Statistical Analysis of a Spike Train Distance in Poisson Models

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***Abstract*—Several spike train metrics have been proposed in the last years for the evaluation of neural responses. In this letter, we perform deep statistical analysis on an important metric. This metric evaluates the dissimilarity between spike trains by applying a linear filter on the trains and then integrating the squared difference of the result. The statistical analysis is made when the metric is used to evaluate spike trains originated from nonhomogenous Poisson processes. Contrary to previous works, the analytical results have been obtained for the general case and not only for particular limiting conditions. By computing the expected value of the metric, insightful information is retrieved; it allows for the proposal of a normalization factor which addresses several deficiencies when comparing neural responses.**

***Index Terms*—Neural modeling, Poisson process, spike train metric.**

I. Introduction

The modeling and evaluation of neural responses is a theme of increasing interest: it improves the human knowledge of biological systems and allows the development of prostheses intended to circumvent human impairments or of systems that interact and control external devices. Neurons respond to external (biological or electronic) stimuli by eliciting electric pulses (spikes). The modeling of neuron responses can be made using nonhomogenous Poisson processes (NHPPs) [1]. In this case, one must first compute the peristimulus time histogram (PSTH) [2] using the spike trains. Typically, the PSTH is then convolved with a Gaussian filter to obtain the estimated firing rate $\hat{r}(t)$ of the neuron. After obtaining the firing rate, one can generate a sequence of spikes. The evaluation of the model can then be made using rate error metrics, such as the (normalized) mean-squared error [3], or by using spike train metrics [4]–[6].

In [5], van Rossum proposes a computationally fast and biological plausible spike train metric. Given two spike trains

$$\rho_a(t)=\sum_k \delta(t-t_k) \quad \rho_b(t)=\sum_j \delta(t-t_j) \tag{1}$$

where $\delta(t)$ is the Dirac function, and t_k and t_j are the spike instants in train a and b, this spike train metric computes the distance between the two spike trains by applying

$$\mathcal{D}(\rho_a,\rho_b)=\frac{1}{\tau}\int_0^T \big(\varphi_a(t)-\varphi_b(t)\big)^2 dt \tag{2}$$

where T is the length of the spike trains and $\varphi_x(t)$ is a filtered version of $\rho_x(t)$

$$\varphi_x(t)=\rho_x(t)*g(t) \tag{3a}$$

$$g(t)=H(t)e^{-t/\tau} \tag{3b}$$

with $*$ representing the convolution operator, $H(t)$ the Heaviside step function, and $1/\tau$ the exponential decay rate. The value of the parameter τ allows the metric to interpolate between a coincidence detector and a rate difference counter.

For simple cases, analytical results for the metric have already been presented [5]. Herein, we extend those analytical results by computing the mean error between spike trains originated from NHPPs. By applying the metric on Poisson processes, one can decrease the computational cost of estimating the mean error between the spike rate of the real neuron $\hat{r}(t)$ and the spike trains originated from a Poisson-based model. The performed comparison also gives insightful knowledge about the choice of the decay rate $1/\tau$ of the convolution function $g(t)$. By using this knowledge, we propose the normalization of the van Rossum's error metric [5].

This letter is organized as follows. Section II derives analytical results for the expected value of the metric when the spike trains under comparison are originated from NHPPs. In Section III, additional results are presented for some particular cases. From these results, we propose the normalization of the metric in Section IV. Finally, Section V ends this letter by drawing the conclusions.

II. Distance Between Nonhomogenous Poisson Processes

Given two models $\mathcal{M}_a$ and $\mathcal{M}_b$, one can compute the distance $\mathcal{D}(\rho_a,\rho_b)$ between two randomly generated spike trains $\rho_a(t)$ and $\rho_b(t)$. Considering that the probability to generate the spike train $\rho_x(t)$ is p_x, with $x\in\{a,b\}$, the expected value of the distance is

