

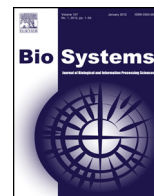


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Review Article

A review of the methods for neuronal response latency estimation

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ABSTRACT

Neuronal response latency is usually vaguely defined as the delay between the stimulus onset and the beginning of the response. It contains important information for the understanding of the temporal code. For this reason, the detection of the response latency has been extensively studied in the last twenty years, yielding different estimation methods. They can be divided into two classes, one of them including methods based on detecting an intensity change in the firing rate profile after the stimulus onset and the other containing methods based on detection of spikes evoked by the stimulation using interspike intervals and spike times. The aim of this paper is to present a review of the main techniques proposed in both classes, highlighting their advantages and shortcomings.

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Contents

1. Introduction.....	00
2. Methods based on the estimated firing rate profile.....	00
2.1. Half-height method.....	00
2.2. Rate change method.....	00
2.3. Method of <i>t</i> -tests in a sliding window.....	00
2.4. Double sliding window technique.....	00
2.5. Bayesian binning.....	00
2.6. Method of Poissonian <i>p</i> -values.....	00
2.7. Maximum-likelihood and least-squares method.....	00
3. Methods based on spike times and interspike intervals.....	00
3.1. Estimation based on interspike intervals.....	00
3.1.1. Detection of change points by maximum likelihood method.....	00
3.1.2. Bayesian method.....	00
3.2. Methods detecting evoked spikes.....	00
3.2.1. Methods for excitatory response without spontaneous activity.....	00
3.2.2. Methods for excitatory response in presence of spontaneous activity.....	00
3.2.3. Properties of the time to the first evoked spike.....	00
3.2.4. Methods for inhibitory response.....	00
4. Conclusions.....	00
Acknowledgments.....	00
References.....	00

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1. Introduction

A common experimental paradigm, in particular for studying sensory systems, is repetitive presentation of a stimulus and recording the neuronal spiking activity. It has been experimentally and theoretically shown that the spike latency, vaguely described as the time between stimulation and neuronal reaction (Friedman and Priebe, 1998, 1999), contains important information in auditory, visual, olfactory, and somatosensory modalities (Deger et al., 2010; Fulcher et al., 2008; Furukawa and Middlebrooks, 2002; Guyonneau et al., 2005; Kalluri and Delgutte, 2003; Krishna, 2002; Kwapien et al., 2000; Panzeri et al., 2001; Reich et al., 2001; Rospars et al., 2003; Tuckwell and Wan, 2005; Wainrib et al., 2010, and many others). The precise definition and determination of the response latency is therefore a crucial problem. The methods proposed in the last twenty years can be divided into two classes: methods to detect an intensity change in the firing rate, and methods based on exact spike times and interspike intervals (ISIs). The aim of this paper is to present a review of the main techniques proposed in both classes.

In the first approach, the estimated latency is given by the first instant following the stimulus onset in which the firing rate changes significantly. In statistical terms, this is a change-point estimation in the intensity (firing rate) function. A common technique involves binning the spike arrival times to form a peri-stimulus time histogram (PSTH) or more sophisticated estimates of the firing rate profile (Baker and Gerstein, 2001; Berényi et al., 2007; Chase and Young, 2008; Friedman and Priebe, 1998; Nawrot et al., 2003; Ventura, 2004).

It is well known that many behavioral responses are completed so fast that the underlying sensory processes cannot rely on estimation of neural firing rate over an extended time window. Then a natural approach is based on finding the first spike which appeared due to the stimulation (Heil, 2004; Hurley and Pollak, 2005; Pawlas et al., 2010; Tamborrino et al., 2012, 2013). This implicitly assumes that the response is excitatory, but specific techniques accounting for inhibitory response have recently been introduced (Levakova et al., 2014; Tamborrino et al., 2014). Both approaches are illustrated in Fig. 1.

Most of the statistical procedures for latency estimation require data of spike times from n repeated trials. In all these trials experimental conditions must be kept identical. Nevertheless, there are also a few methods for estimating latency based on a single trial. Throughout the paper, we always assume to have data from repeated trials. If a single spike train is sufficient, it is mentioned explicitly. Likewise, we always assume the response is excitatory, unless otherwise stated.

