

# The Statistics of Spike Trains

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In this lecture we will cover:

- descriptions of spike trains
- point processes
- the homogeneous Poisson process
- the inhomogeneous Poisson process
- general point processes
- PSTHs and correlation functions

## 1 Spike Trains

The timecourse of every action potential (AP) in a cell measured at the soma might not be identical, due to differences in the open channel configuration. However, axons tend to contain only the  $\text{Na}^+$  and  $\text{K}^+$  channels needed for AP propagation, and therefore exhibit little or no timecourse variation. Further, there is no experimental evidence I am aware of to indicate that AP shape affects vesicle release.

Thus, from the point of view of inter-neuron communication the only thing that matters about an AP or spike is its time of occurrence.

A **spike train** is the sequence of times at which a cell spikes:

$$\mathcal{S} = \{t_1, t_2, \dots, t_N\}.$$

It is often useful to write this as a function in time using the Dirac-delta form,

$$s(t) = \sum_{i=1}^N \delta(t - t_i)$$

(D&A call this  $\rho(t)$ ) or using a counting function,

$$N(t) = \int_0^{\rightarrow t} d\xi s(\xi)$$

(where  $\rightarrow t$  in the limit indicates that  $t$  is not included in the integral: this might seem a little counter-intuitive, but will match a later definition),

or as a vector by discretizing with time step  $\Delta t$

$$\mathbf{s} = (s_1 \dots s_{T/\Delta t}); \quad s_t = \int_{t-\Delta t}^{\rightarrow t} d\xi s(\xi)$$

Note that the neural refractory period means that for  $\Delta t \approx 1\text{ms}$ ,  $s_t$  is binary.

## 2 Variability

Empirically, spike train responses to a repeated stimulus are (very) variable. This is particularly true in the cortex, but might be less so at earlier stages. This variability arises in more than one way.

- **Noise.** Perhaps due to vesicle release; or thermal noise in conductances.
- **Ongoing processes.** The brain doesn't just react to sensory input. Ongoing processing is likely to affect firing, particularly in cortex; and there is experimental evidence for this. This might lead to variability on a slower time-scale than noise.

We do not know the relative sizes of these two contributions.

Note that everything about the spike train can be variable, even the spike count on the  $i$ th repetition (or "trial")  $N_i = \int_0^T d\xi s_i(\xi)$

Variability in  $N_i$  is on order of the mean.

Fits of the form  $\text{Var}[N_i] = A \cdot \text{E}[N_i]^B$  yield values of  $A$  and  $B$  between about 1 and 1.5.

All this requires that we be able to treat spike trains statistically.

## 3 Point Processes

A probabilistic process that produces events of the type

$$\mathcal{S} = \{t_1, \dots, t_N\}$$

is called a **point process**. Clearly this is the statistical object best suited for the description of spike trains. Every point process is associated with a dual **counting process** which produces events of the type

$$\begin{aligned} N(t) \text{ such that } N(t) &\geq 0 \\ N(t + \Delta t) &\geq N(t) \\ N(t) - N(s) &= N[s, t) \in \mathbb{Z} \end{aligned}$$

$N(t)$  gives the number of events with  $t_i < t$ .

## 4 Homogeneous Poisson Process: $N_\lambda(t)$

Recall that the Poisson distribution is a distribution on an integer random variable  $n \geq 0$ . If  $n \sim \text{Pois}[\mu]$  then  $\text{P}[n] = \frac{\mu^n e^{-\mu}}{n!}$ . The parameter  $\mu$  is the mean of the distribution.

The most basic point process is called the homogeneous Poisson process. It is parameterised by a single scalar  $\lambda$  which gives the mean rate with which events arrive. Each event is completely independent of all others. Formally, we can define it by way of the associated counting process,  $N_\lambda(t)$ , by imposing two conditions:

1. **Independence.** For all disjoint intervals  $[s, t)$  and  $[s', t')$ ,  $N_\lambda[s, t) \perp N_\lambda[s', t')$ .

There are two ways to write the second condition. If we assume that  $\lim_{ds \rightarrow 0} N_\lambda[s, s + ds) \in \{0, 1\}$  (technically called conditional orderliness – at most one event occurs at one time) then it is sufficient to assume that

2. **Mean event rate.**  $\mathcal{E}[N_\lambda[s, t]] = (t - s)\lambda$ .

