

Change-point detection in neuronal spike train activity

Rama Ratnam^a, Jozien B.M. Goense^{a,c}, Mark E. Nelson^{*,a,b,c}

^aBeckman Institute for Advanced Science and Technology, ^bDepartment of Molecular & Integrative Physiology, ^cCenter for Biophysics & Computational Biology, University of Illinois Urbana-Champaign, Urbana, IL 61801

Abstract: 110 words
Main text: 2300 words (approx)
Figures: 2
References: 9

***correspondence:**

Mark E. Nelson
Beckman Institute
University of Illinois
405 N. Mathews
Urbana, IL 61801

Phone: 217-244-1371
Fax: 217-244-5180
Email: m-nelson@uiuc.edu

Abstract

Animals respond to changes in their environment based on the information encoded in neuronal spike activity. When exploring the neural substrates of behaviors such as prey detection or predator avoidance, one key issue is to determine how quickly and reliably the system can detect that a behaviorally relevant change has taken place. What are the neural mechanisms and computational principles that allow fast, reliable detection of changes in spike activity? Here we present an optimal statistical signal-processing algorithm for change-point detection, known as the CUSUM algorithm. We then show that the performance of a simple neuron model with leaky integrate-and-fire dynamics can approach theoretically optimal performance limits under certain conditions.

Keywords:

spike train analysis, signal detection, change-point detection, CUSUM, neural coding

1. Introduction

An important aspect of behavior is to evaluate choices and make decisions. At the neural level, the information to support these processes is carried in large part by the time varying activity of spiking neurons. For an animal to respond quickly and reliably to changes in the environment, it must draw inferences in real time from neuronal spike train data. It is therefore useful to ask what sorts of neural algorithms might be employed for detecting changes in spike activity in real time, and how does the performance of these neural algorithms compare with known theoretical results on optimal signal detection? Our interest in this topic is motivated, in part, by specific questions about how weakly electric fish are able to detect and localize prey based on subtle changes in electrosensory afferent spike activity [6, 8].

Developing optimal algorithms for detecting changes in time series data is an active area of investigation in the field of statistical signal processing. There are many practical real world applications for change-detection algorithms, such as early detection of impending structural failures in aircraft, on-line quality control of silicon fabrication processes, and detecting changes in patient outcome during ongoing medical trials. For a comprehensive review of change-detection methodologies and applications, see [1].

Here we present an optimal statistical signal-processing algorithm for detecting abrupt changes in spike activity, based on an established technique known as the cumulative sum (CUSUM) method. We then compare the detection performance of a simple neuron model with the optimal signal-processing algorithm. We show that the performance of a neuron model with leaky integrate-and-fire dynamics can approach the theoretically optimal performance under appropriate conditions.

2. Defining the problem

Consider a spike train as a sequence of random interspike intervals (ISIs). Initially the intervals I_1, I_2, \dots are distributed according to some probability density function (PDF) $f_0(I)$, which can be empirically estimated from the ISI distribution. At some unknown point in the ISI sequence, an abrupt shift occurs such that interval m and all subsequent intervals I_m, I_{m+1}, \dots are distributed according to a new PDF $f_1(I)$. The change in the underlying PDF will be reflected as a change in the observed ISI distribution following the change-point m . Before and after the change-point, the distributions are assumed to be stationary and the ISIs are assumed to be independent (i.e., no correlations in the ISI sequence). The method of analysis presented here is general and applies to a broad class of problems (change in mean, variance, burstiness, or other statistical parameters of the ISI distribution).

The main goal of the detection algorithm is to reliably detect a change in the underlying PDF as soon as possible after it has occurred. An equally important, but perhaps less obvious goal, is to minimize the rate of false alarms. False alarms occur whenever the detection algorithm signals that a change has occurred in the absence of any real change in the underlying PDF. In the application presented here, detection performance will be measured in terms of the mean detection delay as a function of the mean time between false alarms.

