Superposition of many independent spike trains is generally not a Poisson process

Benjamin Lindner
Max-Planck-Institut für Physik Komplexer Systeme, Nöthnitzer Str. 38 01187 Dresden, Germany
(Received 9 November 2005; published 23 February 2006)

We study the sum of many independent spike trains and ask whether the resulting spike train has Poisson statistics or not. It is shown that for a non-Poissonian statistics of the single spike train, the resulting sum of spikes has exponential interspike interval (ISI) distributions, vanishing the ISI correlation at a finite lag but exhibits exactly the same power spectrum as the original spike train does. This paradox is resolved by considering what happens to ISI correlations in the limit of an infinite number of superposed trains. Implications of our findings for stochastic models in the neurosciences are briefly discussed.

DOI: 10.1103/PhysRevE.73.022901 PACS number(s): 87.18.Sn, 05.40.Ca, 72.70.+m

Point processes and their associated spike trains play an important role in many fields such as physics (for instance, the shot noise in semiconductors) and neurobiology (action potentials of nerve cells). A basic mathematical object occurring in applications is the superposition of many independent spike trains. Such a problem is encountered, for instance, for a neuron receiving action potentials from about 10^4 other neurons. Taking the presynaptic (input generating) neurons to be independent and assuming a linear summation of the postsynaptic potentials caused by the input spikes, the effective input to the postsynaptic neuron is exactly given by the sum of single spike trains.

It has been widely assumed in recent theoretical work (see, e.g., [1,2]) that the superposition of a large number of independent non-Poissonian spike trains results in a Poissonian spike train, i.e., in a spike train with exponential interspike interval (ISI) probability density functions (PDF), vanishing ISI correlations $\rho_k=0$, and a flat power spectrum of the spike train. Here we show that although the pooled spike train's ISI indeed follows an exponential PDF and ISI correlations at a specific lag vanish (which is the apparently unique signature of a Poisson process from the ISI statistics point of view), the pooled spike train shares the nonflat spectral statistics of the single process and thus, it is *not* a Poisson process. We resolve this paradox by showing that the pooled spike train is *not* a renewal process [3], although by common measures it may look like one.

We consider independent stationary stochastic spike trains given by a sum of δ functions

$$x_n(t) = \sum \delta(t - t_{n,i}). \tag{1}$$

For simplicity we assume that the single spike train $x_n(t)$ is a renewal process, i.e., the interspike intervals (ISIs) between successive spikes

$$T_{n,i} = t_{n,i} - t_{n,i-1} \tag{2}$$

are uncorrelated among each other. This implies that the serial correlation coefficient, given by

$$\rho_k = \frac{\langle (T_{n,i} - \langle T_{n,i}\rangle)(T_{n,i+k} - \langle T_{n,i+k}\rangle)\rangle}{\langle (T_{n,i} - \langle T_{n,i}\rangle)^2\rangle} \tag{3}$$

vanishes at all finite lags k. We note that a renewal process is completely characterized by the probability density of the ISI $p(T_i)$. In particular, the power spectrum of the spike train

$$S(f) = \int_{-\infty}^{\infty} d\tau\, e^{2\pi i f \tau} \langle x(t)x(t+\tau)\rangle \tag{4}$$

[here defined as the Fourier transform of the spike train correlation function $\langle x(t)x(t+\tau)\rangle$] can be expressed by the Fourier transform of the ISI density $\tilde{p}(f)$ as follows [4,5]:

$$S_{renewal}(f) = r\frac{1 - |\tilde{p}(f)|^2}{|1 - \tilde{p}(f)|^2} \quad (f > 0). \tag{5}$$

Here, r denotes the stationary firing rate, i.e., the stationary mean of the spike train $r=\langle x(t)\rangle$, which equals the inverse mean ISI $r=1/\langle T\rangle$.

The Poisson process is a special renewal process with an exponential ISI density and a flat power spectrum of the spike train

$$p_{poi}(T) = r\exp[-rT], \quad S_{poi}(f) = r. \tag{6}$$

Since the ISI density determines uniquely the statistics of a renewal process we may conclude as follows: if a process is renewal and possesses an exponential ISI density, it is a Poisson process and its power spectrum has to be flat [as can be readily checked using Eq. (5)].