Without assuming conditional orderliness, we could instead define the process by giving the whole distribution of  $N_\lambda[s, t]$ . Here, we will use the more restrictive definition assumption to derive this distribution in the restricted case instead.

Consider dividing the interval  $[s, t]$  into  $M$  bins of length  $\Delta$  (i.e.  $M = (t - s)/\Delta$ ). If each bin is small enough (we will take the limit  $\Delta \rightarrow 0$  later) conditional orderliness tells us that the count of spikes in each bin is binary. For a binary random variable, the expected value is the same as the probability of the variable taking the value 1, so we can assume that the expectation  $\lambda\Delta$  gives the *probability* of a spike in each interval. Then the distribution of the number of spikes in the whole interval is given by the binomial distribution

$$\begin{aligned} \mathbb{P}[N_\lambda[s, t] = n] &= \binom{M}{n} (\lambda\Delta)^n (1 - \lambda\Delta)^{M-n} \\ &= \frac{M!}{n!(M-n)!} \left(\frac{\lambda(t-s)}{M}\right)^n \left(1 - \frac{\lambda(t-s)}{M}\right)^{M-n} \end{aligned}$$

write  $\mu = \lambda(t - s)$

$$= \frac{\mu^n}{n!} \frac{M(M-1)\cdots(M-n+1)}{M^n} \left(1 - \frac{\mu}{M}\right)^n \left(1 - \frac{\mu}{M}\right)^{M-n}$$

now take the limit  $\Delta \rightarrow 0$  or, equivalently,  $M \rightarrow \infty$

$$\begin{aligned} &= \frac{\mu^n}{n!} 1^n 1^n e^{-\mu} \\ &= \frac{\mu^n e^{-\mu}}{n!} \end{aligned}$$

So the spike count in any interval is Poisson distributed. This is where the name of the process comes from. As we mentioned above, we could instead have dispensed with the conditional orderliness assumption and instead made this a defining property of the process:

2'. **Count distribution.**  $N_\lambda[s, t] \sim \text{Pois}[(t - s)\lambda]$ .

We now derive a number of properties of the homogeneous Poisson process that will be important. First, the variance of the count distribution (this is really a property of the Poisson distribution). We can write

$$\begin{aligned} \text{Var}[N_\lambda[s, t]] &= \langle (n - \mu)^2 \rangle \\ &= \langle n^2 \rangle - \mu^2 \\ &= \langle n(n-1) + n \rangle - \mu^2 \\ &= \sum_{n=0}^{\infty} n(n-1) \frac{e^{-\mu} \mu^n}{n!} + \mu - \mu^2 \\ &= \sum_{n=0}^{\infty} \frac{e^{-\mu} \mu^{n-2}}{(n-2)!} \mu^2 + \mu - \mu^2 \\ &= 0 + 0 + \sum_{(n-2)=0}^{\infty} \frac{e^{-\mu} \mu^{n-2}}{(n-2)!} \mu^2 + \mu - \mu^2 \\ &= \mu^2 + \mu - \mu^2 \\ &= \mu \end{aligned}$$

Thus we have the third property of the homogeneous Poisson process:

3. **Fano factor**<sup>1</sup>.  $\frac{\mathcal{V}ar [N_\lambda[s, t]]}{\mathcal{E} [N_\lambda[s, t]]} = 1.$

The next few properties relate to the inter-event (or, for neurons, inter-spike) interval (ISI) statistics. First, it is fairly straightforward to see that, since the counting processes before and after an event  $t_i$  are independent, the times to the previous and following spikes are independent from one another.

4. **ISI independence.**  $\forall i > 1, \quad t_i - t_{i-1} \perp t_{i+1} - t_i.$

The full distribution of ISIs can be found from the count distribution:

$$\begin{aligned} \mathbb{P} [t_{i+1} - t_i \in [\tau, \tau + d\tau)] &= \mathbb{P} [N_\lambda(t_i, \tau) = 0] \mathbb{P} [N_\lambda[\tau, \tau + d\tau) = 1] \\ &= e^{-\lambda\tau} \lambda d\tau e^{-\lambda d\tau} \end{aligned}$$

taking  $d\tau \rightarrow 0$

$$= \lambda e^{-\lambda\tau} d\tau$$

5. **ISI distribution.**  $\forall i \geq 1, \quad t_{i+1} - t_i \sim \text{iid Exponential}[\lambda^{-1}].$

From this it follows that

6. **Mean ISI.**  $\mathcal{E} [t_{i+1} - t_i] = \lambda^{-1}$

7. **Variance ISI.**  $\mathcal{V}ar [t_{i+1} - t_i] = \lambda^{-2}$

These two properties imply that the **coefficient of variation** (CV), defined as the ratio of the standard deviation to the mean, of the ISIs generated by an homogeneous Poisson process is 1.