3. The CUSUM algorithm

Consider sampling a single ISI I_k from a spike train without knowing whether it occurred before or after the change point m . We wish to distinguish between two hypotheses: that the ISI occurred before the change (H_0), or that the ISI occurred after the change (H_1). In general, one of the two distributions f_0 or f_1 will be more likely to have generated the sample, thus one of the two

candidate hypotheses will be favored by this single observation. The log-likelihood of H_1 relative to H_0 based on this single observation is:

$$s(I_k) = \ln \frac{f_1(I_k)}{f_0(I_k)} \quad (1)$$

The CUSUM algorithm is an iterative algorithm for processing consecutive samples based on a cumulative sum of log-likelihood ratios. There are two thresholds associated with the CUSUM algorithm. Crossing an upper threshold level h indicates the accumulated evidence in favor of H_1 is sufficient to signal that a change has occurred. Crossing a lower threshold level at zero indicates that the accumulated evidence favors hypothesis H_0 and that the cumulative sum should be reset to zero. Starting with the first ISI in the spike train, I_1 , and proceeding sequentially, the update rule for the CUSUM algorithm is:

$$g_k = \begin{cases} g_{k-1} + s(I_k) & \text{if } g_{k-1} + s(I_k) > 0 \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

with the initial condition $g_0 = 0$. The detection of a change is signaled following observation of the n^{th} ISI, if $g_n \geq h$. The detection delay d , measured in intervals, is defined by $d = n - m + 1$, where m is the index of the first ISI after the actual change-point.

The CUSUM algorithm, which was first introduced by [7], has been shown to be asymptotically optimal, in the limit of low false alarm rates, for solving change detection problems involving independent and identically distributed samples drawn from two known PDFs [3]. Others have extended these results to establish non-asymptotic optimality under certain conditions [4, 9], and optimality for processes that are not necessarily independent and identically distributed [5].

4. Applying CUSUM to spike train data

An application of the CUSUM algorithm to simulated spike train data is illustrated in Fig. 1. ISI values were randomly drawn from a gamma distribution of order n and mean \bar{I} . The gamma distributions is useful for describing a wide range of ISI distributions because the two parameters, \bar{I} and n , allow independent control of the mean and variance of the ISI distribution, respectively. The PDF for a gamma distribution of order n and mean \bar{I} is given by:

$$f(I) = \frac{n^n}{\bar{I}^n (n-1)!} I^{n-1} \exp[-nI / \bar{I}] \quad (3)$$

The parameters for the initial probability density function f_0 were $n = 8$ and $\bar{I}_0 = 0.020$ s (corresponding to a mean rate $\bar{R}_0 = 50$ Hz); the resulting ISI distribution is illustrated in Fig. 1A. After the change-point, the new PDF f_1 had a mean $\bar{I}_1 = 0.015$ s (corresponding to a mean rate $\bar{R}_1 = 66.7$ Hz) and n remained unchanged; the resulting ISI distribution is shown in Fig. 1B. Figure 1C shows a sample spike train before and after the change-point. Note that the intervals tend to be shorter following the change-point.

Following Eqn. 1, the log-likelihood ratio for an ISI of duration I in this example is:

$$s(I) = \ln \frac{f_1(I)}{f_0(I)} = \ln \frac{\frac{n^n}{\bar{I}_1^n (n-1)!} I^{n-1} \exp[-nI / \bar{I}_1]}{\frac{n^n}{\bar{I}_0^n (n-1)!} I^{n-1} \exp[-nI / \bar{I}_0]} = n(\ln \frac{\bar{R}_1}{\bar{R}_0} - \Delta R I) \quad (4)$$

where $\bar{R}_0 = 1 / \bar{I}_0$, $\bar{R}_1 = 1 / \bar{I}_1$, and $\Delta R = \bar{R}_1 - \bar{R}_0$. Substituting numerical values from this particular example yields $s(I) \cong 2.3 - 133 I$. Consequently, ISI values shorter than approximately 0.0173 s will result in a positive value of the log-likelihood ratio, whereas longer ISI values will result in a negative log-likelihood ratio. Using this expression for $s(I)$, the CUSUM update rule (Eqn. 2) is evaluated after the observation of each ISI, as illustrated by the

solid points in Fig. 1D. When the value of g_k (solid points) crosses above the threshold level h (horizontal dashed line), a detection event is signaled and the update process is terminated.

