



A new measure for bursting

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Abstract

We present a new measure, called B_2 , to quantify the degree of bursting in spike trains. The measure is based on a simple argument about the variance of interspike intervals and is related to the first serial correlation coefficient ρ_1 . We have used the measure in a preliminary study about the influence of dendritic morphology on bursting in spike trains.

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1. Burst measure

Although in most cases there will be an agreement on the existence of bursting in spike trains when subjected to visual inspection, the concept of bursting lacks a mathematical definition [1]. In our approach, we consider bursting as the correlated occurrence of two or more spikes in quick succession followed by a long interval. An accidental short-interspike interval would not be considered as bursting. Our approach is statistical in nature, and it is not possible to identify individual bursts; only whole spike trains can be analysed for bursting. This is different from approaches that try to classify individual spikes as intraburst or extraburst, such as, for example, the threshold construction in [1].

Apart from independence of subsequent interspike intervals (ISIs), we make no additional assumptions, such as an underlying Poisson [5] process, about the ISI distributions of the non-bursting situation. We consider bursting to be stronger if the ratio of short to long intervals is smaller. Existing higher order characteristics do not reflect this property. They are either fully sensitive to the average ISI, like the autocorrela-

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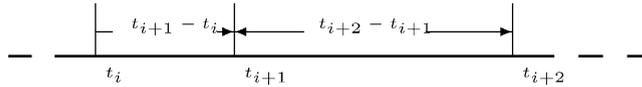


Fig. 1. Interspike intervals.

tion function [4], or not sensitive to the ratio of short to long intervals, like the serial correlation coefficient [2,3].

The burst measure we propose can be understood on the basis of a simple notion. If a spike train consists of single spikes and there is no correlation between the intervals, we expect that the variance of the sums $\tau_i + \tau_{i+1}$ of two subsequent interspike intervals is twice the variance of single intervals τ_i . However, if there is bursting there will be a correlation between two subsequent intervals and this relation is violated. The difference between the actual variance and the expected variance of independent intervals is a measure for the deviation from the situation with independent intervals, and is thus a measure for bursting. This deviation still includes information on the size of the intervals; i.e., a low-frequency spike train that in all properties except frequency is comparable to a high-frequency spike train would show stronger bursting with this measure. If we divide the difference by the squared average ISI, we obtain a normalized burst measure that is only sensitive to the relative size of the intervals and not to the average spike frequency:

$$B_2 = \frac{2\text{Var}(t_{i+1} - t_i) - \text{Var}(t_{i+2} - t_i)}{2E^2(t_{i+1} - t_i)}, \quad (1)$$

where the order has been chosen such that the burst measure will show a positive deviation from zero in case of bursting and t_i is the i th spike in the spike train (see Fig. 1). If we assume that the statistics of the spike train do not vary over time, i.e., the spike train is trend free, we can show that Eq. (1) is equal to

$$B_2 = \frac{E^2(t_{i+1} - t_i) - E((t_{i+2} - t_{i+1})(t_{i+1} - t_i))}{E^2(t_{i+1} - t_i)}. \quad (2)$$

For a trend free spike train, this burst measure differs from the first serial correlation [2,3] coefficient $\rho_1 = E((t_{i+2} - t_{i+1} - \mu)(t_{i+1} - t_i - \mu))/\sigma^2(t_{i+1} - t_i)$ only in its sign and normalization. The serial correlation coefficient uses the variance of the ISI to eliminate the dependence on average ISI size, whereas we use the squared average. As a consequence, the serial correlation coefficient is not sensitive to the relative size of the different ISIs, whereas our burst measure is sensitive to this. This difference in behaviour is most pronounced in the case of periodic bursting. In that case, B_2 reflects the ratio of the different ISIs, while the serial correlation coefficient is always -1 . This is clearly visible in the spike trains obtained from model neurons stimulated by a constant current injection at the soma (see the left panel in Fig. 2), which leads to periodic spike patterns. The right panel of Fig. 2 shows a similar plot for spike trains obtained with random synaptic stimulation of the dendritic tree.