$$\begin{aligned}
&E[\mathcal{D}(\rho_a,\rho_b)]\\
&=\int_a\int_b\frac{1}{\tau}\int_0^T\big(\varphi_a(t)-\varphi_b(t)\big)^2 p_a p_b\,dt\,db\,da\\
&=\frac{1}{\tau}\int_0^T\int_a\int_b\Big[\varphi_a^2(t)-2\varphi_a(t)\varphi_b(t)+\varphi_b^2(t)\Big]p_a p_b\,db\,da\,dt\\
&=\frac{1}{\tau}\int_0^T E\left[\varphi_a^2(t)\right]+E\left[\varphi_b^2(t)\right]-2E[\varphi_a(t)]E[\varphi_b(t)]dt\\
&=\frac{1}{\tau}\int_0^T VAR[\varphi_a(t)]+VAR[\varphi_b(t)]\\
&\quad+\big(E[\varphi_a(t)]-E[\varphi_b(t)]\big)^2 dt.
\end{aligned} \tag{4}$$

While the above definitions are valid for any model—e.g., Poisson [1], [7], or Integrate and Fire [1], [8] models—it is not easy to compute $E[\varphi_x(t)]$ or $E\left[\varphi_x^2(t)\right]$ in general. However, for

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Poisson-based models, it is possible to arrive at simple expressions for both $E[\varphi_x(t)]$ and $E\left[\varphi_x^2(t)\right]$, resulting in a simple and insightful expression for the expected value of the metric.

Since the expectation E is a linear operator, one can write

$$E[\varphi_x(t)] = (E[\rho_x] * g)(t) = (r_x * g)(t) \tag{5}$$

where $r_x(t)$ is the firing rate of model $\mathcal{M}_x$ measured in Hertz; by definition, an NHPP has $E[\rho_x(t)] = r_x(t)$.

However, $E\left[\varphi_x^2(t)\right]$ is harder to compute. To obtain such an expression, a discretization procedure is applied in time bins of Δt. Under the condition

$$\forall_{t\in\mathbb{R}} \quad r_x(t) \ll (\Delta t)^{-1} \tag{6}$$

the probability for the model to fire more than one spike in each time bin can be approximated by zero. In this case, the probability for one spike to be found at bin n is $\mathcal{P}_n = r_x[n]\Delta t$, $r_x[n] = r_x(n\Delta t)$. On the other hand, the probability for no spike to be fired is $\overline{\mathcal{P}}_n = 1 - \mathcal{P}_n = 1 - r_x[n]\Delta t$.

This approximation becomes exact in the case of discretized neural models, where the probability of firing a spike at bin n does not depend on the previous elicited spikes (e.g., [9]). In this case, a spike sequence a is generated by model $\mathcal{M}$ with probability[1] P_a

$$P_a = \prod_{n\in\mathcal{S}} \mathcal{P}_n \prod_{n\notin\mathcal{S}} \underbrace{(1-\mathcal{P}_n)}_{\overline{\mathcal{P}}_n} \tag{7}$$

where $\mathcal{S}$ is the set of bins where spikes were fired: $\rho_a[n] = 1$ for $n \in \mathcal{S}$; otherwise, $\rho_a[n] = 0$.

Under this discretized model, the variance of the filtered spike train is given by Lemma 1.

Lemma 1: By considering a discrete causal temporal linear filter g and a spike train generated by an NHPP with firing probability $\mathcal{P}_n$, the variance of the filtered spike train, $\varphi[n] = (\rho * g)[n]$, is

$$VAR[\varphi[n]] = (\mathcal{P} * g^2)[n] - (\mathcal{P}^2 * g^2)[n]. \tag{8}$$

Proof: Considering (5) and the standard statistics relation, $VAR[\varphi[n]] = E[\varphi^2[n]] - E^2[\varphi[n]]$, Lemma 1 states that

$$E[\varphi^2[n]] = (\mathcal{P} * g^2)[n] + (\mathcal{P} * g)^2[n] - (\mathcal{P}^2 * g^2)[n].$$