Finally, we write down the probability density of observing a spike train  $\{t_1 \dots t_N\}$  in some interval  $T$ , from an homogeneous Poisson process. Recall that spike times are independent of one another and arrive at a uniform rate. This makes it possible to write down the relevant probability as a product of three terms:

$$p(t_1 \dots t_N) dt_1 \dots dt_N = \mathbb{P} [N \text{ spikes in } T] \cdot \mathbb{P} [i\text{th spike} \in [t_i, t_i + dt_i)] \cdot [\# \text{ of equivalent spike orderings}]$$

The first term is given by the Poisson distribution, the second by the uniform distribution of spike times conditioned on  $N$ , and the third is  $N!$ , giving us

$$\begin{aligned} p(t_1 \dots t_N) dt_1 \dots dt_N &= \frac{(\lambda T)^N e^{-\lambda T}}{N!} \cdot \frac{dt_1}{T} \dots \frac{dt_N}{T} \cdot N! \\ &= \lambda^N e^{-\lambda T} dt_1 \dots dt_N \end{aligned}$$

We will see another way to write down this same expression while considering the inhomogeneous Poisson process below.

## 5 Inhomogeneous Poisson Process: $N_{\lambda(t)}(t)$

The inhomogeneous Poisson process generalizes the constant event-arrival rate  $\lambda$  to a time-dependent one,  $\lambda(t)$ , while preserving the assumption of independent spike arrival times. We will quickly summarize the properties of the inhomogeneous process by reference to the homogeneous one.

We begin with the two defining properties, although in this case we will just state the Poisson distribution property directly.

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<sup>1</sup>The term Fano Factor comes from semiconductor physics, where it actually means something slightly different. This use is standard in neuroscience. Note that this ratio (unlike the CV that we will encounter later) is only dimensionless for counting processes, or other dimensionless random variables.

1. **Independence.** For all disjoint intervals  $[s, t]$  and  $[s', t']$ ,  $N_{\lambda(t)}[s, t] \perp N_{\lambda(t)}[s', t']$ .

2. **Count distribution.**  $N_{\lambda(t)}[s, t] \sim \text{Pois}[\int_s^t d\xi \lambda(\xi)]$ .

The variance in the counts is simply a consequence of the Poisson counting distribution, and so the next property follows directly.

3. **Fano factor.**  $\frac{\text{Var}[N_{\lambda(t)}[s, t]]}{\mathcal{E}[N_{\lambda(t)}[s, t]]} = 1$ .

Also, independence of counting in disjoint intervals means that ISIs remain independent.

4. **ISI independence.**  $\forall i > 1, \quad t_i - t_{i-1} \perp t_{i+1} - t_i$ . pp

The full distribution of ISIs is found in a similar manner to that of the homogeneous process distribution:

$$\begin{aligned} \text{P}[t_{i+1} - t_i \in [\tau, \tau + d\tau]] &= \text{P}[N_{\lambda(t)}(t_i, t_i + \tau) = 0] \text{P}[N_{\lambda(t)}[t_i + \tau, t_i + \tau + d\tau] = 1] \\ &= e^{-\int_{t_i}^{t_i+\tau} \lambda(\xi) d\xi} e^{-\int_{t_i+\tau}^{t_i+\tau+d\tau} \lambda(\xi) d\xi} \int_{t_i+\tau}^{t_i+\tau+d\tau} \lambda(\xi) d\xi \end{aligned}$$

taking  $d\tau \rightarrow 0$

$$\begin{aligned} &= e^{-\int_{t_i}^{t_i+\tau} \lambda(\xi) d\xi} e^{-\lambda(t_i+\tau)d\tau} \lambda(t_i + \tau) d\tau \\ &= e^{-\int_{t_i}^{t_i+\tau} \lambda(\xi) d\xi} \lambda(t_i + \tau) d\tau \end{aligned}$$

5. **ISI distribution.**  $\forall i \geq 1, \quad p(t_{i+1} - t_i) = e^{-\int_{t_i}^{t_{i+1}} \lambda(\xi) d\xi} \lambda(t_{i+1})$ .

