# Understanding a Measure for Synchrony: Spike Time Tiling Coefficient Method

Evan Huang<sup>\*</sup>, Kevin Li<sup>†</sup>, and Bill Sun<sup>\*</sup>

Project Advisors: Dr. Yunjiao Wang<sup>‡</sup> and Dr. Maria Leite<sup>§</sup>

#### Abstract

Synchrony is an important feature of brain activities for the coordination of neural information and is also related to some neuronal disorders. Around 40 different measures have been proposed in literature for quantifying the synchrony of spike trains and the list is still growing. The main issue is that it is not clear to users which one to use and how measurements correspond to different features of synchrony. In this work, instead of looking at all methods at once, we focus on investigating one of the popular measures in the field of neuroscience: Spike Time Tiling Coefficient (STTC) proposed by Cutts and Eglen in 2014. We simulate three scenarios of neural spike trains and study how STTC values depend on distributions and phase shifts of spike trains. Firstly, we study pairs of simple periodic binary time series. We derive an analytical formula showing that the dependence of the STTC value on the phase shift is symmetric and has a general trend where the maximum value of STTC occurs when the phase shift is zero and the minimum value occurs when the phase shift is half of the period. Secondly, we investigate pairs of "periodic" normally distributed spike trains. While we observe the similar trends shown in the first scenario, we notice an exception. We also observe a general trend where the STTC value decreases as the standard deviation of the normal distribution increases. Thirdly, we study pairs of Poisson distributed spike trains. Using properties of the Poisson distribution, we generate pairs of Poisson distributed spike trains with certain overlap ratios and study the relationship between STTC and the overlap ratio. In general, this relationship is nonlinear. We observe that as the synchronicity window decreases towards zero, this nonlinear relationship tends toward a linear relationship. We derive analytical formulas to describe this nonlinear relationship and quantitatively evaluate its closeness to a linear relationship as the synchronicity window decreases towards zero. Through studying STTC, we notice that when the synchronicity window is too large, the problem of dividing by zero occurs in the calculation of STTC. To avoid such a problem, we derive an upper bound for the synchronicity window. We also argue that STTC can only approach -1, and show a case to demonstrate this argument.

<sup>\*</sup>Seven Lakes High School

 $<sup>^{\</sup>dagger}$ Corresponding author: kevinli.yili@gmail.com, previously with Seven Lakes High School, currently with Texas Academy of Mathematics and Science

<sup>&</sup>lt;sup>‡</sup>Texas Southern University: yunjiao.wang@tsu.edu

<sup>&</sup>lt;sup>§</sup>University of South Florida, St. Petersburg

## 1 Introduction

Neurons use action potentials, which are also called spikes, to signal over long distances. It is believed that the timing of individual spikes carries most of the information [6]. The detailed voltage waveform is often converted into binary events where "1" represents a spike and "0" means no spike. The binary sequence is referred to as a spike train. When comparing a pair of spike trains, we can always convert them to binary representations so that the pair has the same unit time step since any arrival time is assumed to be a rational number. Bursting refers to groups of relatively high-frequency spikes that are separated by quiescence [8]. Each such group of high-frequency spikes is called a burst. In binary representation, a burst refers to a piece of signal that satisfies [1]: (a) consisting of consecutive 1s and 0s, (b) starting and ending with 1, (c) being separated from neighboring bursts by relatively long consecutive 0s.

The study of synchrony between spike trains has many applications [3]. For example, synchrony is an important feature of brain functions [5, 7, 9], and it is also related to pathological states [2]. Around 40 different measures for synchrony of spike trains have been proposed, and several papers have been devoted to comparing some or all of the existing methods [2, 4]. However, it is still not clear to a practitioner on which one to use and how to interpret resulting measurements if the signals are not in complete synchrony.

In this work, instead of looking at all measurements at once, we focus on investigating in a great detail in one of the popular measurements in the field of neuroscience: Spike Time Tiling Coefficient (STTC) Method proposed by Cutts and Eglen [4]. We study STTC for signals generated by three models, namely periodic binary time series, "periodic" normalbursting, and Poisson spiking trains. Our choice of the three models was inspired by the test setting in [4]. The measure STTC was tested in [4] for pairs of synthetic spike trains generated by the Poisson spiking model, Poisson burst model and out-of-synchrony spiking and bursting models. The Poisson spiking model assumes that spike trains A and B fire Poissondistributed spikes, and a certain proportion of spikes from the two trains are synchronous and also follow the Poisson distribution. It is not hard to see that increasing the proportion of synchronous spikes increases the mean STTC value. However, it is not transparent how exactly STTC values depend on the proportion of synchrony. We are interested in finding out the relation between these two quantities by following [4] to further study STTC values of pairs of signals generated by the Poisson spiking model. The Poisson burst model in [4] is a doubly stochastic process: the center-points of bursts are generated by the Poisson process and then the positions of spikes relative to the center-point of each burst follow either a normal distribution or a continuous uniform distribution. As the measure was also tested for out-of-synchrony (anti-phase) spiking and bursting models, a natural question arises for this testing scenario: suppose a signal is periodic, how does STTC value depend on the phase shift? To seek the answer to this question, we choose to start with a simplistic model: a periodic binary time series with a repeated pattern in the form  $1 \cdots 10 \cdots 0$ . The model is simple enough for easy calculations of STTC values while still capturing the main feature of bursts. We then ask the same question when the signals are generated by the "periodic" normally distributed burst model, in which center-points of bursts are equally spaced and the positions of spikes relative to the center-point of each burst follow a normal distribution.

For the binary time series model, we are able to derive an analytical formula demonstrating how STTC values depend on the phase shift and how this dependence is determined by the number of spikes in the spike trains. In general, the dependence of STTC values on the phase shift is symmetric and has a general trend where the maximum value of STTC occurs when the phase shift is zero and the minimum value occurs when the phase shift is half of the period. This simple case provides a perspective to gain a basic understanding of STTC measure.

For "periodic" normally distributed spike trains, while we observe similar trends shown in the first scenario, we notice an exception that when the the synchronicity window for calculating STTC is large relative to the period, the maximum value of STTC occurs when the phase shift is half of the period and the minimum value occurs when the phase shift is zero. This is opposite to the case when the synchronicity window is small relative to the period. We also observe a general trend that STTC value decreases as the standard deviation of the normal distribution increases.

In the case of the Poisson spiking model, using properties of the Poisson distribution, we generate pairs of Poisson distributed spike trains with certain overlap (synchrony) ratios and study the relationship between STTC and the overlap ratio. In general, this relationship is nonlinear. We observe that as the synchronicity window decreases towards zero, this nonlinear relationship tends to a linear relationship with a slope of  $\frac{\lambda_a + \lambda_b}{2\lambda_b}$  and a *y*-intercept of zero, where  $\lambda_a \leq \lambda_b$  are the rates of pairs of Poisson distributed spike trains. We derive analytical formulas to describe this nonlinear relationship and quantitatively evaluate its closeness to this linear relationship as the synchronicity window decreases towards zero.

Through studying STTC, we realize that when the synchronicity window is too large, the problem of dividing by zero occurs in the calculation of STTC. To avoid such a problem, we derive an upper bound for the synchronicity window. We also argue that STTC can only approach -1, and show a case to demonstrate this argument.

The paper is organized as follows. In Section 2, we briefly review the STTC measure. In Section 3, we derive an analytical formula for the STTC measure for pairs of simple periodic binary time series. In Section 4, we present experimental results for the STTC measure for pairs of "periodic" normally distributed spike trains. In Section 5, we present both experimental and analytical results for STTC measure for pairs of Poisson distributed spike trains. We discuss some general observations about STTC in Section 6 and finally, draw some conclusions in Section 7.