Although the CUSUM output g_k is defined only at the end of each ISI, the form of the log-likelihood function $s(I)$ suggests an interpolation that will be useful when drawing analogies with neural implementations. Note that $s(I)$ consists of a constant term, $n \ln(\bar{R}_1 / \bar{R}_0)$, and a term that scales linearly with the duration I of the ISI, $-n\Delta R I$. We can construct an interpolated version of g that decays linearly with a slope of $-n\Delta R$ between spikes and is boosted by a constant amount $n \ln(\bar{R}_1 / \bar{R}_0)$ upon the arrival of a spike at the end of each ISI, as shown in Fig. 1D.

The saw tooth pattern of boosts and decays seen in the interpolated version of the CUSUM algorithm in Fig. 1D immediately suggests a possible neural implementation. The time course of the interpolated CUSUM variable g is strikingly similar to the changes in membrane potential that are associated with leaky integration of spike events by a postsynaptic neuron. This point is illustrated using a simple leaky integrate-and-fire neuron model in Fig. 1E. We will explore this neural implementation in more detail in section 6, but first we wish to establish some performance measures for the CUSUM algorithm and revisit the issue of optimality.

5. CUSUM performance and statement of optimality

Once the PDFs, f_0 and f_1 , have been defined, the CUSUM algorithm has only one free parameter, the threshold level h . As h is increased, both the mean time between false alarms \bar{T} and the mean detection delay \bar{d} will increase. This tradeoff is illustrated in Fig. 2 for the change-detection problem formulated in Fig. 1. Empirically, the mean number of intervals between false alarms scales exponentially with threshold level, $\bar{T} \propto e^h$, while the mean detection delay (in intervals)

scales linearly with threshold level, $\bar{d} \propto h$. Thus a semi-logarithmic plot of \bar{d} versus \bar{T} for the CUSUM algorithm results in a nearly straight line, as shown in Fig. 2A.

It is also useful to consider a quantity known as the worst-case mean delay \bar{d}_{wc} , or simply the *worst mean delay*. Just prior to the change-point, the state-variable g_k of the CUSUM algorithm can potentially take on any value between 0 and h due to intrinsic fluctuations in the baseline activity. The worst case, in terms of detection delay will occur when g_k happens to start off at its lowest possible value, namely 0. This will occur whenever the accumulated evidence just prior to the change-point favors hypothesis H_0 . A careful comparison of the solid lines in Figs. 2A and 2B will show that the worst mean delay is always slightly longer than the actual mean delay, and hence provides an upper bound. The motivation for introducing the worst mean delay, is that the statement of optimality for the CUSUM algorithm is stated in terms of this quantity.

Asymptotically, as $\bar{T} \rightarrow \infty$, the CUSUM algorithm can be shown to produce the minimum worst mean delay \bar{d}_{wc} for a fixed mean time between false alarms \bar{T} [1, 3].

6. Leaky integrate-and-fire as a biologically plausible implementation

How might a neuron in the brain implement a CUSUM-like detection algorithm? As mentioned earlier, the time course of the interpolated CUSUM state variable suggests a plausible implementation based on leaky integration by the post-synaptic neuron. This idea can be captured in a leaky integrate-and-fire neuron model, in which the membrane potential obeys a differential equation of the form:

$$\frac{dv}{dt} = -\frac{v}{\tau} + \frac{x(t)}{\tau} \quad (5)$$

where $x(t)$ is the input spike train, represented as a series of delta functions at the time of each input spike. For convenience, we have scaled the input in Eqn. 5 to give unity gain at DC. The

membrane voltage is integrated according to Eqn. 5 until it reaches a threshold level h , at which point an output spike is generated, signaling that a change has been detected. To parallel the structure of the CUSUM algorithm, we can recast Eqn. 5 in terms of a discrete update rule that is evaluated at the end of each ISI I_k :

$$v_k = v_{k-1} \exp(-I_k / \tau) + 1 / \tau \quad (6)$$

Thus the membrane voltage decays exponentially between spikes and is boosted by a constant amount $1/\tau$ upon the arrival of a spike at the end of each ISI.