As the ISI distribution is not *iid* it is not very useful to consider its mean or variance. Instead we pass directly to the probability density of the event  $\{t_1 \dots t_N\}$  which can be derived by setting the count in intervals between spikes to 0, and the count in an interval around  $t_i$  to 1. This gives

$$p(t_1 \dots t_N) dt_1 \dots dt_N = e^{-\int_0^T \lambda(\xi) d\xi} \prod_{i=1}^N \lambda(t_i) dt_1 \dots dt_N$$

Finally, we derive an additional important property of the inhomogeneous process. Let us rewrite the density above, by changing variables from  $t$  to  $u$  according to

$$u(t) = \int_0^t \lambda(\xi) d\xi \quad \text{i.e.} \quad u_i = \int_0^{t_i} \lambda(\xi) d\xi$$

Then

$$\begin{aligned} p(u_1 \dots u_n) &= p(t_1 \dots t_n) / \prod_i \frac{du_i}{dt_i} \\ &= e^{-u(T)} \prod_{i=1}^N \lambda(t_i) / \prod_{i=1}^N \lambda(t_i) \\ &= e^{-u(T)} \end{aligned}$$

Comparison with the density for a homogeneous Poisson process shows that the variables  $u_i$  are distributed according to a homogeneous Poisson process with mean rate  $\lambda = 1$ .

This result is called **time rescaling**, and is central to the study of point processes.

## 6 Other Point Processes

### 6.1 Self-exciting point processes

A self-exciting process has an intensity function which is conditioned on past events

$$\lambda(t) \rightarrow \lambda(t|N(t), t_1 \dots t_{N(t)})$$

This is actually the most general form of a point process – we can re-express any (conditionally orderly) point process in this form. To see this, consider the point process to be the limit as  $\Delta \rightarrow 0$  of a binary time series  $\{b_1, b_2, \dots, b_{T/\Delta}\}$  and note that

$$P(b_1, b_2, \dots, b_{T/\Delta}) = \prod_i P(b_i | b_{i-1} \dots b_1)$$

### 6.2 Renewal processes

If the intensity of a self-exciting process depends only the time of the last spike, i.e.

$$\lambda(t) \rightarrow \lambda(t|t_{N(t)})$$

then the process is called a **renewal** process. ISIs from a renewal process are iid and so we could equivalently have defined the process by its ISI density. The **gamma process**

$$t_{i+1} - t_i \stackrel{\text{iid}}{\sim} \text{Gamma}[\alpha, \beta]$$

where

$$t \sim \text{Gamma}[\alpha, \beta] \Rightarrow p(t) = \frac{\beta^\alpha}{\Gamma(\alpha)} t^{\alpha-1} e^{-\beta t}$$

is an important renewal process in theoretical neuroscience, because the ISI distribution has a refractory-like component.

A homogeneous Poisson process is a gamma process (and therefore a renewal process) with  $\alpha = 1$ . The parameter  $\alpha$  is sometimes called the order of the gamma process. You might wish to show that a gamma process of integral order  $\alpha$  can be constructed by selecting every  $\alpha$ th event from a homogeneous Poisson process.

### 6.3 Birth process

The intensity of a birth process depends only on the *number* of events so far:

$$\lambda(t) \rightarrow \lambda(t|N(t))$$

### 6.4 Doubly stochastic Poisson process

In the doubly stochastic process,  $\lambda(t)$  is itself a random variable; or depends on another random process  $x(t)$ . An example is the randomly scaled IHPP:

$$\lambda(t) = s \cdot \rho(t) \quad \text{with } \rho(t) \text{ fixed and } s \sim \text{Gamma}(\alpha, \beta)$$

These models have been the subject of some recent attention, as a way to model a stimulus-dependent response  $\rho(t)$  which is modulated by cortical excitability. The counting process for such a DSPP has a Fano factor  $> 1$ .