## 2 Preliminary

In this section, we briefly review the method of Spike Time Tiling Coefficient (STTC) [4]. This method was proposed for quantifying the correlation between pairs of spike trains. In this method the authors defined four variables,  $T_A$ ,  $T_B$ ,  $P_A$ , and  $P_B$ , as shown in the following diagram from the original paper, where  $T_A$  is the proportion of the total recording time that falls within the synchronicity window  $\pm \Delta t$  of any spike from signal A, and  $P_A$  is the proportion of spikes from signal A that falls within  $\pm \Delta t$  of any spike from signal B.  $T_B$  and  $P_B$  are calculated in a similar way.

## **Spike Time Tiling Coefficient - STTC**

**T<sub>A</sub>:** the proportion of total recording time which lies within  $\pm\Delta t$  of any spike from A. **T<sub>B</sub>** calculated similarly.



 $T_A$  is given by the fraction of the total recording time (black) which is covered (tiled) by blue bars. Here  $T_A$  is 1/3.

**P<sub>A</sub>:** the proportion of spikes from A which lie within  $\pm\Delta t$  of any spike from B. **P<sub>B</sub>** calculated similarly.



number of spikes in A (5). Here  $P_A$  is 3/5.

Figure 1: Definition of STTC. This figure is taken from [4] Fig.1.

In calculating  $T_A$  or  $T_B$ , if  $\Delta t$  overlaps multiple spikes, then we only count the overlapping areas once. The authors argued that STTC should be symmetric to combine the contributions from both spike trains. In summary, the authors define the STTC formula as follows:

$$STTC = \frac{1}{2} \left( \frac{P_A - T_B}{1 - P_A T_B} + \frac{P_B - T_A}{1 - P_B T_A} \right)$$

The authors indicate that STTC ranges from -1 to 1 and is equal to 1 for autocorrelation and -1 when  $P_A = 0$  and  $T_B = 1$ . However, we argue that STTC can only approach but never equal -1 since if  $T_B = 1$ , then  $P_A \neq 0$ , and vice versa (assume that spike trains A and B contain at least one spike, respectively). We demonstrate this argument in Section 6.

# **3** STTC of Pairs of Periodic Binary Time Series

In this section, we study pairs of simple periodic binary time series. The pairs have the following format: binary time series A is periodic in the form

$$A: \underbrace{\overline{1\cdots 1}}_{m} \underbrace{0\cdots 0}_{n} \tag{3.1}$$

Binary time series B is a k-shift of A, with  $0 \le k \le (m+n)$ . For example, when m = 3, n = 5, k = 1

 $A:\overline{11100000}$ 

 $B:\overline{011100000}$ 

If we choose the synchronicity window  $\Delta t = 0.5$ , then

$$T_A = T_B = \frac{3}{8}$$
$$P_A = P_B = \frac{2}{3}$$

 $\operatorname{So}$ 

$$STTC = \frac{1}{2} \left( \frac{P_A - T_B}{1 - P_A T_B} + \frac{P_b - T_A}{1 - P_B T_A} \right) = \frac{P_A - T_B}{1 - P_A T_B} = \frac{\frac{2}{3} - \frac{3}{8}}{1 - \frac{2}{3} \cdot \frac{3}{8}} = \frac{7}{18}$$

if  $\Delta t = 1$ , then

$$T_A = T_B = \frac{4}{8} = \frac{1}{2}$$
$$P_A = P_B = 1$$
$$STTC = \frac{P_A - T_B}{1 - P_A T_B} = 1$$

**Theorem 3.1.** Let A be a periodic binary time series of the form of (3.1) and B is a k phase shift of A with  $0 \le k \le (m+n)$ , where m > 0. If we choose the synchronicity window  $\Delta t$  to be 0.5, then

$$STTC = \begin{cases} \frac{mn - (m+n)k}{mn + mk}, & 0 \le k < \min\{m, n\} \\ Z, & \min\{m, n\} \le k \le \max\{m, n\} \\ \frac{mn - (m+n)q}{mn + mq}, & \max\{m, n\} < k \le (m+n) \end{cases}$$
(3.2)

where q = (m+n) - k and

$$Z = \begin{cases} -\frac{m}{m+n}, & m < n \\ -\frac{1}{2}, & m = n \\ -\frac{n}{2m}, & m > n \end{cases}$$

*Proof.* When the synchronicity window  $\pm \Delta t$  centered with each number in the binary time series fully covers a 1 or 0, *i.e.*,  $\Delta t = 0.5$ , then  $T_A$  and  $T_B$  can be simply calculated by counting the number of 1s and 0s in the time series. Also because of periodicity, we just need to count spikes over one period. So  $T_A$  is equal to the ratio of the number of spikes over one period and the total number of time steps over a period, *i.e.*,

$$T_A = T_B = \frac{m}{m+n}$$

Similarly,  $P_A$  and  $P_B$  can be found by counting spikes over a period as well. When k is in the range of  $0 \le k < min\{m, n\}$ , the number of overlap over one period is m - k. Hence,

$$P_A = P_B = \frac{m-k}{m}$$

When k is in the range of  $max\{m,n\} < k \leq (m+n)$ , the number of overlap over one period is k-n. Hence,  $P_A$  and  $P_B$  is,

$$P_A = P_B = \frac{k-n}{m}$$

When k is in the range of  $min\{m, n\} \le k \le max\{m, n\}$ , there are two cases. Case 1: If  $m \le n$ , then  $m \le k \le n$  and the two trains have no overlapping spike. Hence,

$$P_A = P_B = 0$$

Case 2: If m > n, then  $n \le k \le m$  and the two trains have exactly m - n number of spikes overlapped. Hence,

$$P_A = P_B = \frac{m-n}{m}$$

From the definition of STTC, the STTC value for the pair of periodic binary time series A and B is derived as follows.

1) When  $0 \le k < \min\{m, n\},\$ 

$$STTC = \frac{\frac{m-k}{m} - \frac{m}{m+n}}{1 - \frac{m-k}{m}\frac{m}{m+n}} = \frac{nm - (m+n)k}{mn + mk}$$

2) When  $max\{m, n\} < k \le (m+n)$ ,

$$STTC = \frac{\frac{k-n}{m} - \frac{m}{m+n}}{1 - \frac{k-n}{m}\frac{m}{m+n}} = \frac{nm - (m+n)q}{mn + mq}$$

where q = (m+n) - k.

3) When  $min\{m,n\} \le k \le max\{m,n\},\$ 

if m < n, then

$$STTC = -\frac{m}{m+n}$$

if m = n, then

$$STTC = -\frac{1}{2}$$

if m > n, then

$$STTC = -\frac{n}{2m}$$

In summary, the STTC for the pair of periodic binary time series A and B can be written as the expression in (3.2).

#### **Remark:**

- 1) Z is the minimum value of STTC, which is greater than or equal to  $-\frac{1}{2}$ , with equality when m = n. It only depends on the number of consecutive 1s and 0s in the binary time series of the form of (3.1) and is independent of the shift k.
- 2) STTC reaches the minimum value when shift  $k = min\{m, n\}$ , and remains the minimum value until k is beyond the value of  $max\{m, n\}$ .
- 3) STTC is symmetric around  $k = \frac{1}{2}(m+n)$ .

