Neuronal Activities of Response Onset and Offset in Macaque Visual Neurons

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Abstract—Temporal modulation of statistics on point process has not been examined fully in experimental data analysis. We proposed analysis methods for measuring several time-varying statistics, including local statistics. We applied our methods to the physiological spike data, which were recorded from macaque visual neurons. From the results of temporally changing behavior of the spike train statistics observed from the visual neurons, local statistics of the spike train temporally change, which is independent of firing rates. These findings may provide novel insights into the neuronal codes of visual neurons.

1. Introduction

Temporal modulation of statistics on point process has not been examined fully in experimental data analysis, while first-order statistics have been commonly employed to analyze complex data [1]. Many stochastic systems require multiple trials to estimate their time-varying statistics. Time-varying statistics are often estimated by employing a time window of a certain length over trials.

In Ref. [2] and [3], we proposed analysis methods for measuring several time-varying statistics, including local statistics. These methods calculate a local measure by extracting a short segment of data within a predefined time bin and connecting the segments with each other. We numerically confirm that these analysis methods are reliable for estimating the statistics of several stochastic processes, such as nonstationary Poisson process and gamma process. Next, we applied our estimation methods to the physiological spike data, which were recorded from the LGN of Macaca fascicularis anesthetized with sufentanil and paralyzed with vecuronium [4]. The recordings from LGN were obtained while a drifting sinusoidal grating was presented. Our result of temporal modulation of the statistics may provide novel insights into the neuronal codes of LGN.

2. Statistics

The local variation L_V is known to be independent of first order statistics [5], and is defined as follows:

$$L_V = \frac{1}{N-1} \sum_{i=1}^{N-1} \frac{3(T_i - T_{i+1})^2}{(T_i + T_{i+1})^2}, \qquad (1)$$

where T_i represents the ith interspike interval (ISI) and N is the number of ISIs. L_V expresses the local firing irregularity, and $L_V = 1$ for infinitely long purely Poisson series of events, and $L_V = 0$ for perfectly periodic sequences.

Davies et al. proposed another irregularity measure IR that is also independent of the first order statistics [6]. IR is defined as follows:

$$IR = \frac{1}{N-1} \sum_{i=1}^{N-1} |\log(T_{i+1}) - \log(T_i)|, \qquad (2)$$

where $IR = 2\log 2$ for an infinitely long purely Poisson series of events and $IR = 0$ for perfectly periodic sequences.

It has been reported that not only the firing rates, but also the values of L_V and IR of neural spike trains are important indexes for the analysis of neuronal response and may provide insights into the neuronal codes [5, 6]. For example, L_V can be used for the classification of types of neurons, and IR can be used for representing particular information with behavioral context. From these viewpoints, methods for analyzing such modulations have been important research topics [2, 3, 7].

3. Analysis methods

To measure the time-varying statistics, the point process is devided by small bins and instantaneous statistics are measured. By shifting the bin, temporal changes of the statistics during the experiment can be obtained. However, there could be several methods to measure the instantaneous statistics. The simplest method of measuring the time-varying statistics is the method of measuring the statistics within a bin of each trial and averaging those statistics over the trials, which is employed in Ref. [2, 6]. The method is executed as follows.

Step 1: All the trials are aligned to the stimulus (or event) marker and divided by a certain time length.

Step 2: The statistics are calculated within each bin. In this step, ISIs in the edges of the bins would be cut off and not calculated. If no ISIs exist in a certain bin, the statistics for this bin will not be measured.

Step 3: The statistics are averaged over the trials.

This method is called the "edge-excluding averaging method", abbreviate as "EX". In the EX, all the ISIs used for obtaining the statistics exist in the original spike train,

although there is a bias that the ISIs which are longer than the bin width will be neglected.

In Ref. [2], we proposed another method for measuring the time-varying statistics on the basis of connecting trials within each bin and measuring the statistics. The method for connecting trials is called the "edge-connecting method" (CN).

Step 1: All trials are aligned to the stimulus (or event) marker and they are divided by the time bin.

Step 2: The jth bins with a fixed j are connected over trials i and a new set of ISIs is produced.

Step 3: The statistics are measured for each set of ISIs produced in the **Step 2**.

