# Variance stabilization of spike trains via non-renewal mechanisms: The impact on the speed and reliability of signal detection

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**Abstract**

Detecting a signal that is buried in a noisy background is important to all organisms. How this is achieved at the level of single neurons is as yet unknown. Here we examine how the properties of the input affect the ability of a biologically plausible neuron to detect a signal. Two kinds of input are examined, 1) an experimentally obtained non-renewal spike train that exhibits anti-correlations in the interspike interval sequence, and 2) a renewal spike train without serial correlations. We show that anti-correlations enable a detector neuron to detect a change in the input quickly and reliably, and this is possible even when the integration time is varied over a large range. For renewal input, performance is overall poor, and is sensitive to the integration time. We show that anti-correlations in the neural spike train stabilize the variance of the detector's membrane potential, keeping it roughly constant over multiple time scales. The mechanism may provide the nervous system with the flexibility to detect signals robustly, independent of membrane characteristics.

## 1 Introduction

The fundamental dilemma in neural decision making is the trade-off between speed and reliability. On the one hand, sufficient information must be gathered to make a reliable decision, but this takes time. On the other hand, decisions must be made quickly, but this means acting on incomplete information. The simplest decision making task concerns detecting a behaviorally relevant stimulus in a background of unwanted and interfering signals. It is not yet known how neurons achieve this trade-off between speed and reliability in a detection task.

Here we suggest that a mechanism to achieve this may be based on the intrinsic structure of the baseline (or spontaneous) activity of spike trains. Using spontaneous activity recorded from the electrosensory afferents of weakly electric fish, we show that speed and reliability of decision making may be enhanced as by a non-renewal spiking mechanism. The non-renewality entails the presence of anti-correlations in the interspike interval sequence. These correlations are known to stabilize the firing rate of the neuron over multiple time scales, as can be observed by counting spikes over different time windows. The variance of the count stays nearly constant over time scales extending from a few to hundreds of milliseconds [3,7]. Earlier studies have shown that stabilization of rate makes it possible to detect extremely weak signals in fixed sample size tasks [1, 3, 7] and in sequential or dynamic detections tasks [5, 6]. Here we look at both speed and reliability of signal detection, and compare the detection performance for the neuron with a renewal spike train. We show that the non-renewal mechanism enables post-synaptic detector neurons to detect signals embedded in the input quickly and reliability, and that this is possible in a biologically realistic manner in continuous time. When the input is renewal, the detection performance was degraded.

# 2 Methods

## 2.1 Electrophysiology

Extracellular recordings were made from P-type electrosensory afferent nerve fibers of paralyzed weakly electric fish *Apternotus leptorhynchus*. The fish were anesthetized with tricaine methanesulfonate and paralyzed with an intramuscular injection of gallamine triethiodide [10]. The neurogenic electric organ is unaffected by the immobilizing agents, and recordings were made in the presence of the ongoing electric organ discharge. The activity under these conditions is called "baseline" activity as opposed to spontaneous activity obtained if the EOD was silenced. Neural activity was recorded with glass microelectrodes (10-30 M$\Omega$) filled with 3M KCl solution. Data were analyzed using MATLAB (The MathWorks). Surgical and experimental protocols were approved by the animal care committee, University of Illinois at Urbana-Champaign.

## 2.2 Theory and Analysis

The afferent spike times were converted to a sequence of interspike intervals (ISIs). The afferent spike trains have strongly correlated ISIs, and constitute a non-renewal process exhibiting high-order dependencies in the ISI sequence [7]. A renewal spike train was created by randomly sampling the afferent ISI distribution. This is a zeroth-order Markov model (M0 model). The two spike trains, for each afferent fiber, thus have identical ISI distributions. However, the serial dependencies exhibited in the ISIs of the neural data were not present in the M0 spike train (see [7]). The afferent and M0 spike trains are considered to be noise-only conditions in a binary hypothesis task, with ISI distributions $f_0$ under the null hypothesis ($H_0$).

In weakly electric fish, the P-type afferents encode signals by modulating the spike rate. They increase their spike rate when a conducting object is placed in their receptive field [2]. To simulate a signal, the ISIs of the spike trains were synthetically shortened by 10%, thereby increasing their spike rate. P-type afferents respond to stimuli of moderate strength by shortening their ISIs but preserved the statistical structure in the ISI sequence [8]. Thus, interval shortening may be well-supported for moderately strong stimuli. The modified experimental and model spike trains are considered to be the signal plus noise conditions, with ISI distributions $f_1$ under the alternate hypothesis ($H_1$).

The sequential detection task was formulated as follows: At some unknown point in time (the change point), the baseline spike train statistics ($f_0$ given $H_0$) changes abruptly to the statistics of the driven response ($f_1$ given $H_1$). The task was to detect this change reliably and quickly. A hypothetical post-synaptic neuron with a single membrane time-constant served as a detector (this is the well known leaky-integrate and fire neuron). The neuron integrated a spike train from a single pre-synaptic afferent, and output a spike when the membrane potential exceeded a threshold, signaling a detection. The detection was classified as a false alarm when it occurred while the input followed $f_0$, and classified as a correct detection when the input followed $f_1$. The threshold of the detector was adjusted so that the false alarm rate was 1 spike/s. This may be considered to be the "spontaneous rate" of the detector neuron. In weakly electric fish, such a detector neuron may be located in the electrosensory lateral line (ELL) lobe where the afferents converge.