These observations are illustrated in Figure 2, where the combinations of m and n include  $(m, n) = \{(10, 10), (15, 5), (5, 15)\}$ . We can see that the dependence of STTC value on k is symmetric, and has a general trend where the maximum value of STTC occurs when shift k is zero, and the minimum value of STTC occurs when k is half of the period (m + n). This simple case demonstrates how the STTC value is determined by the number of spikes, m, in the spike trains and the period (m + n) and provides a perspective to gain a basic understanding of the STTC measure.



Figure 2: Dependence of the STTC value on phase shift k for pairs of periodic binary time series in the form of (3.1), where the period is (m + n) and the combinations of m and n include  $(m, n) = \{(10, 10), (15, 5), (5, 15)\}.$ 

# 4 STTC Measure for Pairs of "Periodic" Normally Distributed Spike Trains

In this section, we study pairs of "periodic" normally distributed spike trains. We investigate how STTC values depend on the phase shift and the standard deviation of the normal distribution, respectively. We further investigate how the synchronicity window affects the dependence of STTC values on the phase shift. We generate normally distributed spike trains for each period independently, which implies that the resulting spike trains are not exactly periodic though the standard deviation is the same. Figure 3 shows an example of such periodic spike trains, where period W = 10, standard deviation  $\sigma = 1$ , and the mean of the normal distribution is an integer multiple of the period. In the figure, a pair of 5 periods of normally distributed spike trains are shown, and in each period, there are 20 spikes that follow the normal distribution. The pair has a half-period phase difference, and the histogram for the pair is plotted along with the distribution of spikes. More specifically, spike locations in each period follow a normal distribution.



Figure 3: A pair of 5 periods of normally distributed spike trains and their histogram, with period W = 10, standard deviation  $\sigma = 1$ . The number of spikes in each period is 20.

### 4.1 Dependence of STTC on Phase Shift

We calculate STTC values as phase shift k changes from 0 to a period, W = 10, with increments of 0.2. For each k, we generate 100 pairs of normally distributed spike trains with standard deviation  $\sigma = 1$ . For each pair, we generate 10 periods of spike trains, and in each period, there are 20 spikes that follow the normal distribution. We calculate STTC for each pair with synchronicity window  $\Delta t = 0.5$ . We use the mean value of such 100 STTC values for the corresponding phase shift k. Figure 4 shows the experimental result. We observe similar trends shown in the scenario of pairs of simple periodic binary time series. That is, the dependence of STTC values on the phase shift is symmetric, and has a general trend that the maximum value of STTC occurs at the location where the phase shift k is half of the period W.



Figure 4: Dependence of the expected value of STTC on phase shift k for pairs of "periodic" normally distributed spike trains, with period W = 10, standard deviation  $\sigma = 1$  and synchronicity window  $\Delta t = 0.5$ .

### 4.2 Dependence of STTC on Standard Deviation

We calculate STTC values for pairs of "periodic" normally distributed spike trains with various standard deviations  $\sigma$ , ranging from 0.25 to a period, W = 10, with increments of 0.25. For each  $\sigma$ , we generate 100 pairs of normally distributed spike trains. For each pair, we generate 10 periods of spike trains, and in each period, there are 20 spikes that follow a normal distribution. We calculate STTC for each pair with phase shift k = 0 and synchronicity window  $\Delta t = 0.1$ . We use the mean value of such 100 STTC values for the corresponding standard deviation  $\sigma$ . Figure 5 shows the experimental results, where two different cases are demonstrated. In the first case, the standard deviation used to generate both signals in the pair is the same, *i.e.*,  $\sigma_a = \sigma_b = \sigma$ . In the second case, the standard deviation for the other changes, *i.e.*,  $\sigma_b = \sigma$ . We can see that in general for both cases the STTC value decreases as standard deviation  $\sigma$  increases. However, it is interesting to note that when  $\sigma$  continues increasing so that  $2\sigma$  is close to and greater than period W, the STTC value no longer decreases and even increases a little bit. The reason could be that as the standard deviation deviation increases beyond certain point, the spikes act more like random noise.



Figure 5: Dependence of the expected value of STTC on standard deviation  $\sigma$  for pairs of "periodic" normally distributed spike trains, with period W = 10, phase shift k = 0 and synchronicity window  $\Delta t = 0.1$ .

#### 4.3 Effects of Synchronicity Window on STTC Measure

We are interested in how the dependence of STTC values on phase shift k is affected by synchronicity window  $\Delta t$ . We investigate a set of  $\Delta t$ , represented in the form of a ratio of  $\Delta t$  over period W, that is,  $\Delta t/W = [0.01, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6]$ , where W = 10. For each  $\Delta t$ , we calculate STTC values as phase shift k changes from 0 to a period, W = 10, with increments of 0.2. For each k, we generate 100 pairs of normally distributed spike trains with standard deviation  $\sigma = 1$ . For each pair, we generate 10 periods of spike trains, and in each period, there are 20 spikes that follow the normal distribution. We calculate STTC for each pair with synchronicity window  $\Delta t$  selected from the set of  $\Delta t/W$ . We use the mean value of such 100 STTC values for the corresponding phase shift k. Figure 6 shows the experimental results. It is interesting to note that when  $\Delta t/W$  is large, indicating that synchronicity window  $\Delta t$  is large relative to the period W, the general trend observed in Section 3 and Section 4.1 is inverted. That is, the maximum value of STTC occurs at the location where phase shift k is half of the period W, and the minimum value of STTC occurs at the location where phase shift k is zero. The reason could be that the synchronicity window is large enough to include spikes in neighboring period intervals in the calculation of the STTC. As a result, when the phase shift is at half the period, it appears that pairs of spike trains have a better correlation.



Figure 6: Effects of synchronicity window  $\Delta t$  on the dependence of the expected value of STTC on phase shift k for pairs of "periodic" normally distributed spike trains, with period W = 10 and standard deviation  $\sigma = 1$ .

# 5 STTC Measure for Pairs of Poisson Distributed Spike Trains

In this section we study pairs of Poisson distributed spike trains with certain overlaps. The overlapped parts of the pair of spike trains contain shared spikes and thus are synchronous, and the non-overlapped parts are statistically independent. We generate a pair of overlapped Poisson distributed spike trains by combining two separate Poisson distributed spike trains. One is the synchronous spike train containing shared spikes, and the other is the independent spike train. Let the rates of a pair of overlapped Poisson distributed spike trains be  $\lambda_a$  and  $\lambda_b$ , and without loss of generality, let  $\lambda_a \leq \lambda_b$ , then the rate of the synchronous spike train is  $\lambda_s = r\lambda_a$ , with  $0 \leq r \leq 1$  being the overlap ratio, and the rates of independent spike trains are  $\lambda_a - \lambda_s$  and  $\lambda_b - \lambda_s$ , respectively. Figure 7 shows an example of a pair of Poisson distributed spike trains with r = 0.5,  $\lambda_a = \lambda_b = 2$ , and time limit T = 20. We investigate the relationship between STTC and overlap ratio r for pairs of Poisson distributed spike trains.



Figure 7: An example of a pair of Poisson distributed spike trains with overlap ratio r = 0.5, rates  $\lambda_a = \lambda_b = 2$ , and time limit T = 20.

## 5.1 Relationship Between STTC and Overlap Ratio

To investigate the relationship between STTC and overlap ratio r, we calculate STTC values for pairs of Poisson distributed spike trains as overlap ratio r changes from 0 to 1. Given a pair of spiking rates  $\lambda_a$  and  $\lambda_b$ , for each r from 0 to 1 with increments of 0.02, we generate 100 pairs of Poisson distributed spike trains with time duration T = 100, and compute the mean STTC. We repeat the process for different values of synchronicity window  $\Delta t$ . The result for  $\lambda_a = \lambda_b = 2$  is shown in Figure 8. We observe that in general the relationship between the expected value of STTC and the overlap ratio is nonlinear. For a fixed  $\lambda$ , as synchronicity window  $\Delta t$  decreases, the relationship tends to be linear. We find that this observation remains the same as we change the spiking rates  $\lambda_a$  and  $\lambda_b$  to other values.