Let us denote by $\varphi^2[n; M]$ the value of $\varphi^2[n]$ when the filter g is truncated to M samples. The lemma therefore states that the expected value of this variable is

$$\begin{aligned} &E[\varphi^2[n;M]] \\ &\quad = \sum_{k=0}^{M-1} \mathcal{P}_{n-k} g^2[k] \\ &\qquad + \sum_{k=0}^{M-1} \mathcal{P}_{n-k} g[k] \sum_{k=0}^{M-1} \mathcal{P}_{n-k} g[k] - \sum_{k=0}^{M-1} \mathcal{P}_{n-k}^2 g^2[k] \\ &\quad = \sum_{k=0}^{M-1} \mathcal{P}_{n-k} g^2[k] + 2\sum_{k=0}^{M-1}\sum_{j=k+1}^{M-1} \mathcal{P}_{n-k}\mathcal{P}_{n-j} g[k]g[j]. \end{aligned} \tag{9}$$

[1]The use of a capital letter in the discrete case arises from the fact that the number of possible cases becomes finite.

This result can be proven by induction. By definition, the expected value for $M = 1$ is

$$\begin{aligned} E\left[\varphi^2[n;1]\right] &= \mathcal{P}_n (1\cdot g[0])^2 + \overline{\mathcal{P}}_n \cdot (0 \cdot g[0])^2 \\ &= \sum_{k=0}^{0} \mathcal{P}_n g^2[k] + 2\sum_{k=0}^{0}\sum_{j=k+1}^{0} \mathcal{P}_{n-k}\mathcal{P}_{n-j} g[k]g[j]. \end{aligned}$$

For increased filter length, $M' = M + 1$, one can write

$$\begin{aligned} \varphi^2[n;M'] &= \left(\sum_{k=0}^{M} \rho[n-k]g[k]\right)^2 \\ &= \left(\sum_{k=0}^{M-1} \rho[n-k]g[k] + \rho[n-M]g[M]\right)^2. \end{aligned}$$

Two cases can occur:

C1: a spike was NOT fired at time bin $n - M$ ($\rho[n-M] = 0$): φ is unchanged, $\varphi[n; M+1] = \varphi[n; M]$; this hypothesis has probability $\overline{\mathcal{P}}_{n-M}$;

C2: a spike was fired at time bin $n - M$ ($\rho[n - M] = 1$): $g[M]$ is added to φ so that $\varphi[n; M+1] = \varphi[n; M] + g[M]$; the expected value for this case is $E[\varphi^2[n; M + 1]] = E[(\varphi[n; M] + g[M])^2]$; this hypothesis has probability $\mathcal{P}_{n-M}$.

Combining the two cases in a mathematical expression results

$$\begin{aligned} &E\left[\varphi_x^2[n;M+1]\right] \\ &\quad = \overbrace{\overline{\mathcal{P}}_{n-M} E\left[\varphi^2[n;M]\right]}^{\mathbf{C1}} + \overbrace{\mathcal{P}_{n-M} E\left[(\varphi[n;M] + g[M])^2\right]}^{\mathbf{C2}} \\ &\quad = \overline{\mathcal{P}}_{n-M} E\left[\varphi^2[n;M]\right] + \mathcal{P}_{n-M} E\left[\varphi^2[n;M] \right. \\ &\qquad \left. + 2g[M]\varphi[n;M] + g^2[M]\right] \\ &\quad = E\left[\varphi^2[n;M]\right] + 2\mathcal{P}_{n-M} E\left[\varphi[n;M]\right] g[M] + \mathcal{P}_{n-M} g^2[M] \\ &\quad = \sum_{k=0}^{M-1} \mathcal{P}_{n-k} g^2[k] + 2\sum_{k=0}^{M-1}\sum_{j=k+1}^{M-1} \mathcal{P}_{n-k}\mathcal{P}_{n-j} g[k]g[j] \\ &\qquad + 2\mathcal{P}_{n-M} E\left[\varphi[n;M]\right] g[M] + \mathcal{P}_{n-M} g^2[M] \\ &\quad = \sum_{k=0}^{M} \mathcal{P}_{n-k} g^2[k] + 2\sum_{k=0}^{M-1}\sum_{j=k+1}^{M-1} \mathcal{P}_{n-k}\mathcal{P}_{n-j} g[k]g[j] \\ &\qquad + 2\sum_{k=0}^{M-1} \mathcal{P}_{n-M}\mathcal{P}_{n-k} g[k]g[M] \\ &\quad = \sum_{k=0}^{M} \mathcal{P}_{n-k} g^2[k] + 2\sum_{k=0}^{M}\sum_{j=k+1}^{M} \mathcal{P}_{n-k}\mathcal{P}_{n-j} g[k]g[j] \end{aligned}$$