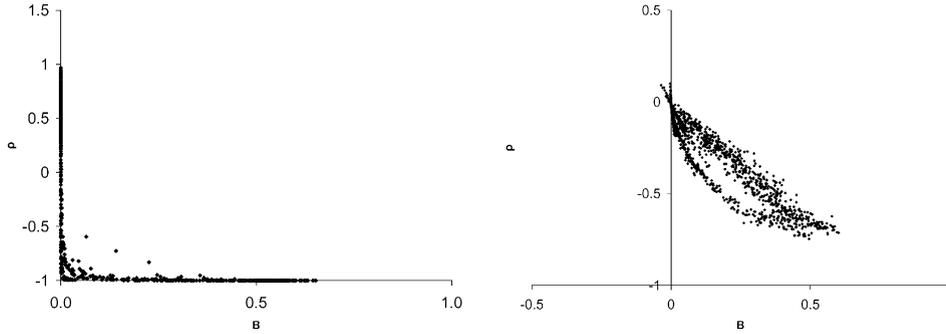


Fig. 2. First serial correlation coefficient ρ_1 versus our burst measure B_2 , for spike trains obtained from model neurons stimulated by a constant current injection at the soma (left) and by Poissonian synaptic stimulation of the dendritic tree (right). See also Section 3.

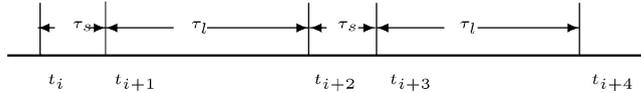


Fig. 3. Spike train showing periodic bursting.

If we apply B_2 to a periodic train of two-spike bursts (see Fig. 3), we obtain the following value for B_2 :

$$B_2 = \left(\frac{\mu_{\tau_L} / \mu_{\tau_s} - 1}{1 + \mu_{\tau_L} / \mu_{\tau_s}} \right)^2, \tag{3}$$

where μ_{τ_L} and μ_{τ_s} are the average long and short intervals, respectively. This result shows a few important properties of our burst measure: it generally takes on values between 0 and 1; if the “short” interval has the same length as the “long” interval, we indeed detect no bursting; and from the burst measure we can reconstruct the ratio of the ISIs associated with different stochasts.

2. Markov chain analysis of B_2

If we consider the interspike and intrabursts intervals as realizations of stochastic variables $\tau_{\alpha_{i+1}, \alpha_i}$ whose realization is selected by a Markov process, it is possible to express B_2 in the parameters of this process. Let us denote a spike train by spike times t_i , with $t_{i+1} > t_i$, and assume that an interspike interval $t_{i+1} - t_i$ is a realization of one of the stochasts $\tau_{\alpha_{i+1}, \alpha_i}$, where α_i denotes the nature or state of the spike, i.e., single isolated spike, or first, second spike in a doublet, or first, second, third spike in a triplet, etc. The whole set of states will be denoted by S . The transition between these states is assumed to be probabilistic and given by the transition probabilities $p_{\alpha_{i+1}, \alpha_i}$. If only two states are involved and the stochasts $\tau_{\alpha_{i+1}, \alpha_i}$ are independent of either α_{i+1} or α_i , the final model reduces to the semi-alternating renewal model [2,3].



Fig. 4. Transition from a train of single spikes to bursting; $B_2 = 0.055$, $\rho_1 = -0.95$.

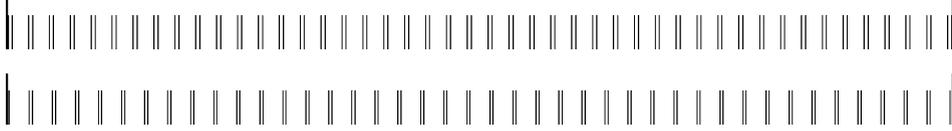


Fig. 5. Periodic trains of bursts. Top: $B_2 = 0.38$, $\rho_1 = -1.0$. Bottom: $B_2 = 0.53$, $\rho_1 = -1.0$.

By the definition of a Markov process, the probability $\pi_{\alpha,i}$ that spike i has state α is related to the probabilities of the preceding spike, spike $i-1$, by $\pi_{\alpha,i} = \sum_{\beta} P_{\alpha,\beta} \pi_{\beta,i-1}$. For our purposes, we assume that the spike train represents the asymptotic state π of the Markov process; i.e., for all states α , the probability is stable: $\pi_{\alpha,i+1} = \pi_{\alpha,i}$. This assumption can be fulfilled if the stimulation regime is stochastic and if the spike train is recorded from a region that is not dominated by onset phenomena. As a consequence, Markov models cannot be applied to a spike train such as in Fig. 4, because the spike train is still dominated by the onset. Markov models with transition probabilities exclusively equal to 1 or 0 apply to situations where the stimulus is not stochastic and no internal sources of noise are present. The first two scenarios that we present below are of this type; the third scenario is truly non-deterministic.