Figure 8: Relationship between the expected value of STTC and overlap ratio r for pairs of Poisson distributed spike trains, where  $\lambda = 2$ , T = 100, and  $\Delta t = [0.01, 0.05, 0.2]$ .

We further derive an analytical formula to estimate STTC,

$$STTC_E(r, \Delta t, \lambda_a, \lambda_b) = \frac{1}{2} \left( \frac{r}{1 + (1 - r)(1 - e^{-2\Delta t\lambda_b})} + \frac{\beta r}{1 + (1 - \beta r)(1 - e^{-2\Delta t\lambda_a})} \right)$$
(5.3)

where  $STTC_E$  denotes an estimate of the expected value of STTC,  $\lambda_a \leq \lambda_b$ , and  $\beta = \frac{\lambda_a}{\lambda_b}$ . The analytical result of 5.3 closely follows the experimental result of the sample mean of STTC, as shown in Figures 9 and 10 for Examples 5.1 and 5.2, respectively. Appendix A shows the details of how we arrive at the expression of  $STTC_E$ . When  $\Delta t \to 0$ ,  $STTC_E \to \frac{\lambda_a + \lambda_b}{2\lambda_b}r$ , which implies that the expected value of STTC tends to linearly depend on overlap ratio r.

#### **Remark:**

- 1)  $STTC_E$  is an increasing function of r, for given  $\Delta t$ ,  $\lambda_a$  and  $\lambda_b$ . It has a minimum value, denoted as  $STTC_{E,min}$ , at r = 0 and a maximum value, denoted as  $STTC_{E,max}$ , at r = 1. Substituting r = 0 and r = 1 into 5.3, respectively, we have  $STTC_{E,min} = 0$ , and  $STTC_{E,max}(\Delta t, \lambda_a, \lambda_b) = \frac{1}{2} \left[ 1 + \frac{\beta}{1 + (1 \beta)(1 e^{-2\Delta t \lambda_a})} \right]$ .
- 2)  $STTC_{E,max}$  is a function of  $\Delta_t$ ,  $\lambda_a$  and  $\lambda_b$ , and has a range of  $0.5 < STTC_{E,max} \leq 1$ . For a given  $\Delta t$ ,  $STTC_{E,max}$  increases as  $\beta$  increases.

3) For a given  $\lambda_a \leq \lambda_b$ ,  $STTC_{E,max}$  increases as  $\Delta t$  decreases. When  $\Delta t \to 0$ ,  $STTC_{E,max} \to \frac{\lambda_a + \lambda_b}{2\lambda_b}$ .

**Example 5.1.** We conduct experiments similar to ones shown in Figure 8, with parameters  $\lambda_a = \lambda_b = \lambda = 2$ , T = 100, and  $\Delta t = [0.01, 0.05, 0.2]$ . We calculate  $STTC_{E,max}$  with the same parameters and plot both experimental and analytical results side by side in Figure 9. We also plot the straight line  $L(r, \Delta t, \lambda_a, \lambda_b) = sr$ , where the slope s is equal to  $STTC_{E,max}$ , and thus a function of  $\Delta t$ ,  $\lambda_a$  and  $\lambda_b$ . In this example, since  $\beta = 1$ , s = 1, regardless of the  $\Delta_t$  value. We observe that analytical results of  $STTC_E$  closely follow experimental results of the sample mean of STTC. We also observe that the nonlinear curves of  $STTC_E$  for different  $\Delta t$  are hanging below one single straight line L(r) = r, since  $\beta = 1$ , and sharing the same endpoints at r = 0 and r = 1, corresponding to  $S_{E,min} = 0$ , and  $S_{E,max} = 1$ , respectively. As  $\Delta t$  decreases, the nonlinear curve of  $STTC_E$  tends toward to the straight line L(r) = r.



Figure 9: Relationship between the expected value of STTC and overlap ratio r for pairs of Poisson distributed spike trains when  $\lambda_a = \lambda_b$ , where  $\lambda_a = \lambda_b = \lambda = 2$ , T = 100, and  $\Delta t = [0.01, 0.05, 0.2]$ .

**Example 5.2.** We conduct a similar experiments for the case of  $\lambda_a \neq \lambda_b$ , with parameters  $\lambda_a = 2, \lambda_b = 3, T = 100$ , and  $\Delta t = [0.01, 0.05, 0.2]$ . The results are shown in Figure 10. We observe the similar trends as seen in Example 5.1. The difference is that the endpoint at  $r = 1, i.e., STTC_{E,max}$ , varies with  $\Delta t$ , since  $\beta \neq 1$ . Specifically,  $STTC_{E,max}$  is less than 1 and increases as  $\Delta t$  decreases, which makes the nonlinear curves of  $STTC_E$  tend toward to the straight lines  $L(r, \Delta t) = sr$ , depending on the values of  $\Delta t$ , with  $s = STTC_{E,max} = 0.5 + \frac{1}{4-e^{-4\Delta t}}$ . When  $\Delta t \to 0, STTC_{E,max} \to \frac{\lambda_a + \lambda_b}{2\lambda_b} = \frac{5}{6}$ , or  $s = STTC_{E,max} = 0.5 + \frac{1}{4-e^{-4\Delta t}} \to \frac{5}{6}$ .



Figure 10: Relationship between the expected value of STTC and overlap ratio r for pairs of Poisson distributed spike trains when  $\lambda_a \neq \lambda_b$ , where  $\lambda_a = 2$ ,  $\lambda_b = 3$ , T = 100, and  $\Delta t = [0.01, 0.05, 0.2]$ .

### 5.2 Measuring Closeness to Linear Relation

We have observed that given the rates of pairs of Poisson distributed spike trains,  $\lambda_a \leq \lambda_b$ , when synchronicity window  $\Delta t$  decreases, the nonlinear relationship between  $STTC_E(r)$ and overlap ratio r tends toward a linear relationship with a form of  $L(r, \Delta t, \lambda_a, \lambda_b) = sr$ , where  $s = STTC_{E,max} = \frac{1}{2} \left[ 1 + \frac{\beta}{1+(1-\beta)(1-e^{-2\Delta t\lambda_a})} \right]$  with  $0 < \beta \leq 1$ . We are interested in quantitatively evaluating the closeness between the nonlinear curve  $STTC_E(r)$  and the straight line L(r), for a given  $\Delta t$ ,  $\lambda_a$  and  $\lambda_b$ . We use a relative area between  $STTC_E(r)$ and L(r) as a measure of closeness. Note the area between  $STTC_E(r)$  and L(r) is equal to the area of the triangle, defined by (0, 0),  $(1, STTC_{E,max})$  and (1, 0), subtracted by the area underneath the curve  $STTC_E(r)$  with  $STTC_E(r) \geq 0$ . Since the area of the triangle is  $\frac{s}{2}$ , the area between  $STTC_E(r)$  and L(r) is  $A = \frac{1}{2}s - \int_0^1 STTC_E(r) dr$ . We define the measure for closeness as a relative area  $A_{\varepsilon} = \frac{A}{s/2}$ . That is,

$$A_{\varepsilon} = 1 - \frac{2}{s} \int_0^1 STTC_E(r) \, dr$$

Using standard integration techniques, we can find that

$$A_{\varepsilon} = 1 - 2 \left[ \frac{\left(\frac{1}{b} + \frac{a \ln|a|}{b^2}\right) + \beta \left(\frac{1}{d} - \frac{c(\ln|c+d| - \ln|c|)}{d^2}\right)}{1 + \frac{\beta}{c+d}} \right]$$

where  $a = 2 - e^{-2\Delta t\lambda_b}$ ,  $b = e^{-2\Delta t\lambda_b} - 1$ ,  $c = 2 - e^{-2\Delta t\lambda_a}$  and  $d = -\beta(1 - e^{-2\Delta t\lambda_a})$ . Appendix C shows the detailed calculation. We say that the smaller the area is, the closer the nonlinear

curve  $STTC_E(r)$  and the straight line L(r) are, and the better the linearity of the relationship between the expected value STTC and overlap ratio r for pairs of Poisson distributed spike trains.