With the gain fixed, the leaky integrate-and-fire model has two free parameters, the integration time constant τ and the threshold level h . As was done previously for the CUSUM model, we can characterize the performance by plotting the mean detection delay versus mean time between false alarms for different values of h . However, we now have an additional free parameter—the integration time constant τ . If τ is very small, the voltage will decay to zero before the next spike, and spike events will not summate; if τ is very large, summation will occur, but the system will be slow to respond. Intuitively, there should be an intermediate value of τ that will yield the best detection performance. A full parametric study of this issue is beyond the scope of this paper. For illustration purposes we have chosen $\tau = 0.150$ s, which was empirically determined to yield the best detection performance for the particular set of parameters used in this example.

The dashed lines in Fig. 2 show the detection performance of the leaky integrate-and-fire model, in comparison to the theoretically optimal CUSUM algorithm. In terms of the mean detection delay, the performance of the integrate-and-fire model closely approaches the CUSUM model over much of the range, as shown in Fig. 2A. In terms of the worst mean delay, however, the integrate-and-fire model does considerably worse (Fig. 2B). Unlike the CUSUM algorithm, the neuron model does not have a reset mechanism when the accumulated evidence has swung in

favor of hypothesis H_0 . Thus random fluctuations in baseline activity just prior to the change-point can allow the membrane voltage to decay significantly below its baseline level, leading to longer detection delays. Despite poorer performance on worst-case scenarios, the typical performance of the leaky integrate-and-fire model is near optimal over a broad operating range.

7. Discussion

Based on the analytical formulation of the CUSUM update rule and log-likelihood ratio (Eqns. 2 and 4), it might not be readily apparent how the nervous system could implement such an algorithm. Observing the time course of the CUSUM state variable (Fig. 1D), however, suggests that leaky integration of spike activity could provide a biologically plausible approximation to the CUSUM algorithm. Indeed, we have shown that a neuron model with leaky integrate-and-fire model dynamics can approach the performance of the theoretically optimal algorithm in one particular example (Fig. 2A). Detailed simulations (non presented here) generalize this result to a broad class of change-detection problems involving a shift in the mean of the ISI distribution. Other sorts of changes in the ISI distribution, such as changes in variance, or changes in burst properties, will require somewhat more elaborate neural implementations. The success of the simple integrate-and-fire mechanism leaves us optimistic that biologically plausible solutions to these more complex problems will also exhibit near-optimal performance characteristics. Recently, we have used the leaky integrate-and-fire neuron model to detect changes in empirical spike train data recorded from primary electrosensory afferents [2]. The results of this empirical study reveal an impressive sensitivity of the detection algorithm to small changes in electrosensory afferent spike activity. In addition, the empirical results raise interesting questions regarding the potential role of bursts in the change-detection process.

Acknowledgements

This work was supported by a grant from the National Science Foundation (IBN 0078206).