Thus, having proven (9), we have demonstrated (8) in Lemma 1. ■

Let us now extend the obtained results in Lemma 1 to the continuous mode.

Lemma 2: The variance of the convolution between a spike train ρ, generated by an NHPP with finite rate $r(t)$, and a linear filter g is

$$VAR\left[\varphi(t)\right] = (\mathcal{P} * g^2)(t). \tag{10}$$

Proof: When applying the limit $\Delta t \to 0$ to (8), the first term corresponds to the discretization of the convolution operator in the continuous mode, while the second term corresponds to the discretization of the convolution $(r^2 * g^2)(t)$ multiplied

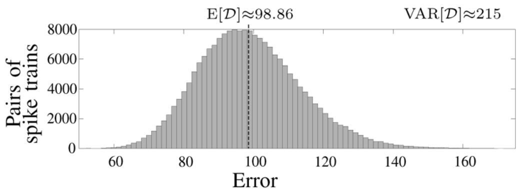

Fig. 1. Distribution of the van Rossum metric when comparing spike trains generated by the same Poisson process.

by the discretization step Δt. This last term can thus be ignored as long as $r(t) \in \mathbb{R}$. Thus

$$VAR[\varphi(t)] = \lim_{\Delta t \to 0} \Delta t (r * g^2)[n] - \underbrace{(\Delta t)^2 (r^2 * g^2)[n]}_{=0} = (r * g^2)(t).$$

■

Lemma 3: The variance of the convolution between a spike train ρ, generated by an NHPP with impulsive firing rate $r(t) = \sum_k \delta(t - t_k)$, and a linear filter g is zero.

Proof: When $\Delta t \to 0$, for impulsive firing rate, $\forall_{\Delta t, n} \mathcal{P}_n \in \{0, 1\}$. Thus, $\mathcal{P}_n = \mathcal{P}_n^2$ and

$$VAR[\varphi_x(t)] = \lim_{\Delta t \to 0} ((\mathcal{P} - \mathcal{P}^2) * g^2)[n] = 0.$$

In other words, there is exact knowledge that one spike is fired at time instants $t_1, \ldots, t_K$; the spike train becomes deterministic. ■

By applying (5) and (10) in (4), the expected error between two spike trains ρ_a and ρ_b generated by models $\mathcal{M}_a$ and $\mathcal{M}_b$, with finite firing rates $r_a(t) \in \mathbb{R}$ and $r_b(t) \in \mathbb{R}$ is

$$E[\mathcal{D}(\rho_a, \rho_b)] = \frac{1}{\tau} \int_0^T \big((r_a + r_b) * g^2\big)(t) + \big((r_a - r_b) * g\big)^2(t) dt. \quad (11)$$

Expression (11) allows to compute the error between two Poisson models without having to generate spike trains for each model. From the computational point of view, this can be an important advantage, namely, for large firing rates where the variance of the metric can be considerably large. As an example, let us consider the experimental evaluation of spike trains with length $T = 1$ s, generated by a model with constant firing rate, $r(t) = 100$ Hz, a sampling period of 1 ms, and a decay of $\tau = 10$ ms. Fig. 1 presents the histogram of the error when comparing 200.000 random pairs of spike trains; it fits a gamma distribution with scale $\theta \approx 2.15$ and shape $k \approx 46$ (computed by using maximum likelihood estimation). The experimental and theoretical mean error is $E[\mathcal{D}] \approx 98.86$. Notice that, for computing the expected value of the error, the term $(\Delta t)^2 (r^2 * g^2)[n]$ must be subtracted from (11): it is only null in the continuous case. As can be seen by the histogram, the experimental variance of the error is considerably large ($VAR[\mathcal{D}] \approx 215$); this forces the generation of a large number of spike trains in order to obtain a precise experimental evaluation of the mean error.