We plot the relationship between  $A_{\varepsilon}$  and  $\Delta t$  for a given  $\lambda_a \leq \lambda_b$  in Figure 11, where the combinations of  $\lambda_a$  and  $\lambda_b$  include  $(\lambda_a, \lambda_b) = \{(2, 2), (4, 4), (8, 8), (2, 3), (2, 5), (2, 7)\}$ . We can see that when  $\Delta t$  decreases,  $A_{\varepsilon}$  decreases, implying that the nonlinear relationship between the expected value of STTC and overlap ratio for pairs of Poisson distributed spike trains is closer to a linear relationship.

As an application of this quantitative evaluation of linearity, for any given curve of  $A_{\varepsilon}$ with rates  $\lambda_a$  and  $\lambda_b$ , as shown in Figure 11, we may set a threshold of  $A_{\varepsilon}$ , for example  $A_{\varepsilon} = 0.05$ , for which a threshold of  $\Delta t$ , denoted as  $\Delta t_{TH}$ , can be determined. When we choose any value  $\Delta t \leq \Delta t_{TH}$  to calculate the expected value of STTC for pairs of Poisson distributed spike trains with overlap ratio r, we may use the linear relationship  $L(r) = \frac{\lambda_a + \lambda_b}{2\lambda_b}r$  to quickly obtain an estimation of the expected value of STTC for given rates  $\lambda_a$  and  $\lambda_b$ .



Figure 11: Measure of linearity of the relationship between the expected value of STTC and overlap ratio r for pairs of Poisson distributed spike trains. The smaller the synchronicity window  $\Delta t$  is, the smaller the value of  $A_{\varepsilon}$  is, and the better the linearity.

## 6 Size of Synchronicity Window

The synchronicity window  $\Delta t$  is a key parameter for calculating STTC. Through studying STTC, we have the following general observations about the relation of  $\Delta t$  and STTC values.

- 1) When  $\Delta t$  is small enough to where signal spikes in A and B do not overlap,  $P_A = P_B = 0$ , therefore,  $STTC = -\frac{1}{2}(T_A + T_B)$ .
- 2) When  $\Delta t$  is large enough to where all signal spikes in A and B overlap,  $P_A = P_B = 1$ , therefore, STTC = 1.
- 3) When  $\Delta t$  is too large where  $T_A = T_B = P_A = P_B = 1$ , the problem of dividing by zero occurs.
- 4) To avoid dividing by zero in calculating STTC, neither  $T_A$  nor  $T_B$  can equal 1.

Based on Observation 4, we can derive an upper bound for  $\Delta t$  to avoid dividing by zero in the calculation of STTC. Theorem 6.1 defines such an upper bound.

**Theorem 6.1.** Assuming that signals A and B have a time limit T and contain spikes at locations  $a_i$  for  $i = 1, 2, \dots, N$  and  $b_j$  for  $j = 1, 2, \dots, M$ , respectively, to avoid dividing by zero in calculating STTC, the upper bound for the synchronicity window  $\Delta t$  is the minimum value between  $\Delta t_a$  and  $\Delta t_b$ , that is,

$$\Delta t < \min\left\{\Delta t_a, \Delta t_b\right\}$$

where

$$\Delta t_a = \max \left\{ d_a, a_1, (T - a_N) \right\}$$
$$\Delta t_b = \max \left\{ d_b, b_1, (T - b_M) \right\}$$

where

$$d_a = \max_i \left\{ \frac{1}{2} (a_{i+1} - a_i) \right\}, \ i = 1, 2, \cdots, N - 1$$
$$d_b = \max_j \left\{ \frac{1}{2} (b_{j+1} - b_j) \right\}, \ j = 1, 2, \cdots, M - 1$$

*Proof.* The definition of STTC is

$$STTC = \frac{1}{2} \left( \frac{P_A - T_B}{1 - P_A T_B} + \frac{P_B - T_A}{1 - P_B T_A} \right)$$

To avoid dividing by zero in calculating STTC, it requires  $P_B T_A \neq 1$  and  $P_A T_B \neq 1$ . By definition,  $0 \leq T_A \leq 1$ ,  $0 \leq T_B \leq 1$ ,  $0 \leq P_A \leq 1$ , and  $0 \leq P_B \leq 1$ . Therefore,

- $P_BT_A = 1$  if and only if  $T_A = P_B = 1$
- $P_A T_B = 1$  if and only if  $T_B = P_A = 1$

Also by definition,

- if  $T_A = 1, P_B = 1$
- if  $T_B = 1, P_A = 1$

Therefore, the requirement of  $P_B T_A \neq 1$  and  $P_A T_B \neq 1$  is equivalent to the requirement of  $T_A \neq 1$  and  $T_B \neq 1$ .

According to the definition of the synchronicity window  $\Delta t$ ,

- $T_A \neq 1$  if and only if  $\Delta t < \Delta t_a$
- $T_B \neq 1$  if and only if  $\Delta t < \Delta t_b$

Therefore, the upper bound for  $\Delta t$  is the minimum value between  $\Delta t_a$  and  $\Delta t_b$ , that is,

$$\Delta t < \min\left\{\Delta t_a, \Delta t_b\right\}$$

As another observation about the STTC value, we realize that when defining an STTC value [4], the authors state that "we require the coefficient to be equal to +1 for autocorrelation, to be -1 when  $P_A = 0$ ,  $T_B = 1$  and to have a range of [-1, 1]", but it can be argued that the value of STTC can never equal -1, because if  $T_B = 1$ ,  $P_A \neq 0$ , and if  $P_A = 0$ ,  $T_B \neq 1$  (assume that spike trains A and B contain at least one spike, respectively). It can be further argued that STTC can only approach -1. We demonstrate in Figure 12 that this argument holds true for the following case where spike train A is a periodic signal with a period of  $T_P$ , spike train B is a shift of spike train A by a half of period of  $T_P$ , and  $\Delta t$  is less than  $T_P/2$  but approaching  $T_P/2$ . In this case,  $T_A \to 1$ ,  $T_B \to 1$ ,  $P_A = 0$  and  $P_B = 0$ , and therefore,  $STTC \to -1$ .