## 7 Measuring point processes

We now turn from the probabilistic theory of point processes to the question of how best to characterise a set measured of events. Suppose we repeatedly measure spike trains,  $s(t)$ , elicited from a single neuron under, as far as possible, constant experimental conditions. Let the  $k$ th measured spike train be

$$s^{(k)}(t) = \sum_{i=1}^{N^{(k)}} \delta(t - t_i^{(k)}).$$

We might take one of a number of approaches to characterising  $s^{(k)}(t)$ , and it's relationship to the experimental stimulus (or task):

- Construct a parametric model for the intensity of the point process, possibly dependent on the stimulus  $a(t)$ :

$$s^{(k)}(t) \sim \lambda \left( t, a(t), N^{(k)}(t), t_1^{(k)}, \dots, t_{N^{(k)}(t)}^{(k)}, \theta \right),$$

thus characterising the stimulus-response function of the neuron. This is the **encoding** approach, to be discussed in a subsequent lecture. Here, we just note that the time-rescaling result discussed above provides a way to evaluate the goodness-of-fit of a point-process encoding model.

- Construct an algorithm to estimate  $a(t)$  from  $s^{(k)}(t)$ :

$$\hat{a}(t) = F[s^{(k)}(t)]$$

as accurately as possible. This **decoding** approach (also discussed in a later lecture) may be interpreted as asking what the neuron tells the animal about the outside world.

- Estimate nonparametric features (usually moments) of the distribution of  $s^{(k)}(t)$ . This is what we discuss below.

### 7.1 Mean response functions and the PSTH

The simplest non-parametric characterisation of the process that generated  $s^{(k)}(t)$  is its **mean intensity**:

$$\bar{\lambda}(t) = \langle s(t) \rangle = \lim_{K \rightarrow \infty} \frac{1}{K} \sum_{k=1}^K s^{(k)}(t)$$

Note that this is *not* the intensity function for the point process, unless that process is Poisson. Instead it is the *marginal* intensity, obtained by integrating over all random variables besides time:

$$\bar{\lambda}(t, a(\cdot)) \stackrel{\text{def}}{=} \int dN(t) \int dt_1 \dots dt_{N(t)} p(t_1 \dots t_{N(t)}) \lambda(t, a(\cdot), N(t), t_1, \dots, t_{N(t)})$$

For finite  $K$ , estimating  $\bar{\lambda}$  by summing  $\delta$ -functions yields spiky results. Instead, we usually construct a histogram

$$\widehat{N}[t, t + \Delta t] = \frac{1}{K} \sum_{k=1}^K N^{(k)}[t, t + \Delta t]$$

This is called the Post- (or Peri-) Stimulus-Time Histogram or PSTH.

If we expect  $\bar{\lambda}(t)$  to be a smooth function of time, we might instead use a kernel  $\phi(\tau)$  to construct the estimate:

$$\widehat{\bar{\lambda}}(t) = \frac{1}{K} \sum_{k=1}^K \int d\tau \phi(\tau) s^{(k)}(t - \tau)$$

There has been some work (which we won't discuss here) on choosing the width of  $\phi$  adaptively, possibly even in a way that depends on the local density of spikes. [Note: the literature contains many examples where a histogram is constructed first and then smoothed with a kernel. There is little theoretical justification for this practice, rather than sampling the smoothed kernel estimate given above.]

## 7.2 Correlation functions and Correlograms

The autocorrelation function for a process that generates spike trains  $s(t)$  is:

$$R_{ss}(\tau) = \left\langle \frac{1}{T} \int dt s(t)s(t-\tau) \right\rangle$$

where the angle brackets indicate expectation with respect to random draws of  $s(t)$  from the process. This is the time-averaged local second moment of the joint distribution on  $s(t)$ ; by contrast,  $\bar{\lambda}(t)$  was the (non-time-averaged) first moment. Note that, since  $s(t)$  is a sum of  $\delta$  functions,  $R_{ss}(0) = \infty$  for this definition.

An alternative definition for  $R_{ss}$  is in terms of a time-averaged conditional first moment. It is the mean intensity at time  $t + \tau$ , conditioned on an event having occurred at time  $t$ , and averaged over  $t$ . That is,

$$R_{ss}^{alt}(\tau) = \frac{1}{T} \int dt \langle \lambda(t + \tau, \eta | t_i = t) \rangle,$$

where the conditioning means that  $t_i = t$  for some  $i$ , and the angle brackets represent expectation with respect to  $N(T)$  and the times of all but the  $i$ th event. In this case,  $R_{ss}^{alt}(0)$  gives the average probability of two events occurring at the same time, which is 0, by definition, for a conditionally orderly process. In what follows, we will stick to the first (i.e., second moment) definition.