References

- [1] M. Basseville and I.V. Nikiforov, Detection of abrupt changes: theory and application (Prentice-Hall, Englewood Cliffs, NJ, 1993). This out-of-print book can be downloaded at <http://www.irisa.fr/sigma2/kniga/>
- [2] J. B. M. Goense, R. Ratnam, and M. E. Nelson, Burst firing improves the detection of weak signals in spike trains (this issue) *submitted*.
- [3] G. Lorden, Procedures for reacting to a change in distribution. Ann. Math. Stat. 42 (1976) 1897-1908.
- [4] G. V. Moustakides, Optimal stopping times for detecting changes in distributions, Ann. Statist. 14 (1986) 1379-1387.
- [5] G. V. Moustakides, Quickest detection of abrupt changes for a class of random processes. IEEE Trans. Info. Theory 44, (1998) 1965-1968.
- [6] M. E. Nelson and M. MacIver, Prey capture in the weakly electric fish *Apteronotus albifrons*: sensory acquisition strategies and electrosensory consequences. J. Exp. Biol. 202 (1999) 1195-1203.
- [7] E. S. Page, Continuous inspection schemes, Biometrika 14 (1954) 100-115.
- [8] Ratnam, R. and M. E. Nelson, Nonrenewal statistics of electrosensory afferent spike trains: implications for the detection of weak sensory signal, J. Neurosci. 20 (2000) 6672-6683.
- [9] Y. Ritov, Decision theoretic optimality of the CUSUM procedure. Ann. Statist. 18 (1990) 1464-1469.

Figure Captions

Fig. 1 Change-point detection in simulated spike train data. (A) ISI distribution before the change-point. (B) ISI distribution after the change-point. For reference the original ISI distribution is shown as a solid line. (C) Spike train data before and after the change-point, which is indicated by the vertical dotted line. (D) The CUSUM algorithm applied to the spike train data. Filled points represent the discrete values of g_k evaluated at the end of each ISI according to Eqn. 2. The saw tooth pattern is the continuous interpolation of g described in the text. Horizontal dashed line is the threshold level h ; vertical dashed line indicates the detection time. (E) Response of a leaky integrate-and-fire neuron model to the spike train data. Line-style conventions are as above. The membrane time constant is $\tau = 0.150$ s.

Fig. 2. Performance comparison between the optimal CUSUM algorithm (solid lines, filled circles) and a leaky integrate-and-fire neuron model (dashed lines, open circles), for different threshold levels h . (A) Mean detection delay versus the mean time between false alarms (B) Worst mean detection delay versus mean time between false alarms. The membrane time constant for the integrate-and-fire model is $\tau = 0.150$ s. The mean time between false alarms was computed from a random sequence of 10^6 ISIs drawn from the baseline distribution f_0 . The mean detection delay was evaluated based on 10^3 random trials involving a change in the underlying PDF from f_0 to f_1 . For evaluating worst-case delays, the relevant state-variable (g or v) was set to zero just prior to the change-point.