Figure 12: Demonstration of STTC approaching -1

# 7 Conclusions

We studied one of the popular measures in the field of neuroscience, Spike Time Tiling Coefficient (STTC), for quantifying the synchrony of spike trains. Through numerical simulations and analytical study, we derived several interesting properties of the STTC measure that provides a better understanding of the information encoded by the measure. It is expected that increasing the proportion of synchronous spikes increases the STTC value. However, the exact relation between STTC and the proportion is not transparent. In this work, we characterized this relation: when pairs of spike trains are generated from Poisson processes and synchronicity window is very small, STTC measures the proportion of synchrony. That means, in this setting, STTC is generally non-negative. It was shown in [4] that STTC could also measure the anti-phase relation, which is what negative values imply. We explored a little further this aspect and showed how STTC could measure phase-shifts of periodic bursts. Interestingly, what we observed in a simple burst model was also observed in periodic-centered bursts with random spikes: STTC decreases as phase-shift increases from 0 to half of the period, and has a minimum value at half of the period. In [4], the range of STTC was designed to be any value between -1 and 1. However, we showed that the value of -1 could never be reached. We also addressed the effect of the synchronicity window on the STTC measure. In general applications, the synchronicity window is selected to be relatively small. As the synchronicity window becomes too large, the problem of dividing by zero occurs in the calculation of STTC. We derived an upper bound for the synchronicity window to avoid such a problem.

This study was not intended to be a systematic study of the STTC measure, but to provide some insights on how to interpret the values of STTC. For this reason, we did not study more complex bursting models. In this study, we presented an analytical expression to describe the relation between the ratio of synchronous spikes and an estimate of the expected value of STTC for pairs of Poisson distributed spike trains. While the analytical result of the estimation of the expected value of STTC closely follows the numerical result of the sample mean of STTC, we have yet to find a rigorous expression for the expected value of STTC. These could be interesting aspects to investigate in the future.

## 8 Acknowledgment

We are sincerely grateful to Dr. Yunjiao Wang, Department of Mathematical Sciences, Texas Southern University, for initiating this scientific research project. We could not have completed this project without Dr. Wang's guidance and advice. We have learned a lot from insightful discussions with Dr. Wang. We also thank Dr. Maria Leite for initial discussions and suggestions for writing, Dr. Alona Ben-Tal for discussion regarding binary representation of spike trains, and Dr. Rafael J. Villanueva for very helpful feedback.

# References

- [1] A. Ben-Tall, Y. Wang, and M. C. Leite. The logic behind neural control of breathing pattern. *Scientific Reports*, 9, 2019.
- [2] Manuel Ciba, Robert Bestel, Christoph Nick, Guilherme Ferraz de Arruda, Thomas Peron, Comin César Henrique, Luciano da Fontoura Costa, Francisco Aparecido Rodrigues, and Christiane Thielemann. Comparison of Different Spike Train Synchrony Measures Regarding Their Robustness to Erroneous Data From Bicuculline-Induced Epileptiform Activity. *Neural Computation*, 32(5):887–911, 05 2020.
- [3] Manuel Ciba, Takuya Isomura, Yasuhiko Jimbo, Andreas Bahmer, and Christiane Thielemann. Spike-contrast: A novel time scale independent and multivariate measure of spike train synchrony. *Journal of Neuroscience Methods*, 293:136–143, 2018.
- [4] C. S. Cutts and S. J. Eglen. Detecting Pairwise Correlations in Spike Trains: An Objective Comparison of Methods and Application to the Study of Retinal Waves. *Journal of Neuroscience*, 34(43):14288–14303, October 2014.
- [5] Andreas K. Engel, Pascal Fries, and Wolf Singer. Dynamic predictions: Oscillations and synchrony in top-down processing. *Nature Reviews Neuroscience*, pages 704 – 716, 2001.
- [6] Thomas Kreuz, Julie S. Haas, Alice Morelli, Henry D.I. Abarbanel, and Antonio Politi. Measuring spike train sychrony. *Journal of Neuroscience Methods*, 165:151–161, 2007.
- [7] Robert Rosenbaum, Tatjana Tchumatchenko, and Rubén Moreno-Bote. Correlated neuronal activity and its relationship to coding, dynamics and network architecture. Frontiers in Computational Neuroscience, 8, 2014.
- [8] J. Shao, Y. Liu, D. Gao, J. Tu, and F. Yang. Neural burst firing and its roles in mental and neurological disorders. *Front Cell Neurosci.*, 15, 2021.
- [9] L. M. Ward. Synchronous neural oscillations and cognitive processes. rends Cogn Sci., pages 553–9, 2003.

## **A Derivation of** (5.3)

We derive (5.3) using the following steps:

- 1) Estimate  $\mathbb{E}[P_A]$  and  $\mathbb{E}[P_B]$
- 2) Compute  $\mathbb{E}[T_B]$  and  $\mathbb{E}[T_A]$
- 3) Estimate  $\mathbb{E}[STTC]$  by  $\frac{1}{2}\left(\frac{\mathbb{E}[P_A] \mathbb{E}[T_B]}{1 \mathbb{E}[P_A] \mathbb{E}[T_B]} + \frac{\mathbb{E}[P_B] \mathbb{E}[T_A]}{1 \mathbb{E}[P_B] \mathbb{E}[T_A]}\right)$

Estimate  $\mathbb{E}[P_A]$  and  $\mathbb{E}[P_B]$  Let the rates of a pair of overlapped Poisson distributed spike trains, A and B, be  $\lambda_a$  and  $\lambda_b$ , and without loss of generality, let  $\lambda_a \leq \lambda_b$ , then the rate of the synchronous spike train, S, is  $\lambda_s = r\lambda_a$ , with  $0 \leq r \leq 1$  being the overlap ratio, and the rates of independent spike trains,  $I_A$  and  $I_B$ , are  $\lambda_a - \lambda_s$  and  $\lambda_b - \lambda_s$ , respectively. Let  $N_S$ be the number of spikes in Train S,  $N_a$  be the number of spikes in Train  $I_A$  and  $N_{AB}$  be the number of spikes in  $I_A$  within  $\pm \Delta t$  range of the spikes of  $I_B$  or S, then the total number of spikes in Train A is  $N_A = N_S + N_a$ . By definition of  $P_A$ , we have

$$P_A = \frac{N_S + N_{AB}}{N_A}$$

It follows that

$$\mathbb{E}(P_A) = \mathbb{E}\left[\frac{N_S + N_{AB}}{N_S + N_a}\right] = \mathbb{E}\left[\frac{N_S}{N_A}\right] + \mathbb{E}\left[\frac{N_{AB}}{N_A}\right]$$

Since  $I_A$  is independent of  $I_B$  and S, we estimate  $\mathbb{E}\left[\frac{N_{AB}}{N_A}\right]$  by  $(1-r)\mathbb{E}[T_B]$  (we add a factor (1-r) for we exclude the synchronous portion). To get a rough estimation, we use  $\frac{\mathbb{E}[N_S]}{\mathbb{E}[N_A]} = \frac{\lambda_s}{\lambda_a} = r$  as an estimate of  $\mathbb{E}\left[\frac{N_S}{N_A}\right]$ . As a result, we have an estimate of  $\mathbb{E}[P_A]$ , denoted as  $P_{A,E}$ ,

$$P_{A,E} = r + (1-r) \mathbb{E}[T_B]$$

Similarly, we have an estimate of  $\mathbb{E}[P_B]$ , denoted as  $P_{B,E}$ ,

$$P_{B,E} = r + (1 - r\beta) \mathbb{E}[T_A]$$

where  $\beta = \frac{\lambda_a}{\lambda_b}$ .

