense in terms of thinking of the density of the 2D signal as each spike train contributes its density of β.

Now, a Poisson spike train is memoryless, in that spikes have no memory of previous spiking events or inter spike intervals. This means that the **autocorrelation** of a spike train with itself at *different* times is the same as the crosscorrelation of two spike trains with the same intensity: $\rho_{w_i}(\Delta \neq 0) = \beta^2$. This amounts to the density of the 2D signal *away* from the diagonal being β^2.

For no lag ($\Delta = 0$, on the diagonal), however, each spike lines up with itself, such that if there is a spike at time t, the autocorrelation at time t will obtain a contribution from this spike. Since these spikes occur with density β (for stationary Poisson process) in the spike train $w_i(t)$, and the spike train product $w_i(t)w_i(t)$ at lag zero is exactly the same as the initial spike train (because $\sum_{jj} \delta(t-t_j)\delta(t-t_j) = \sum_j \delta(t-t_j)$), we thus know that the product spike train also has density β. Note, for the diagonal we are no longer taking the density over an area, but over a 1D line. Thus, the autocorrelation must also obtain a contribution of size β at lag zero. This means we obtain

$$\rho_{w_i w_j}(\Delta) = \beta\delta(\Delta) + \beta^2.$$

Problem 2.2: Putting everything together **2 points**

Use your results for the previous problems to calculate the autocorrelation $\rho_{x_i x_i}(\Delta)$ of one of the inputs $x_i(t)$ and the crosscorrelation $\rho_{x_i x_j}(\Delta)$ between two inputs $x_i(t)$ and $x_j(t)$.

Solution.

Calculating the auto- or crosscorrelation is relatively easy due to the linearity of the expectation operator. Knowing this, the **autocorrelation** of $x_i(t)$ is

$$\begin{aligned}
\rho_{x_i x_i}(\Delta) &= \mathbb{E}[x_i(t+\Delta)x_i(t)] \\
&= \mathbb{E}[w_u(t+\Delta)w_u(t)] + \mathbb{E}[w_u(t+\Delta)w_i(t)] + \mathbb{E}[w_i(t+\Delta)w_u(t)] + \mathbb{E}[w_i(t+\Delta)w_i(t)] \\
&= \rho_{w_u(t)w_u(t)}(\Delta) + \rho_{w_u(t)w_i(t)}(\Delta)\rho_{w_i(t)w_u(t)}(\Delta) + \rho_{w_i(t)w_i(t)}(\Delta) \\
&= \alpha\delta(\Delta) + \alpha^2 + \alpha\beta + \beta\alpha + \beta\delta(\Delta) + \beta^2 \\
&= (\alpha+\beta)\delta(\Delta) + (\alpha+\beta)^2.
\end{aligned}$$

As for the **crosscorrelation**:

$$\begin{aligned}
\rho_{x_i x_j}(\Delta) &= \mathbb{E}[x_i(t+\Delta)x_j(t)] \\
&= \mathbb{E}[w_u(t+\Delta)w_u(t)] + \mathbb{E}[w_u(t+\Delta)w_j(t)] + \mathbb{E}[w_i(t+\Delta)w_u(t)] + \mathbb{E}[w_i(t+\Delta)w_j(t)] \\
&= \rho_{w_u(t)w_u(t)}(\Delta) + \rho_{w_u(t)w_j(t)}(\Delta)\rho_{w_i(t)w_u(t)}(\Delta) + \rho_{w_i(t)w_j(t)}(\Delta) \\
&= \alpha\delta(\Delta) + \alpha^2 + \alpha\beta + \beta\alpha + \beta^2 \\
&= \alpha\delta(\Delta) + (\alpha+\beta)^2.
\end{aligned}$$

We see that the autocorrelation is the same as the crosscorrelation, expect that it has an increased Dirac delta peak at $\Delta = 0$ due to the addition of the same spike train $w_i(t)$ on top of $w_u(t)$.

Problem 3: Auto- and crosscovariance 4 points

One can make an equivalent notion to covariance (equation 1) for processes or signals (functions of time) by calculating the crosscorrelation of the two centred processes $\bar{R}(s) = R(s) - \mathbb{E}[R(s)]$ and $\bar{S}(t) = S(t) - \mathbb{E}[S(t)]$, where $\mathbb{E}[R(s)]$ is the mean of the process R *at time* s, for example. In this way, the **crosscovariance** is defined as

$$\gamma_{RS}(s,t) = \mathbb{E}\left[\big(R(s) - \mathbb{E}[R(s)]\big)\big(S(t) - \mathbb{E}[S(t)]\big)\right] = \mathbb{E}[R(s)S(t)] - \mathbb{E}[R(s)]\,\mathbb{E}[S(t)]. \quad (8)$$

By comparing to equation 1, one sees that the crosscovariance gives the covariance of the two processes at each pair of time points (s,t).