In what follows, we will use for illustration a non-Poissonian renewal process $x_n(t)$ the ISIs of which are distributed according to the density

$$p_\alpha(T) = 4r^2 T\exp[-2rT]. \tag{7}$$

This density has a unimodal shape with a peak at finite ISI (see Fig. 1, midpanel in the first row). The spike rate is given by r and the single ISI can be generated as a sum of two exponentially distributed random numbers with mean value $1/(2r)$. The power spectrum of the spike train can be obtained from Eq. (5) and reads

$$S_\alpha = r\left[1 - \frac{2r^2}{4r^2 + (\pi f)^2}\right]. \tag{8}$$

The spectrum is not flat but shows a dip at low frequencies and saturates in the high frequency limit at the firing rate r (see Fig. 2, left upper panel).

In the following we focus on the superposition of the trains $x_n(t)$ with $n=1,\ldots,N$. We rescale this sum by the number N of pooled spike trains, i.e., we consider

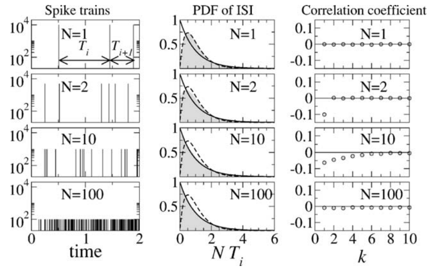

FIG. 1. Simulation results for the ISI statistics of $X(t)$ with $x_n(t)$ being a renewal process with PDF according to Eq. (7) and $r=1$. The simulation was performed for 2^{17} spikes. Left column: the summed spike train $X(t)$ for different numbers N of processes, the height of a single spike is $(N\Delta t)^{-1}$ where we chose an arbitrary value $\Delta=10^{-4}$ (temporal resolution was actually larger); two subsequent ISIs (T_i and T_{i+1}) are indicated in the top panel. Midcolumn: the PDF of a single ISI of $X(t)$, scaled with N (gray area); the PDF of the single spike train according to Eq. (7) (dashed line); the exponential PDF $r\exp(-rT)$ of a Poisson process (solid line). Right column: the serial correlation coefficient of the ISIs of $X(t)$.

$$X(t) = \frac{1}{N}\sum_{n=1}^{N} x_n(t) \tag{9}$$

and the question we pose is whether for $N\to\infty$ the pooled train $X(t)$ approaches a Poisson process with amplitude $1/N$ and rate Nr. In order to check this we will study the probability density $p(T_i)$ of a ISI in $X(t)$ defined by $T_i=t_i-t_{i-1}$, where t_i and t_{i-1} are two successive firing times in the pooled spike train. We also ask whether the linear correlations between the intervals T_i and T_{i+k} are zero ($\rho_k=0$ for $k>0$) or not, i.e., whether $X(t)$ is a renewal process or a nonrenewal process. Finally, we look at the power spectrum of $X(t)$ which should tend to $S_{poi}=r/N$ if $X(t)$ tends to a Poisson process.

Why a Poissonian statistics for $X(t)$ may be naively expected. One way to simulate a Poissonian spike train is as follows: Distribute N points uniformly and independently over an interval $[0,T]$. Over a much smaller interval $[0,T']$ (with $T'\ll T$), the resulting point process will have a Poissonian statistics.

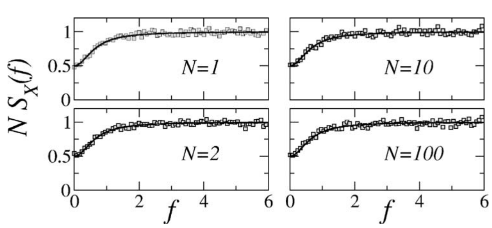

FIG. 2. Scaled power spectra of spike trains for different numbers N of superposed processes $x_n(t)$ with PDF Eq. (7) and $r=1$. Simulation results (symbols) obtained by averaging the spectra of 10^3 spike trains $X(t)$ of length 2^{18} with time step $\Delta t=10^{-2}$ are compared to theory (black lines) according to Eqs. (11) and (8). For clarity, only a fraction of the simulation data is shown, i.e., the actual frequency resolution was much higher than shown. The single processes $x_n(t)$ were generated as explained in Fig. 1. Multiple spikes occurring in the rather large time bin were added up; this only affects the power spectrum at much higher frequencies than shown here.