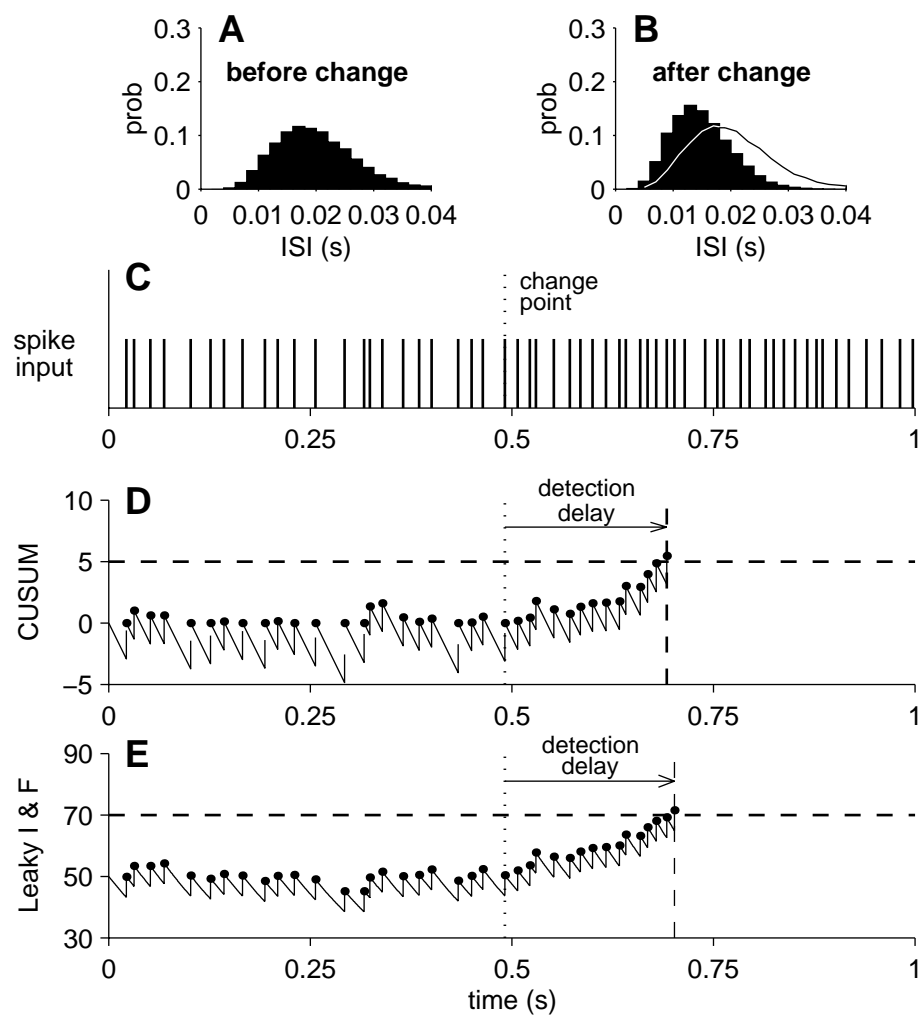


Figure 1

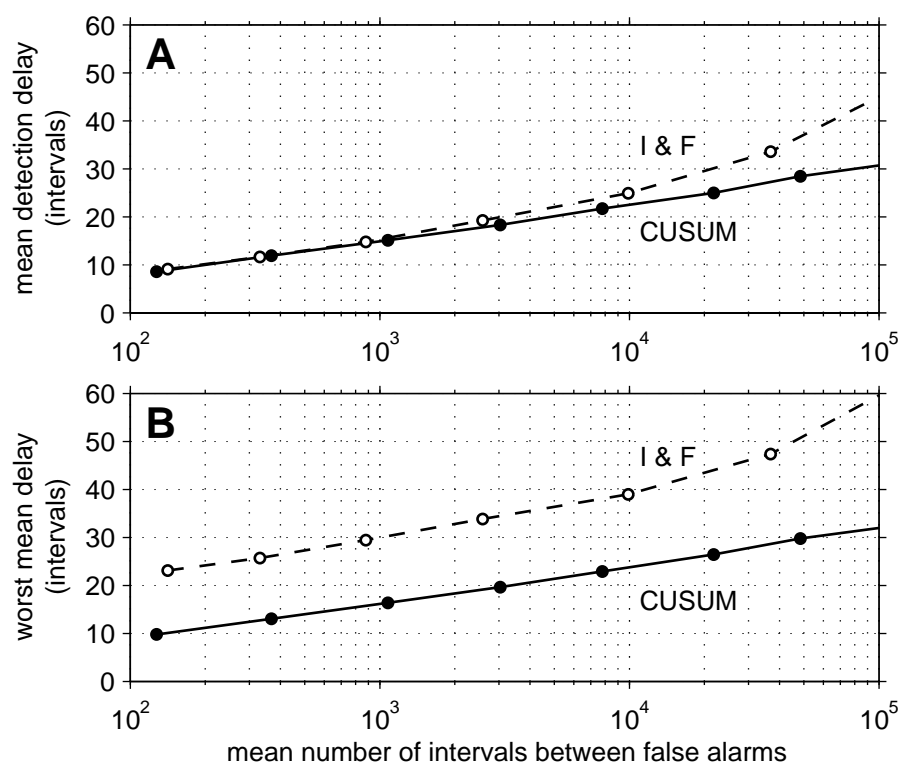


Figure 2