In this method, all the bins, including the ones that have no ISIs, would be connected. With regard to the CN, the fact that the new nonexistent ISI appears as a consequence of connecting the edges may be cause for concern. To avoid such nonexistent ISIs, the ISIs that lie on edges of a bin can be included and averaged over trials. This alternative method is called as "edge-including averaging method"(IN)[3].

4. Numerical simulation

### 4.1. Statistics obtained from the nonstationary Poisson process

We now compare these analysis methods on the basis of the performances of statistics L_V and IR. We use a doubly stochastic Poisson process in which the firing rate is modulated [1]. We consider the case that the random modulation of the firing rate is given by the Ornstein-Uhlenbeck process as follows:

$$\frac{d\lambda}{dt} = -\frac{\lambda - \lambda_0}{s} + D\xi(t), \qquad (3)$$

where λ is the rate of the Poisson process, λ_0 is the mean rate, s is the time scale of the rate change, D is the strength of the noise, and $\xi(t)$ is Gaussian noise with ensemble-averaged quantities $\langle \xi(t) \rangle = 0$ and $\langle \xi(t)\xi(t') \rangle = \delta(t - t')$. The performance of each method is evaluated by the mean error rates $\sigma_{L_V}^2 = \langle (L_V - 1)^2 \rangle_t$ and $\sigma_{IR}^2 = \langle (IR - 2\log 2)^2 \rangle_t$, which measure the differences between the obtained values and theoretical values.

The results of the mean error rate obtained from the EX, IN, and CN in the doubly stochastic Poisson process with physiologically plausible parameter range are shown in Fig. 1. Figure 1 shows that the mean error rates obtained from the CN are smaller than those obtained from the EX. If the time scale of the firing rate modulation is sufficiently shorter than the bin width Δ ($s \ll \Delta = 100$), it is possible to estimate the true statistical value $L_V = 1$ or $IR = 2\log 2$, since the bin width is long enough to neglect the rate nonstationarity. On the other hand, if the time scale of the firing rate is sufficiently longer than the bin width ($s \gg \Delta = 100$), it is possible to estimate $L_V = 1$ or $IR = 2\log 2$, because

the firing rate does not change rapidly within the period of the bin length. When the time scale of the firing rate s is close to the bin width $\Delta = 100$, it is difficult to estimate the accurate statistics because we cannot neglect the rate nonstationarity, resulting in the peak of the error rates around $s = 190$.
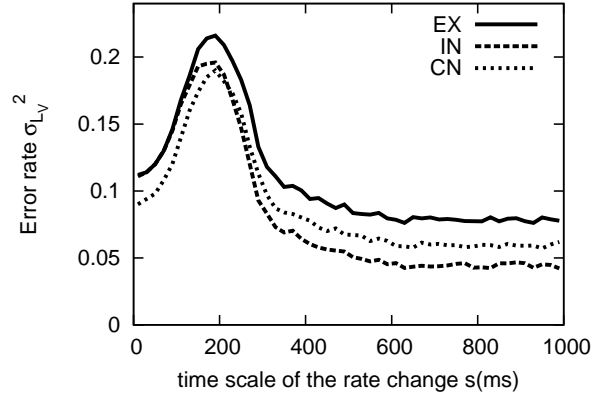
(a)
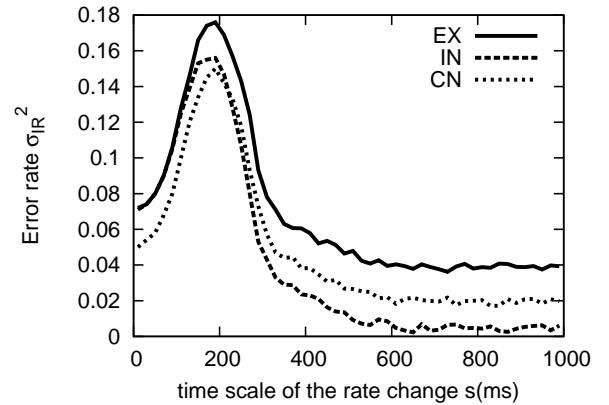
(b)

Figure 1: (a) Mean error rate $\sigma_{L_V}^2 = \langle (L_V - 1)^2 \rangle_t$ and (b) mean error rate $\sigma_{IR}^2 = \langle (IR - 2\log 2)^2 \rangle_t$ obtained from the EX (the solid lines), IN (the heavy dashed lines), and CN (the thin dashed lines) in a doubly stochastic Poisson process with modulating the time scale of the rate change s in a physiologically plausible range. The parameters are set as $\lambda_0 = 0.02$, $D = 0.01$, $s = 100$ and $\Delta = 100$.