If we sum a number of independent non-Poissonian spike trains, then on time scales much smaller than a ISI of the single process $x_n(t)$, we generate *locally* a Poisson process [3] exactly in the way described above. Consider the pooled spike train Eq. (9) for large N. The ISI of the single process $T_{n,i}$ will be split into much smaller subintervals $T_{i'}$ (the ISIs of the superposed spike train) in a completely random fashion. Adding more spike trains we further subdivide these small ISIs and thus remove all correlations present in the spike train. The linear correlations at an arbitrary lag, for instance, are expected to vanish, i.e., $\rho_k\to 0$ as $N\to\infty$. The resulting spike train seems to converge to a renewal process with exponential ISI density—in other words: to a Poisson process.

This line of our somewhat vague reasoning seems to be supported by the numerical results for the ISI statistics shown in Fig. 1.

For $N=1$ (first row), the ISI density (midpanel) corresponds to that of the single process given in Eq. (7) (dashed line in the figure); serial correlations between intervals (right panel) vanish because $x_n(t)$ is a renewal process.

For $N=2$ (second row) the ISI density deviates from Eq. (7) even if we rescale the interval such that the mean interval is the same. Surprisingly, by adding the two independent spike trains, we introduce serial correlations in subsequent intervals (cf. the right panel of the second row), i.e., $X(t)$ is a nonrenewal process (for further results on small N, see Ref. [4]). The (linear) correlations extend over two successive intervals and are negligible for lags larger than lag one.

By adding more spike trains (third and fourth rows), the interval density is getting closer to an exponential PDF (midpanels, theory is shown by the solid lines), in fact, for $N=100$ (fourth row) deviations from the exponential function are extremely small. The serial correlations are getting weaker but extend over more lags. The correlation coefficient ρ_k for $N=100$ is very small at all lags and concluding from the linear correlations as measured by the serial correlation coefficient one is tempted to state that the process $X(t)$ approaches a renewal process in the limit of $N\to\infty$.

As sketched above, it is intuitively clear that the correlations between two intervals T_i and T_{i+k} will decrease further as N grows. So any linear or nonlinear correlations for a certain lag k will vanish as we let N go to infinity. Studying only the ISI statistics (PDF of and correlations between intervals), we may conclude that $X(t)$ approaches a renewal process with exponential ISI density—that means $X(t)$ *approaches a Poisson process*. This line of arguments was used, for instance, in Refs. [1,2].

Why $X(t)$ is not a Poisson process in the limit $N\to\infty$.—Let us consider the correlation function of $X(t)$:

$$\begin{aligned}
K_X(\tau) &= \langle X(t)X(t+\tau)\rangle - \langle X(t)\rangle\langle X(t+\tau)\rangle \\
&= \frac{1}{N^2}\sum_{n,l} \langle x_n(t)x_l(t+\tau)\rangle - \langle x_n(t)\rangle\langle x_l(t+\tau)\rangle \\
&= \frac{1}{N^2}\sum_{n} [\langle x_n(t)x_n(t+\tau)\rangle - \langle x_n(t)\rangle\langle x_n(t+\tau)\rangle] \\
&\quad + \frac{1}{N^2}\sum_{n\neq l} [\langle x_n(t)x_l(t+\tau)\rangle - \langle x_n(t)\rangle\langle x_l(t+\tau)\rangle].
\end{aligned}$$

Since the spike trains are independent the term in the last line drops out and we obtain

$$K_X(\tau) = \frac{1}{N} K_x(\tau). \tag{10}$$

This elementary calculation is analogous to a well-known statistical fact: the variance of the sum of independent random variables equals the sum of the variances of the variables. Likewise, the correlation function of independent stochastic processes equals the sum of the correlation functions of the processes.

For the power spectrum which is the Fourier transform of the autocorrelation function we obtain from Eq. (10)

$$S_X(f) = \frac{1}{N} S_x(f). \tag{11}$$

This means that the power spectrum of the summed spike train is the same (apart from rescaling by $1/N$) as that of the single spike train $x_n(t)$. This is confirmed in Fig. 2 for $x_n(t)$ being the renewal process with density Eq. (7). We can also compare all expressions with the analytical result Eq. (8); the dip at low frequencies which was present for the single process $x_n(t)$ is conserved for all numbers N used in the simulations.

Generally, if we start with a non-Poissonian process for $x_n(t)$ we will keep this non-Poissonian spectral statistics in $X(t)$. Hence, $X(t)$ is *not a Poisson process* (which needs to have a flat "white" power spectrum for all frequencies) in contradiction with what was inferred above.