2.1. Scenario I, single spike only

If no bursting takes place, we assume that there is only the singlet state with the corresponding stochastic, the singlet interspike interval

$$S = \{s\}, \quad p_{s,s} = 1, \quad \mu_{\tau_{s,s}} = \tau. \quad (4)$$

For this scenario, the burst measure $B_2 = 0$.

2.2. Scenario II, only two-spike bursts (examples in Fig. 5)

$$S = \{d_1, d_2\}, \quad p_{d_2,d_1} = p_{d_1,d_2} = 1, \quad \mu_{\tau_{d_2,d_1}} = \tau_s, \quad \mu_{\tau_{d_1,d_2}} = \tau_\ell, \quad (5)$$

where d_i denotes the i th spike in the burst doublet. This scenario leads to periodic bursting; see Eq. (3) for the value of the burst measure.

2.3. Scenario III, single spikes mixed with two-spike bursts (Fig. 6)

$$\begin{aligned} S &= \{s, d_1, d_2\}, \\ p_{d_1,s} &= 1 - p_{s,s} = x, \quad p_{d_2,d_1} = 1, \quad p_{s,d_2} = 1 - p_{d_1,d_2} = y, \\ \mu_{\tau_{s,s}} &= \mu_{\tau_{d_1,s}} = \mu_{\tau_{s,d_2}} = \mu_{\tau_{d_1,d_2}} = \tau_\ell, \quad \mu_{\tau_{d_2,d_1}} = \tau_s. \end{aligned} \quad (6)$$



Fig. 6. Mix of bursts and single spikes; $B_2 = 0.065$, $\rho_1 = -0.59$.

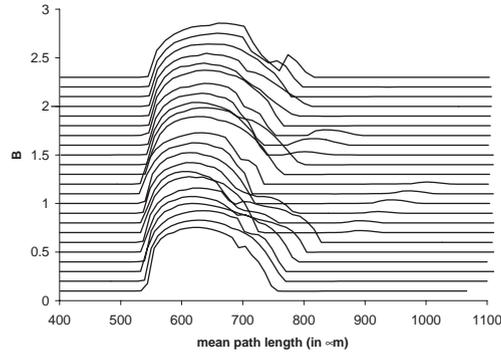


Fig. 7. Burst measure of spike trains obtained from neurons with topologically different dendritic trees plotted against mean path length. The top curve is of the most asymmetric tree, and the bottom curve is of a completely symmetric tree. The neurons were stimulated by a constant current injection at the soma. For clarity, the graphs have an offset; the flat part of each graph corresponds to $B_2 \approx 0$.

We assume that all intervals except the intraburst interval τ_{d_2, d_1} have the same average length. For this scenario, the burst measure will yield

$$B_2 = 1 - (2y + x) \frac{(x^2 + y(2 - y)) \left(\frac{\tau_s}{\tau_l} - 1 \right) + (2y + x)}{\left(y \frac{\tau_s}{\tau_l} + (y + x) \right)^2}. \quad (7)$$

3. Characterization of spike trains obtained from model neurons

We used the burst measure B_2 to study the firing behaviour of model neurons that vary in dendritic topology and total dendritic length but have the same membrane properties and number of terminal segments. We used a set of neurons consisting of all the topologically different dendritic trees with eight terminal segments. All the segments in the tree have the same length. The diameters of the segments obey Rall's power law, with the constraint that all terminal segments have the same diameter. The neurons were simulated at the soma with a constant current injection. We used the NEURON package to carry out the simulations. For details, see [6]. Data from these simulations are used in the left panel of Fig. 2, as well as in Fig. 7, in which B_2 is plotted against the mean path length of the dendritic tree (the sum of all dendritic path lengths in the tree measured from the tip of a terminal segment to the soma divided by the total number of terminal segments). The example spike trains shown in Section 2 were also taken from these simulations.

Fig. 7 shows that both dendritic topology and mean path length influence the amount of bursting in the spike trains. Neurons with a low mean path length all behave approximately the same. At higher mean path lengths, starting from around 600 μm , the different topologies start deviating in their behaviour. The differences between the curves can be related to specific characteristics of the dendritic topologies. Extensive results and analyses will be presented in [7].

4. Conclusions

We have introduced a new, relatively model-free measure to quantify bursting in spike trains. Our burst measure makes it possible to compare in a standardized way the degree of bursting in different spike trains. The measure is sensitive to the ratio of short to long interspike intervals and is independent of the average spike frequency. The usefulness of the measure has been shown in a study about the influence of dendritic morphology on firing patterns.

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