III. Additional Analytical Results

For certain particular cases it is possible to achieve even simpler expressions for the expected value of the metric. These cases are when: 1) τ tends to 0 and ∞; 2) the firing rates of the models under evaluation are the same; 3) the models have constant firing rates; and 4) one model is evaluated against a single spike train.

For performing the evaluation for the given cases, let us first normalize the gains of the filters g and g^2 in Lemma 2. Let h_τ be a linear low pass filter with unitary gain

$$h_\tau(t) = H(t) \frac{1}{\tau} e^{-t/\tau} \text{ with } \int_{-\infty}^{\infty} h_\tau(t) = 1 \quad (12)$$

resulting in $g(t) = \tau h_\tau(t)$, $g^2(t) = \frac{\tau}{2} h_{\tau/2}(t)$, and

$$E[\mathcal{D}(\rho_a, \rho_b)] = \int_0^T \frac{1}{2} \big((r_a + r_b) * h_{\tau/2}\big)(t) + \tau \big((r_a - r_b) * h_\tau\big)^2(t) dt. \quad (13)$$

A. Mean Distance For Extremely High Decay Rates ($\tau \to 0$)

For $\tau \to 0$, the poles of the filters g and g^2 are moved to $s = +\infty$ (all pass filters). In this case, the expected value for the distance between NHPPs is

$$\lim_{\tau \to 0} E[\mathcal{D}(\rho_a, \rho_b)] = \int_0^T \frac{r_a(t) + r_b(t)}{2} dt. \quad (14)$$

The expected value of the metric is the mean firing rate of both models. Since the metric should evaluate the difference between spike trains, this result shows that the value of τ should not be too small.

B. Mean Distance For Extremely Low Decay Rates ($\tau \to \infty$)

From (13), the first term can be neglected when $\tau \to \infty$. Therefore

$$\lim_{\tau \to \infty} E[\mathcal{D}(\rho_a, \rho_b)] = \lim_{\tau \to \infty} \int_0^T \tau ((r_a - r_b) * h_r)^2(t) dt. \quad (15)$$

For a sufficiently large value of τ, the metric evaluates the difference between firing rates: it is similar to the mean-squared error of the firing rates.

Expression (15) differs from [5, (2.5)]. This inconsistency is due to the fact that van Rossum neglected that, in the limit condition of $\tau \to \infty$, the linear function $g(t)$ is proportional to the Heaviside step function. Therefore, the integral converges to $+\infty$.

C. Evaluating Equivalent Poisson Processes

For instance, if the firing rate of models $\mathcal{M}_a$ and $\mathcal{M}_b$ is the same ($r_a(t) = r_b(t) = r(t)$), then

$$E[\mathcal{D}(\rho_a, \rho_b)] = \frac{2}{\tau} \int_0^T (r * g^2)(t) dt. \quad (16)$$

This result implies that the mean error using this metric does not converge to zero for equal NHPPs.

D. Evaluating Homogenous Poisson Processes

If the firing rates of models $\mathcal{M}_a$ and $\mathcal{M}_b$ are constant, $r_a(t) = R_a$ and $r_b(t) = R_b$, then, from (13), it results

$$E[\mathcal{D}(\rho_a, \rho_b)] = T \frac{R_a + R_b}{2} + \tau T (R_a - R_b)^2. \quad (17)$$

E. Mean Error Between a Spike Train and a Poisson Process

When comparing a single spike train $\rho(t)$ with the spike trains $\hat{\rho}$ originated from a Poisson process with firing rate $\hat{r}(t)$, one can consider it as an NHPP with impulsive firing rate $r(t) = \rho(t) =$