Based on the usual decomposition of second moments ( $\langle x^2 \rangle = \langle (x - \mu)^2 \rangle + \mu^2$ ) we can decompose the autocorrelation functions thus:

$$R_{ss}(\tau) = \bar{\Lambda}^2 + \frac{1}{T} \int dt (\bar{\lambda}(t) - \bar{\Lambda})(\bar{\lambda}(t - \tau) - \bar{\Lambda}) + \underbrace{\left\langle \frac{1}{T} \int dt (s(t) - \bar{\lambda}(t))(s(t - \tau) - \bar{\lambda}(t - \tau)) \right\rangle}_{Q_{ss}(\tau)}$$

where  $\bar{\Lambda}$  is the time-averaged mean rate, and  $Q_{ss}(\tau)$  is called the **autocovariance** function. D&A call  $Q_{ss}$  the autocorrelation function; in the experimental literature, estimates of  $Q_{ss}$  are usually called “shift-” or “shuffle-corrected autocorrelograms”.

For an (inhomogeneous) Poisson process  $Q_{ss}(\tau) = \delta(\tau)$ , by independence. For a general self-exciting process, it indicates (to second order) dependence on nearby spike times. Thus, it is often used to look for oscillatory structure in spike trains (where spikes tend to repeat around with fixed intervals, but at random phase with respect to the stimulus) or similar spike-timing relationships. Note, however, that since any (conditionally orderly) point process is a self-exciting process, *any* non-Poisson process will have a non- $\delta$  autocovariance function, even if nearby spike timing relationships are not the most natural (or causal) way to think about the process. In particular, think about the effects of random (but slow) variations in a non-constant  $\lambda(t)$ , as in a DSPP.

Correlation functions are typically estimated by constructing **correlograms**, which are histograms of the time differences between (not necessarily adjacent) spikes. The covariance function is then estimated by subtracting an estimate of the correlation of the mean intensity; this estimate is perhaps best constructed from the PSTH, but, in practice is often obtained by constructing a “shifted” or “shuffled” correlogram where time differences are taken between spikes from two different trials.

## 7.3 Power spectra and coherences

Another way to describe the second order statistics of a process is in the frequency domain, through power-spectra, spectrograms and (for multiple processes) coherence. These are increasingly used in neuroscience, but are beyond our present scope.

## 7.4 Multiple spike trains

Thus far we have restricted ourselves to spike trains from a single cell. Often, we may actually be interested in simultaneously modelling responses from many cells. If no two processes can generate

events at precisely the same time (a form of conditional orderliness), or if simultaneous spiking events are independent, then we can express dependences between the processes generally by dependence on all previous events in all cells:

$$\lambda^{(c)}(t) \rightarrow \lambda^{(c)}\left(t | N^{(c)}(t), t_1^{(c)}, \dots, t_{N^{(c)}(t)}^{(c)}, \{N^{(c')}(t), t_1^{(c')}, \dots, t_{N^{(c')}(t)}^{(c')}\}\right)$$

This is analogous to the self-exciting point process intensity function.

Dependencies can also be expressed by other forms, for example by DSPPs with the latent random process shared (or correlated) between cells. Such representations may often be more natural or causally accurate.

The techniques for measuring relationships between cells are analogous to those described for single processes: namely, by cross-correlogram estimates of the cross-correlation function:

$$R_{s^{(c)}s^{(c')}}(\tau) = \left\langle \frac{1}{T} \int dt s^{(c)}(t) s^{(c')}(t - \tau) \right\rangle;$$

shift- or shuffle-corrected correlogram estimates of the cross-covariance function:

$$Q_{s^{(c)}s^{(c')}}(\tau) = \left\langle \frac{1}{T} \int dt (s^{(c)}(t) - \bar{\lambda}^{(c)}(t))(s^{(c')}(t - \tau) - \bar{\lambda}^{(c')}(t - \tau)) \right\rangle;$$

or by cross-spectra or empirical coherences.

Note that, as for autocovariograms, structure in a cross-covariogram needn't imply that dependencies between individual spike times are the most natural way to think about the interaction between the processes – DSPPs with shared latents may also give significant cross-covariance structure.

Parametric models for multiple spike trains have also recently appeared in the experimental and neural-data-modelling literature. Further discussion of these is beyond our present scope.