Notation. In the following, we assume data from n independent and statistically identical trials. In every trial, a neuron is recorded from time t_0 to t_f and a stimulus is presented at time t_s , $t_0 < t_s < t_f$. The latency is denoted by θ , so the response may start at $t_s + \theta$. $N(t)$ is the number of spikes in the interval $(t_0, t]$, where the capital letter indicates a theoretical random variable. The observed number of spikes up to time t in the i th trial is denoted by $n_i(t)$ and similarly we use $n_i(s, t]$ to refer to the number of spikes observed in the interval $(s, t]$. When we speak about PSTH, M is the number of bins, n_i is the number of spikes in the i th bin and $c_i = \sum_{j=1}^i n_j$ is the cumulative number of spikes up to the i th bin. Furthermore, we denote spike times by t_{ij} and ISIs by x_{ij} , such that $x_{ij} = t_{i(j+1)} - t_{ij}$, where i is the number of the trial and j is the number of that spike among the consecutive spikes within the trial, hereafter referred to as “serial number”. The number of ISIs in the time interval $[t_0, t_s]$, i.e. before the stimulus onset, in the i th repetition is denoted by m_i .

Throughout the paper, capital letters are used for random variables and lowercase letters indicate their realizations. The cumulative distribution function (cdf) of a generic random variable X is denoted by $F_X(x) = P(X \leq x)$, its survival function $1 - F_X(x)$ by $\bar{F}_X(x)$, its probability density function (pdf) by $f_X(x)$, and the empirical cdf (ecdf) by $F_{X,n}(x) = \frac{1}{n} \sum_{i=1}^n \mathbb{1}_{\{x_i \leq x\}}$, where $\mathbb{1}_A$ is the indicator function of the set A . Further, $T_{(i)}$ denotes the i th order statistic of the sample, i.e. $T_{(1)} \leq T_{(2)} \leq \dots \leq T_{(n)}$, with $T_{(1)} = \min(T_1, \dots, T_n)$ and $T_{(n)} = \max(T_1, \dots, T_n)$. Finally, \hat{f} is used to indicate an estimator of the quantity f .

2. Methods based on the estimated firing rate profile

Many statistical methods for neuronal data are based on estimation of the firing rate. The standard definition of the firing rate (Johnson, 1996) is

$$\lambda(t) = \lim_{dt \rightarrow 0} \frac{\mathbb{E}[N(t+dt) - N(t)]}{dt}, \tag{1}$$

which is an intensity function expressing how likely a spike is in an infinitesimal interval after time t . Assuming a stimulus evokes a significant change of the firing rate $\lambda(t)$, the response latency is defined as the time point where $\lambda(t)$ deviates from its level before the stimulus onset.

The simplest and most common estimator of the firing rate is a PSTH. The time axis is divided into M equally sized bins of width Δt with boundaries $t_0 < t_0 + \Delta t < t_0 + 2\Delta t < \dots < t_0 + M\Delta t = t_f$ (an optimum method for selecting the bin width was proposed by Shimazaki and Shinomoto (2007)). For every bin $(t_0 + (k-1)\Delta t, t_0 + k\Delta t]$, $k \in \{1, \dots, M\}$, the number of spikes $n_i(t_0 + (k-1)\Delta t, t_0 + k\Delta t]$ in the bin of the i th trial is summed over all trials and

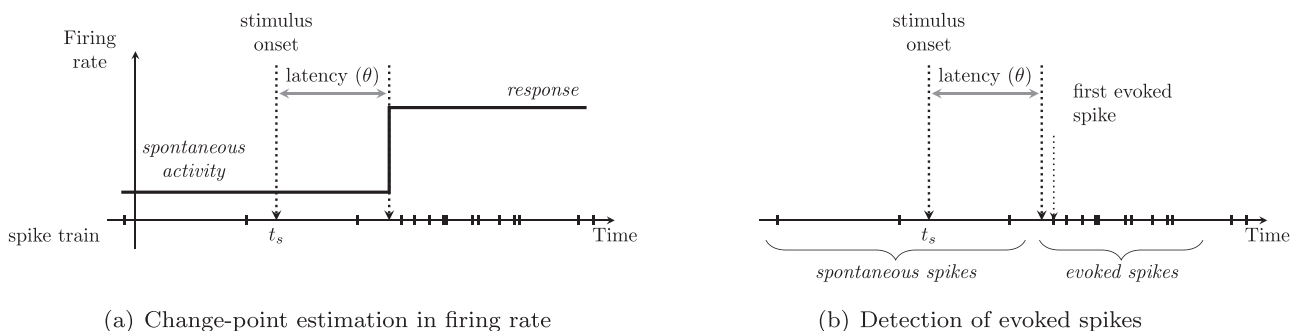


Fig. 1. A schematic illustration of the basic approaches to latency estimation. (a) The change-point methods are based on estimation of the firing rate function and detection of the point in which it changes significantly. The latency is the time from the stimulus onset to the change in the firing rate. (b) When using methods based on detection of spikes evoked by the stimulation, the latency is defined as the time where no evoked spikes can occur. In addition, statistical properties of the time to the first evoked spike are investigated.

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