One can define the **autocovariance** by comparing the process to itself

$$\gamma_{SS}(s,t) = \mathbb{E}[S(s)S(t)] - \mathbb{E}[S(s)]\,\mathbb{E}[S(t)]. \tag{9}$$

As for the auto- and crosscorrelation, both of these may merely dependent on the displacement Δ. Note that for $s = t$ (or $\Delta = 0$), the autocovariance gives the variance $\gamma_{SS}(t,t) = \mathbb{V}\mathrm{ar}[S(t)]$ (or $\gamma_{SS}(0) = \mathbb{V}\mathrm{ar}[S]$).

Problem 3.1: First for $w_i(t)$ **2 points**

Use the results from the last problem to calculate the autocovariance $\gamma_{w_iw_i}(\Delta)$ of a Poisson point process $w_i(t)$ and the crosscovariance $\gamma_{w_iw_j}(\Delta)$ between two such independent processes $w_i(t)$ and $w_j(t)$.

Hint: Remember $\mathbb{E}[w_i(t)] = \beta$ for a stationary Poisson proccess with rate β.

Solution.

Using the solution from Problem 2.2, the **autocovariance** is

$$\begin{aligned}\gamma_{w_iw_i}(t_1,t_2) &= \mathbb{E}[w_i(t_1)w_i(t_2)] - \mathbb{E}[w_i(t_1)]\,\mathbb{E}[w_i(t_2)]\\ &= \rho_{w_iw_i}(t_1,t_2) - \beta\cdot\beta\\ &= \beta\delta(\Delta),\end{aligned}$$

while the **crosscovariance** vanishes

$$\begin{aligned}\gamma_{w_iw_j}(t_1,t_2) &= \rho_{w_iw_j}(t_1,t_2) - \mathbb{E}[w_i(t_1)]\,\mathbb{E}[w_j(t_2)]\\ &= 0.\end{aligned}$$

Problem 3.2: Now for the inputs $x_i(t)$ **2 points**

Use the results from the last question to calculate the autocovariance $\gamma_{x_ix_i}(\Delta)$ of one of the inputs $x_i(t)$ and the crosscovariance $\gamma_{x_ix_j}(\Delta)$ between two inputs $x_i(t)$ and $x_j(t)$.

Solution.

Using the solution from Problem 2.2, the **autcovariance** is

$$\begin{aligned}\gamma_{x_ix_i}(\Delta) &= \mathbb{E}[x_i(t+\Delta)x_i(t)] - \mathbb{E}[x_i(t+\Delta)]\,\mathbb{E}[x_i(t)]\\ &= \rho_{x_ix_i}(\Delta) - \mathbb{E}[w_u(t+\Delta) + w_i(t+\Delta)]\,\mathbb{E}[w_u(t) + w_i(t)]\\ &= (\alpha+\beta)\delta(\Delta) + (\alpha+\beta)^2 - \big[\big(\alpha+\beta\big)\big(\alpha+\beta\big)\big]\\ &= (\alpha+\beta)\delta(\Delta).\end{aligned}$$

Thus the autocovariance is only non-vanishing for zero lag $\Delta = 0$.

For the **crosscovariance**

$$\gamma_{x_ix_j}(\Delta) = \mathbb{E}[x_i(t+\Delta)x_j(t)] - \mathbb{E}[x_i(t+\Delta)]\,\mathbb{E}[x_j(t)]$$

$$
\begin{aligned}
&= \rho_{x_i x_j}(\Delta) - \mathbb{E}[w_u(t+\Delta) + w_i(t+\Delta)]\,\mathbb{E}[w_u(t) + w_j(t)] \\
&= \alpha\delta(\Delta) + (\alpha+\beta)^2 - \big[(\alpha+\beta)(\alpha+\beta)\big] \\
&= \alpha\delta(\Delta),
\end{aligned}
$$

which is again only non-vanishing for zero lag but of smaller amplitude.

Ultimately, the crosscovariance tells us that only on the diagonal (for zero lag) do the signals covary more than independent signals do. In other words, for $\Delta \neq 0$, the inputs $x_i(t)$ are completely independent from themselves and other inputs $x_j(t)$.