**Compute**  $\mathbb{E}[T_B]$  and  $\mathbb{E}[T_A]$  For a Poisson distributed spike train with rate  $\lambda$ , the distance between two neighboring spikes, x, follows an exponential distribution  $\lambda e^{-\lambda x}$  for  $x \geq 0$ . Therefore, based on the definition of  $T_B$ , an expected value of  $T_B$  is

$$\mathbb{E}[T_B] = 2\Delta t \lambda_b - \lambda_b \int_0^{2\Delta t} \left[ (2\Delta t - x)(\lambda_b e^{-\lambda_b x}) \right] dx$$

where  $\Delta t$  is the size of the synchronicity window. The first term on the right-hand side of the formula is the total time covered by the synchronicity window given rate  $\lambda_b$ , and the second

term is the overlapping time when the synchronicity window overlaps two spikes. Since the definition of calculating  $T_B$  states that the overlapping area counts only once, the second term is subtracted from the first term. Using the integral formula for exponential functions

$$\int e^{ax} dx = \frac{1}{a} e^{ax}$$
$$\int x e^{ax} dx = \frac{ax - 1}{a^2} e^{ax}$$

we have

$$\mathbb{E}[T_B] = 2\Delta t\lambda_b - \lambda_b \int_0^{2\Delta t} (2\Delta t\lambda_b e^{-\lambda_b x}) \, dx + \lambda_b \int_0^{2\Delta t} (\lambda_b x e^{-\lambda_b x}) \, dx$$
$$= 2\Delta t\lambda_b + 2\Delta t\lambda_b (e^{-2\Delta t\lambda_b} - 1) - \lambda_b \left[ 2\Delta t e^{-2\Delta t\lambda_b} + \frac{1}{\lambda_b} (e^{-2\Delta t\lambda_b} - 1) \right]$$
$$= 1 - e^{-2\Delta t\lambda_b}$$

Similarly, we have

$$\mathbb{E}[T_A] = 1 - e^{-2\Delta t \lambda_c}$$

**Estimate**  $\mathbb{E}[STTC]$  Using  $\mathbb{E}[T_B]$ ,  $\mathbb{E}[T_A]$ ,  $P_{A,E}$  and  $P_{B,E}$  for  $T_B$ ,  $T_A$ ,  $P_A$  and  $P_B$ , respectively, in the definition of STTC, an estimate of expected value of STTC, denoted as  $STTC_E(r, \Delta t, \lambda_a, \lambda_b)$ , is

$$STTC_{E}(r, \Delta t, \lambda_{a}, \lambda_{b}) = \frac{1}{2} \left( \frac{\left[ r + (1-r) \mathbb{E}[T_{B}] \right] - \mathbb{E}[T_{B}]}{1 - \left[ r + (1-r) \mathbb{E}[T_{B}] \right] \mathbb{E}[T_{B}]} + \frac{\left[ r\beta + (1-r\beta) \mathbb{E}[T_{A}] \right] - \mathbb{E}[T_{A}]}{1 - \left[ r\beta + (1-r\beta) \mathbb{E}[T_{A}] \right] \mathbb{E}[T_{A}]} \right)$$

$$= \frac{1}{2} \left( \frac{r(1 - \mathbb{E}[T_{B}])}{\left( 1 + \mathbb{E}[T_{B}] - r \mathbb{E}[T_{B}] \right) \left( 1 - \mathbb{E}[T_{B}] \right)} + \frac{r\beta \left( 1 - \mathbb{E}[T_{A}] \right)}{\left( 1 + \mathbb{E}[T_{A}] - r\beta \mathbb{E}[T_{A}] \right) \left( 1 - \mathbb{E}[T_{A}] \right)} \right)$$

$$= \frac{1}{2} \left( \frac{r}{1 + (1-r) \mathbb{E}[T_{B}]} + \frac{\beta r}{1 + (1-\beta r) \mathbb{E}[T_{A}]} \right)$$

$$= \frac{1}{2} \left( \frac{r}{1 + (1-r)(1 - e^{-2\Delta t\lambda_{b}})} + \frac{\beta r}{1 + (1-\beta r)(1 - e^{-2\Delta t\lambda_{a}})} \right)$$

When  $\lambda_a = \lambda_b$ ,  $\beta = 1$ , and  $\mathbb{E}[T_A] = \mathbb{E}[T_B]$ , and thus

$$STTC_E(r, \Delta t, \lambda_a, \lambda_b) = \frac{r}{1 + (1 - r)(1 - e^{-2\Delta t\lambda_a})}$$

Note that in general  $\mathbb{E}[\frac{A}{B}] \neq \frac{\mathbb{E}[A]}{\mathbb{E}[B]}$  or  $\mathbb{E}[AB] \neq \mathbb{E}[A] \mathbb{E}[B]$ . In this sense,  $STTC_E$  is an estimate of the expected value of STTC, and  $P_{A,E}$  and  $P_{B,E}$  are estimates of the expected values of  $P_A$  and  $P_B$ , respectively. However, in our case the analytical result  $STTC_E(r, \Delta t, \lambda_a, \lambda_b)$ 

closely follows the numerical result of the sample mean of STTC. We think it is a very interesting observation though we have yet to find a rigorous expression for the expected value of STTC.

#### **Remark:**

- 1)  $P_{A,E}$  and  $P_{B,E}$  are dependent on overlap ratio r. For a given  $\mathbb{E}[T_B]$  and  $\mathbb{E}[T_A]$ , the dependence is linear, that is,  $P_{A,E} = r + (1-r) \mathbb{E}[T_B]$  and  $P_{B,E} = r\beta + (1-r\beta) \mathbb{E}[T_A]$ .
- 2) The relationship between STTC and overlap ratio r is reflected in  $P_{A,E}$  and  $P_{B,E}$ , but not in  $\mathbb{E}[T_A]$  or  $\mathbb{E}[T_B]$  since they are independent of r. This is consistent with the definition of these variables, that is,  $P_A$  and  $P_B$  reflect the relations between the paired signals, and  $T_A$  and  $T_B$  contain information about the signals themselves.

## **B** More Numerical Examples

**Example B.1.** We conduct an experiment with a fixed  $\lambda_a$  and  $\Delta t$ , but a varying  $\beta = \frac{\lambda_a}{\lambda_b}$ . Specifically, we use parameters  $\Delta t = 0.1$ ,  $\lambda_a = 2$  and  $\lambda_b = [3, 5, 7]$ , which indicates  $\beta = [0.67, 0.4, 0.29]$ . The results are shown in Figure 13. We observe that as  $\beta$  decreases,  $STTC_{E,max}$  decreases, where  $STTC_{E,max} = \frac{1}{2} \left[ 1 + \frac{\beta}{1 + (1-\beta)\mathbb{E}[T_A]} \right] = 0.5 + \frac{\beta}{2 + 0.66(1-\beta)}$ . Also, we observe that analytical results  $STTC_E$  closely follow experimental results of expected values of STTC.



Figure 13: Relationship between the expected value of STTC and overlap ratio r for pairs of Poisson distributed spike trains with fixed  $\lambda_a$  and  $\Delta t$ , but varying  $\beta = \frac{\lambda_a}{\lambda_b}$ , where  $\lambda_a = 2$ ,  $\lambda_b = [3, 5, 7], T = 100$ , and  $\Delta = 0.1$ .

**Example B.2.** We conduct an experiment with a fixed  $\beta = \frac{\lambda_a}{\lambda_b} = 1$ , and a fixed product  $\lambda \Delta t = 0.2$ , where  $\Delta t = [0.01, 0.05, 0.1]$  and  $\lambda = [20, 4, 2]$ . The results are shown in Figure 14. As expected, the nonlinear curves of  $STTC_E$  for the three different cases are the same since  $\beta$  and  $\lambda \Delta t$  are the same. Again, we observe that analytical results  $STTC_E$  closely follow experimental results of expected values of STTC.



Figure 14: Relationship between the expected value of STTC and overlap ratio r for pairs of Poisson distributed spike trains with fixed  $\beta = \frac{\lambda_a}{\lambda_b} = 1$  and product  $\lambda \Delta t = 0.2$ , where  $T = 100, \lambda = [20, 4, 2]$  and  $\Delta t = [0.01, 0.05, 0.1]$ , respectively.