Interestingly, the mean error rates of the IN are high compared with other methods when the time scale of the rate change s is short; on the other hand, they take small values when the time scale s is long. If the time scale of the rate change is short, the IN has low temporal resolution because it includes the ISIs from adjacent bins. Therefore, the statistics obtained by this method cannot represent the underlying statistics well. However, if the time scale of the rate change s is long, it enables us to estimate the true underlying statistics well because including adjacent ISIs en-

sures a larger number of samples in each bin, which leads to small statistical fluctuations. On the other hand, in the EX and the CN, each bin undergoes larger statistical fluctuations because of a paucity of data samples in each bin.

4.2. Statistics obtained from the gamma process

We compare the IN and the CN in the case of the non-Poisson process. The value of L_V was analytically obtained as $L_V = 3/(2\kappa + 1)$ for the gamma process in which the ISIs are derived from the gamma distribution of the order κ, $p_\kappa(t) = \lambda^\kappa t^{\kappa-1}\exp(-\lambda t)/\Gamma(\kappa)$, where $\Gamma(\kappa) = \int_0^\infty t^{\kappa-1}\exp(-t)dt$ is the gamma function [5].

We study the case of varying the irregularity parameter κ from irregular to regular. Increasing the parameter κ makes the gamma process more regular. When $\kappa = 1$, the gamma process is equivalent to the Poisson process, and thus, the expectation value of L_V is unity. If $\kappa = 2$, the expectation value of L_V is 0.6. The performance of each method is evaluated by the mean error rate $\sigma^2 = \langle(L_V - \hat{L}_V)^2\rangle_t$, which measures the difference between each obtained L_V and the real L_V value $\hat{L}_V$. When we vary κ from irregular to regular, the performance of the two methods reverses as shown in Fig. 2. In case with $\kappa > 4.24$, the performance of the IN is better than that of the CN. This phenomenon occurs because of the disadvantage of the CN that the new ISIs appearing through the connecting operations do not preserve the gamma distribution. This disadvantage affects the statistics substantially when the spike sequences are regular. For example, perfectly regular but not trial-synchronized spike sequences do not take $L_V = 0$ in the CN, while the IN provides $L_V = 0$.
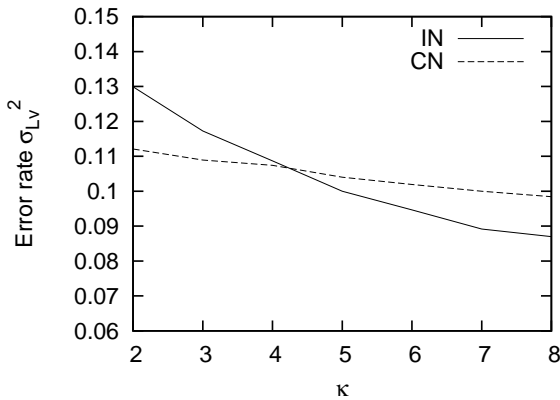

Figure 2: Results of mean error rates $\sigma^2_{L_V}$ obtained from the IN and the CN in case of the gamma processes in a physiologically plausible range. The irregularity parameter κ is changed. With small κ, $\sigma^2_{L_V}$ obtained from CN take small values, while those from IN take small values with large κ. The parameters are set as $\lambda = 0.02$ and $\Delta = 50$.

As shown in Fig. 2, the performance of the CN is better in the time series with low κ. When κ is 4, L_V is 0.33

and C_V, the coefficient of variation, is 0.5. These L_V and C_V values are relatively lower than those observed in many cortical areas [5, 8]. Therefore, the CN may be well applicable to spike data from cortical areas, as well as to the irregular time series ($L_V > 0.33$) in general stochastic processes. From the results shown in Figs. 1 and 2, the CN is more powerful when applied to irregular and rapid data, while the IN is more powerful when applied to regular and slow (with long-range dynamics) data.