Resolution of the paradox and conclusions. The paradox is as follows: the ISI statistics (PDF of the ISI and serial correlation coefficient) as well as intuitive reasoning seems to tell us that $X(t)$ is a renewal process with exponential density of the ISI. Since a renewal process is completely and uniquely characterized by the PDF of the ISI, this tells us that the process is a Poisson process. On the other hand, we could show with a simple calculation that the power spectrum of $X(t)$ is not flat as expected and necessary for a Poisson process but proportional to the (nonflat) power spectrum of the single process $x_n(t)$.

The resolution of this apparent contradiction is that $X(t)$ is *not* a renewal process but a somewhat strange type of nonrenewal process. For $N\to\infty$ it has infinitesimally small correlations for any lag between two intervals but these vanishing correlations extend over an infinite number of lags and therefore affect the spectral statistics. This can be seen as follows. For the specific process $x_n(t)$ with PDF according to Eq. (7), the spectrum has a dip; in particular, for zero frequency, the power spectrum is according to Eq. (8)

$$S_\alpha(0) = r/2 \tag{12}$$

while for a Poisson process it should be $S_{poi}(0)=r$.

For a general stationary stochastic point process, there is a simple relation between the power spectrum at frequency zero on the one hand and the ISI statistics on the other hand [6]

$$S(0) = r^3\langle (T_i - \langle T_i \rangle)^2 \rangle \left[1 + 2\sum_{k=1}^{\infty} \rho_k \right]. \tag{13}$$

In the limit of large N, we have seen that the ISIs of $X(t)$ are exponentially distributed and thus the prefactor of the brackets is r [for a Poisson process we have $\langle (T_i-\langle T_i\rangle)^2\rangle = 1/r^2$].

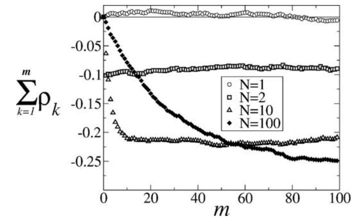

FIG. 3. Partial sum over the serial correlation coefficients (data shown in Fig. 1) up to lag m for different numbers N of superposed processes as indicated.

To get the correct limit for the power spectrum at vanishing frequency [i.e., $NS_X(0)=r/2$], we can only hope for the correction factor within the bracket. We have seen that for $N=100$ we still get some weak correlations in the ISI sequence and we argued that these correlations will become smaller and smaller as N increases. However, when summing those weak correlations over all lags for $N=100$ (compare the black diamonds in Fig. 3), we obtain indeed a finite contribution which is $\Sigma\rho_k \approx -\frac{1}{4}$. Inserting this into Eq. (13) gives us $NS_X(0)=r/2$ in agreement with our findings in the spectral domain.

Correlations in the ISI sequence also have an impact on the power spectrum at *finite* frequency and thus shape the power spectrum such that it does not change for an increasing number N of pooled spike trains. Again, the fact that the correlations vanish at a specific lag but their cumulative effect over many lags is finite in the limit $N\to\infty$ is essential to understand why a non-Poissonian (nonflat) power spectrum for $X(t)$ results.

We can learn a few more things from the partial sum shown in Fig. 3. First of all, the sum does not converge for all N to $-\frac{1}{4}$. This is plausible for the single renewal process $x_n(t)$ itself [i.e., $X(t)$ with $N=1$] for which the sum should fluctuate around zero (which it does). For N larger than 1 but not too large ($N=2,10$), the sum approaches a value larger than $-\frac{1}{4}$—in this case the prefactor in Eq. (13) will not be r (the ISI density is not yet exponential) but smaller, such that the product in Eq. (13) is again $r/2$.

The sum approaches its asymptotic value slower with increasing N. This is in agreement with the decrease of the interspike interval correlations at a given lag. With growing N the correlations are distributed over more and more lags. For $N\to\infty$ we end up with a process that has an infinitesimally small correlation at a given lag but the correlations extend over an infinite number of lags such that the sum of the correlation coefficients is $-\frac{1}{4}$. This process certainly cannot be easily recognized as a nonrenewal spike train. Our results show that with a large but finite sample of data a similar problem is already encountered for a rather modest number of superposed processes ($N=100$).

The thermodynamic limit $N\to\infty$ considered above has, of course, no direct application to the neurobiological or other problems involving superpositions of a limited number of spike trains. It helps us, though, to understand that the nonrenewal character of $X(t)$ is *not* a finite-size effect.