**Example B.3.** In calculating STTC, we need first determine the values of  $T_A$ ,  $T_B$ ,  $P_A$ ,  $P_B$ . To get an explicit impression of relationships between them, we present both experimental and analytical results of the expected values of STTC,  $T_A$ ,  $T_B$ ,  $P_A$ , and  $P_B$  side by side in Figures 15 and 16 for cases of  $\lambda_a = \lambda_b$  and  $\lambda_a \neq \lambda_b$ , respectively. Parameters used are  $\Delta t = 0.1$ , T = 100. In Figure 15, with  $\lambda_a = \lambda_b = \lambda = 2$ , we observe that  $\mathbb{E}[T_A] = \mathbb{E}[T_B] =$ 0.33 and  $P_{A,E} = P_{B,E} = 0.67r + 0.33$ . At r = 0,  $P_{A,E} = P_{B,E} = 0.33$  and  $STTC_E = 0$ ; at r = 1,  $P_{A,E} = P_{B,E} = 0.1$  and  $STTC_E = 1$ . In Figure 16, with  $\lambda_a = 2$  and  $\lambda_b = 3$ , we observe that  $\mathbb{E}[T_A] = 0.33$ ,  $\mathbb{E}[T_B] = 0.45$ ,  $P_{B,E} = 0.45r + 0.33$  and  $P_{A,E} = 0.55r + 0.45$ . At r = 0,  $P_{A,E} = \mathbb{E}[T_B] = 0.45$ ,  $P_{B,E} = \mathbb{E}[T_A] = 0.33$  and  $STTC_E = 0$ ; at r = 1,  $P_{A,E} = 1$ ,  $P_{B,E} = 0.78$  and  $STTC_E = 0.8$ . In both Figure 15 and Figure 16, we observe that analytical results  $STTC_E$ ,  $\mathbb{E}[T_B]$ ,  $\mathbb{E}[T_A]$ ,  $P_{A,E}$  and  $P_{B,E}$  closely follow experimental results of expected values of STTC,  $T_B$ ,  $T_A$ ,  $P_A$  and  $P_B$ .



Figure 15: Relationship between the expected value of STTC,  $T_A$ ,  $T_B$ ,  $P_A$ ,  $P_B$  and overlap ratio r for pairs of Poisson distributed spike trains when  $\lambda_a = \lambda_b$ , where  $\lambda_a = \lambda_b = \lambda = 2$ , T = 100, and  $\Delta t = 0.1$ .



Figure 16: Relationship between the expected value of STTC,  $T_A$ ,  $T_B$ ,  $P_A$ ,  $P_B$  and overlap ratio r for pairs of Poisson distributed spike trains when  $\lambda_a \neq \lambda_b$ , where  $\lambda_a = 2$ ,  $\lambda_b = 3$ , T = 100, and  $\Delta t = 0.1$ .

# **C** Calculation of $A_{\varepsilon}$

Given the nonlinear curve,

$$STTC_E(r, \Delta t, \lambda_a, \lambda_b) = \frac{1}{2} \left( \frac{r}{1 + (1 - r) \mathbb{E}[T_B]} + \frac{\beta r}{1 + (1 - \beta r) \mathbb{E}[T_A]} \right)$$

and the straight line

$$L(r,\Delta t,\lambda_a,\lambda_b) = sr$$

the area between  $STTC_E(r)$  and L(r) for a given  $\Delta t$ ,  $\lambda_a$  and  $\lambda_b$  is,

$$A = \frac{1}{2}s - \int_0^1 STTC_E(r) \, dr$$

where

$$s = STTC_E(r=1) = \frac{1}{2} \left[ 1 + \frac{\beta}{1 + (1-\beta)\mathbb{E}[T_A]} \right]$$

The closeness between  $STTC_E(r)$  and L(r) is measured by a relative area,  $A_{\varepsilon}$ , which defined as a ratio of A over  $\frac{1}{2}s$ , that is,

$$A_{\varepsilon} = 1 - \frac{2}{s} \int_0^1 STTC_E(r) \, dr$$

The smaller  $A_{\varepsilon}$  is, the closer  $STTC_E(r)$  and L(r) are, and the closer to a linear relation between the expected value of STTC and r.

When  $\lambda_a = \lambda_b$ ,  $\beta = 1$ , and thus s = 1 and

$$\int_0^1 STTC_E(r) \, dr = \int_0^1 \frac{r}{1 + \mathbb{E}[T_B] - r \,\mathbb{E}[T_B]} \, dr$$

Letting  $a = 1 + \mathbb{E}[T_B]$  and  $b = -\mathbb{E}[T_B]$ , we have

$$\int_0^1 STTC_E(r) \, dr = \int_0^1 \frac{r}{a+br} \, dr$$

Using the integral formula

$$\int \frac{x}{u+vx} dx = \frac{1}{v} \int \left(1 - \frac{u}{u+vx}\right) dx$$
$$= \frac{1}{v} \int 1 dx - \frac{u}{v^2} \int \left(\frac{1}{u+vx}\right) d(u+vx)$$
$$= \frac{1}{v}x - \frac{u}{v^2} \ln|u+vx|$$

we have

$$\int_0^1 STTC_E(r) dr = \int_0^1 \frac{r}{a+br} dr$$
  
=  $\frac{1}{b} - \frac{a}{b^2} (\ln|a+b| - \ln|a|) = \frac{1}{b} + \frac{a\ln|a|}{b^2}$ 

Therefore,

$$A_{\varepsilon} = 1 - \frac{2}{s} \int_0^1 STTC_E(r) dr$$
$$= 1 - 2\left(\frac{1}{b} + \frac{a\ln|a|}{b^2}\right)$$

When  $\lambda_a \neq \lambda_b$ ,

$$s = \frac{1}{2} \left[ 1 + \frac{\beta}{1 + (1 - \beta) \mathbb{E}[T_A]} \right]$$

and

$$\int_0^1 STTC_E(r) \, dr = \frac{1}{2} \int_0^1 \left( \frac{r}{1 + \mathbb{E}[T_B] - r \,\mathbb{E}[T_B]} + \frac{\beta r}{1 + \mathbb{E}[T_A] - r\beta \,\mathbb{E}[T_A]} \right) \, dr$$

Letting  $c = 1 + \mathbb{E}[T_A]$  and  $d = -\beta \mathbb{E}[T_A]$ , we have

$$s = \frac{1}{2} \left( 1 + \frac{\beta}{c+d} \right)$$

and

$$\int_0^1 STTC_E(r) \, dr = \frac{1}{2} \int_0^1 \left( \frac{r}{a+br} + \frac{\beta r}{c+dr} \right) \, dr$$

Using the same integral formula, we have

$$\int_{0}^{1} STTC_{E}(r) \, dr = \frac{1}{2} \left[ \left( \frac{1}{b} + \frac{a \ln |a|}{b^{2}} \right) + \beta \left( \frac{1}{d} - \frac{c(\ln |c + d| - \ln |c|)}{d^{2}} \right) \right]$$

Therefore,

$$A_{\varepsilon} = 1 - \frac{2}{s} \int_{0}^{1} STTC_{E}(r) \, dr = 1 - 2 \left[ \frac{\left(\frac{1}{b} + \frac{a \ln |a|}{b^{2}}\right) + \beta \left(\frac{1}{d} - \frac{c(\ln |c+d| - \ln |c|)}{d^{2}}\right)}{1 + \frac{\beta}{c+d}} \right]$$