5. Response onset and offset in Macaque visual neurons

We applied our estimation methods of the CN and the IN to the physiological spike data. The data we used are publicly available from the Neural Signal Archive ([9], http://www.neuralsignal.org). The spike data were recorded from the LGN of Macaca fascicularis anesthetized with sufentanil and paralyzed with vecuronium [4]. The recordings from LGN were obtained while a drifting sinusoidal grating was presented (duration: 5,138 milliseconds, 27 trials). Experimental detail is described in Ref. [4].

For the analysis, we excluded the spike trains which have a mean firing rate of less than 10 spikes per second, because the data with too low firing rates are inappropriate for the accurate analysis. We used the CN and the IN for estimating the statistics of the spike data.

We started the analyses from the time that the drifting grating was presented to the Macaca fascicularis.
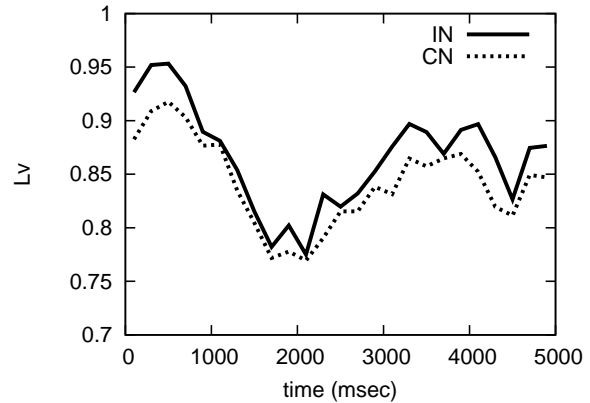

Figure 3: L_V obtained from the spike trains from the LGN of Macaca fascicular [9].

Figure 3 shows temporally changing L_V behavior of the spike trains observed from the LGN of Macaca fascicular. The value of L_V has a similar tendency for both the IN and the CN. In the experiment, the time of 0 corresponds to the time that the drifting grating was presented to the Macaca fascicularis. In Fig. 3, irregularity of the spike train is high in the early stage, then gradually decreases until the time of 2,000 milliseconds, and finally increases again (statisti-

cally significant, $p < 0.05$). When we define the average ISI as $\langle T \rangle$, correlation coefficients of the statistics L_V and $\langle T \rangle$ (expressed as $\mathrm{COR}(L_V, \langle T \rangle)$) is shown in the Table 1.

Table 1: Correlation coefficients between L_V and $\langle T \rangle$ for each analysis method using the spike trains from the LGN of Macaca fascicular [9].

Analysis method	$\mathrm{COR}(L_V, \langle T \rangle)$
IN	-0.129
CN	-0.021

From Table 1, low correlation coefficients which are nearly 0 mean that the modulation of the statistics L_V is independent of that of the average ISI. This result implies that the statistics L_V may possess information different from firing rates in visual neurons.

In the LGN of Macaca fascicular, it is reported that the mean firing rate changes with time while a drifting sinusoidal grating was presented [4]. However, temporal changes of other statistics such as L_V which is independent of firing rates has not been investigated. At present, it is difficult to understand the physiological meaning of these significant temporal changes of L_V, but further investigation may provide novel insights into the neuronal codes of LGN.

6. Conclusion

The temporal modulation of statistics on the point process has not been examined fully in experimental data analysis, while the first-order statistics have been commonly employed to analyze complex data. In this paper, we compared three analysis methods, the edge-excluding averaging method, the edge-including averaging method and the edge-connecting method [2, 3]. Using the edge-including averaging method and the edge-connecting method, the variation of the underlying statistics can be well represented. We numerically showed the performance of each method in the nonstationary Poisson process and the gamma process. The edge-connecting method is a powerful tool when applied to data with a short time scale or highly irregular data. On the other hand, the edge-including averaging method is powerful when applied to data with a long time scale or quasi-regular data. It is useful to recognize advantages and limitations of these methods when analyzing actual experimental data.

We applied our method to physiological spike data [9]. The spike data were recorded from the LGN of Macaca fascicularis, while a drifting sinusoidal grating was presented. During the sinusoidal grading, temporal changes of the statistics independent of first-order statistics have not been sufficiently investigated in physiological data. Significant temporal changes may indicate some sort of information in spike trains, and may provide novel insights to

neural codes. Further application of our method to experimental data in other fields such as biology, economics and finance may provide us with new insights on the underlying mechanisms for producing point processes in each field.

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