$\sum_k \delta(t-t_k)$. By applying (5) and Lemmas 2 and 3 to (4), it results

$$E[\mathcal{D}(\rho,\hat{\rho})] = \frac{1}{\tau}\int_0^T \left(\hat{r}*g^2\right)(t) + \left((\rho-\hat{r})*g\right)^2(t)dt. \quad (18)$$

Notice that if we consider a second Poisson process $\hat{r}(t) = \hat{\rho}(t) = \sum_k \delta(t-\hat{t}_k)$, it results in the original metric

$$E[\mathcal{D}(\rho,\hat{\rho})] = \frac{1}{\tau}\int_0^T \left((\rho-\hat{\rho})*g\right)^2(t)dt. \quad (19)$$

IV. Improving the Error Metric

Using expression (11), one observes that, for Poisson processes, the expected value of the metric has contributions from two terms: 1) the average firing rate of the models, $C^+(t) = (r_a(t)+r_b(t))/2$, and 2) the difference of firing rates, $C^-(t) = r_a(t)-r_b(t)$. Notice also that this result is independent of the convoluting function $g(t)$. If, as suggested by van Rossum [5], $g(t)$ assumes the shape of the spike-triggered average, the result will still hold.

Ideally, one would like to maximize the contribution from the difference of firing rates, $C^-(t)$, while minimizing the contribution from the mean firing rate $C^+(t)$. This can be achieved for a sufficiently high value of τ. However, for such case, the metric is not normalized: as τ increases, so does the value of the metric.

A second problem of the metric is concerned with its dependence on the length T of the spike trains under evaluation. This is a well-known problem in neural modeling which makes difficult the evaluation and comparison of models.

A solution for these two problems can be achieved by slightly changing the metric. For reducing the metric dependency with τ, we propose to normalize the gain of the linear filter by replacing function $g(t)$ with $h_\tau(t)$

$$\varphi^*(t) = (\rho_x * h_\tau)(t). \quad (20)$$

On the other hand, the dependence with the length of the spike train can be minimized by replacing the integration of the error in time with the computation of the expected value of the error in time

$$\mathcal{D}^*(\rho_a(t),\rho_b(t)) = \frac{1}{T}\int_0^T (\varphi_a^*(t)-\varphi_b^*(t))^2 dt. \quad (21)$$

In this case, and by following (11), the expected value of the proposed metric $\mathcal{D}^*$ when comparing spike trains originated from two NHPPs is

$$E[\mathcal{D}^*(\rho_a,\rho_b)] = \frac{1}{T}\int_0^T \frac{1}{2\tau}\left((r_a+r_b)*h_{\tau/2}\right)(t) + \left((r_a-r_b)*h_\tau\right)^2(t)dt. \quad (22)$$

The change in the metric is therefore just a scaling factor: it does not change the quantity being measured, only the resulting amplitude is different. However, this scaling factor has some important benefits. The comparison between a spike train $\rho(t)$ and a model $\mathcal{M}$ which fires no spikes no longer depends on τ; instead, the metric returns the number of spikes in $\rho(t)$. Moreover, the maximum value for the metric when comparing two spike trains is the sum of spikes in both trains.

If we reevaluate the limiting cases of the decay rate $1/\tau$, we now conclude that for $\tau \rightarrow 0$, the metric converges again to $+\infty$. However, since τ should not be too small, it is not an important factor.

V. Conclusions

This letter demonstrates how to compute the expected error of the van Rossum spike train metric when applied to nonhomogenous Poisson models. The obtained results are valid both for the original van Rossum metric and for any other metric of the same class, such as those obtained by convolving the spike train with any causal linear filter.

The application of the developed expression for the expected value of the metric decreases the computational cost of evaluating Poisson processes. Moreover, when the original van Rossum metric is used with an exponential function, it is possible to obtain simpler expressions for spike trains originated from Poisson processes. The information obtained from these results allowed us to improve the metric by changing the gain of the error function. This change consists on normalizing the result by the inverse of the decay rate of the exponential function, and by the length of the spike train.

The derived expressions can also be useful for optimizing the parameters of a Poisson model: instead of using a mean-squared error metric of the firing rate, one can directly tune a Poisson model using the van Rossum metric.

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