Consulting the classical literature on point processes [3,6,7] (see also the recent study of the sum of correlated trains [8]), we find that the original formulation of the convergence to a Poisson process always meant a Poisson process *local in time*, i.e., in a small time window T. Put differently, if the single spike train $x_n(t)$ is sparse enough compared to the time window T for which we consider the superposition of point processes

$$T \ll r^{-1} \tag{14}$$

then on this short time scale T, the process $X(t)$ constitutes a Poisson process. This amounts in the frequency domain to ignoring the low frequency range (in our example, this was $0<f<2$) where interesting non-Poissonian spectral features (e.g., the dip in our example) can be found.

Alternatively, instead of looking only at small time scales, the rate r could be rescaled with growing N such that the above inequality becomes true for arbitrary time window T, i.e., if one makes the spike trains $x_n(t)$ more and more sparse as N increases. This has been done, for instance, in the classical proof [7] on the convergence of pooled spike trains to a Poisson train. A simple way to achieve this is by choosing the rate of the single process to be $r \to r/N$ or equivalently by stretching the time axis (and keeping the rate constant)

$$\hat{X} = \sum x_n(Nt). \tag{15}$$

Note that in this case we do not need the prefactor $1/N$ to keep the mean value of the spike train constant since the spike rate of the superposition will equal r. The spectrum of this process for $x_n(t)$ being the renewal process with PDF given in Eq. (7) can be calculated

$$S_{\hat{X},\alpha} = r\left[1 - \frac{2r^2}{4r^2 + (\pi f N)^2}\right]. \tag{16}$$

We see in Fig. 4 that indeed for this rescaled system the spectral dip is moved to lower and lower frequencies as N grows. In accordance with Eq. (16), for $N \to \infty$ the spectrum approaches a constant for all finite frequencies. This is merely due to the fact that in this limit already the spectrum of the single process becomes flat at arbitrary but finite frequency.

We would like to point out that the limit in Eq. (15), i.e., a scaling of the rate of the single process with $1/N$ *or*—at fixed rate—the restriction to small time windows is not appropriate for many applications of the superposition problem. In neural systems, for instance, the relevant time scale of the output of a neuron which is driven by a superposition of many input spike trains is the same as the time scale of the single input generating neurons. Typically, this time scale includes a few spikes $1/r$ at least and hence on the relevant time scale the effective (superposed) spike train input to the postsynaptic cell will not be a Poisson process.

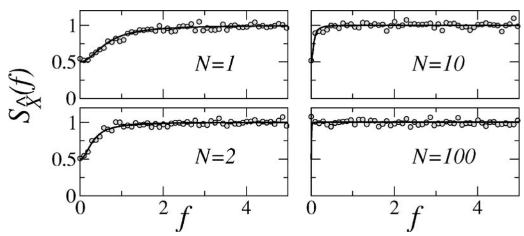

FIG. 4. Power spectra of the superposed process $\hat{X}(t)$ for which the rates of the single processes $x_n(t)$ scale with $1/N$. The simulation method is as in Fig. 2. For all simulation data, we averaged over 10^2 random spectra and additionally over ten frequency bins; each realization had a length of 2^{20} time steps of size $\Delta t = 0.01$. As in Fig. 2, only a fraction of the simulation data (i.e., a diluted data set) is shown for clarity.

Specifically, if the input neuron fires strongly enough such that refractory effects come into play, its power spectrum will exhibit a dip very similar to the one in our numerical example [9]. This dip will still be seen in the superposition of many such independent spike trains and thus also in the effective input of a postsynaptic neuron receiving these stimuli. Worse situations can be thought of: the presynaptic neurons may exhibit a strong periodic component—then the power spectrum of $x_n(t)$ will show strong peaks that also persist in the spectrum of the superposed process $X(t)$. In this case the conclusion that the superposed train has Poissonian statistics would be particularly misleading.

Our results also show that caution has to be used analyzing spike trains both from experiments and theoretical models. What may seem to be close to a renewal or even a Poissonian process from the view point of the ISI statistics, may be a process with strong nonrenewal properties and pronounced spectral features. This indicates that the ISI statistics and spike train (in particular, spectral) statistics should both be studied—neglecting one of them may give a wrong picture of the process at hand.

Note added in proof. In an independent study [10], Câteau and Reyes discuss the non-Poissonian features of summed spike trains and its consequences for signal propagation in feedforward networks.

Fruitful discussions with Nils Becker, Diego Pazo Bueno, and Frank Jülicher are gratefully acknowledged.

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