The detection task is sequential as opposed to fixed sample hypothesis testing, because the neuron tests the input continuously and the signal onset time is unknown. For the nervous system, sequential hypothesis testing is important because neurons continuously integrate their inputs and have no prior knowledge of the time of occurrence of a signal. The performance of the leaky integrator for detecting transient perturbations have been studied by Goense and Ratnam [5], and its role in optimum change point detection has been discussed by Ratnam *et al.* [9]. Here we focus on the influence of the statistical properties of the input spike train on the speed of detection.

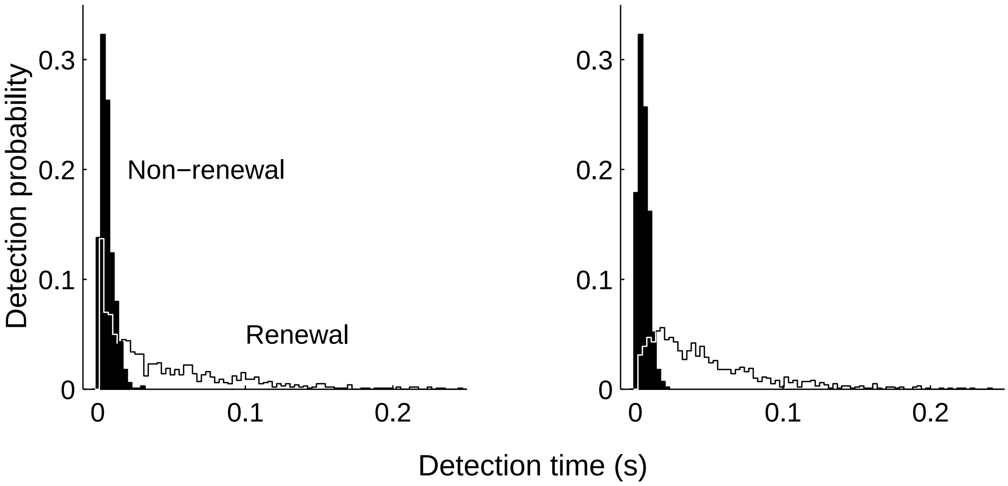


Figure 1: The effect of non-renewality on the probability of detecting a change point as a function of time. A hypothetical detector neuron had to detect an abrupt increase in the pre-synaptic spike rate, and the influence of input statistics and membrane time-constant was investigated. Panels show the histograms of the time to detection following the change point for a spike train with anti-correlated ISIs (black) and the equivalent renewal spike train (white). The time constant of the leaky integrator was 15 ms (left panel) and 50 ms (right panel). The false alarm rate was fixed at 1 spike/s. Anti-correlated ISIs provide rapid detection with a variability in latency that is robust to changes in the integrator time constant.

# 3 Results

Baseline spiking activity was recorded from 49 afferents. The neurons had a spike rate of about 300 spikes/s, and mean ISIs ranged from 0.5-15 ms, averaging about 5 ms over the population [7]. All afferents were non-renewal and their ISIs were strongly anti-correlated, i.e., a long ISI was followed by a short ISI and *vice versa*. The long-short patterning of afferent spike trains has been observed in many sensory systems, but has received most attention in weakly electric fish [1,3,5–7]. These patterns reduce the amplitude and duration of fluctuations in baseline spike rate [5,7]. These factors make it easy to detect a weak signal embedded in an anti-correlated spike train compared to a renewal spike train with the same spike rate.

## 3.1 Speed and reliability of detection

Detector neurons with membrane time constant of 15 ms and 50 ms were used to examine the influence of non-renewal statistics on change point detection. The signal was a 10% increase in the spike rate. Figure 1 shows the distribution of times to first detection following the change point for the afferent spike train (black histogram) and the renewal spike train (white histogram), for a detector with time constant 15 ms (left panel) and 50 ms (right panel). The distributions prior to the change point ($f_0$) and posterior to it ($f_1$) are the same.

Figure 1 indicates that most detections for the afferent spike train are localized within a short period of time, whereas for the M0 spike train, the spread is much greater with detections taking as long as 500 ms in some trials (not shown). The median detection times for afferents were 11 ms ($\tau = 15$ ms), and 7 ms ($\tau = 50$ ms). For the M0 model, the detection times were 108 ms ($\tau = 15$ ms), and 104 ms ($\tau = 50$ ms). The median detection times for the non-renewal spike train are well within the integration time of the detector neuron, whereas for the M0 spike train, the integration must persist for a duration that is much longer than the time-constant. Further, the afferent spike train offers an improvement in speed of detection over the M0 spike train by a factor of $\sim$10 for both time-constants.

### 3.2 Influence of detection window and time-constant

Detectability of short signals was studied by determining the number of correct detections in a fixed time window of 15 ms after the change point. The percentage of correct detections within this time window was examined for both renewal and non-renewal spike trains as a function of detector time-constant (Fig. 2, left panel). As the integration time was increased, the probability of detection increased for the afferent, whereas it decreased for the M0 model.

An increase in time-constant suggests that the integrator can take correspondingly greater time to arrive at a decision, and thus make a more reliable decision. The right panel of Fig. 2 shows that this is indeed the case for both the renewal and non-renewal spike trains. Here, the proportion of hits that occur in a time window equal to the integrator time-constant are shown as a function of the time-constant. If the decision period is increased proportionately to the integration time, the detection probability increases for both spike trains, although the probabilities are significantly higher for a non-renewal spike train. In the left panel of Fig. 2, we note that restricting the decision window to 15 ms irrespective of the integrator time-constant causes no decrease in performance for the an anti-correlated spike train. This indicates that detectors that receive non-renewal input, are robust in their performance, and can have sufficient flexibility in adjusting their time-constants, without trading speed for reliability. Physiologically, this is meaningful because neurons exhibit a

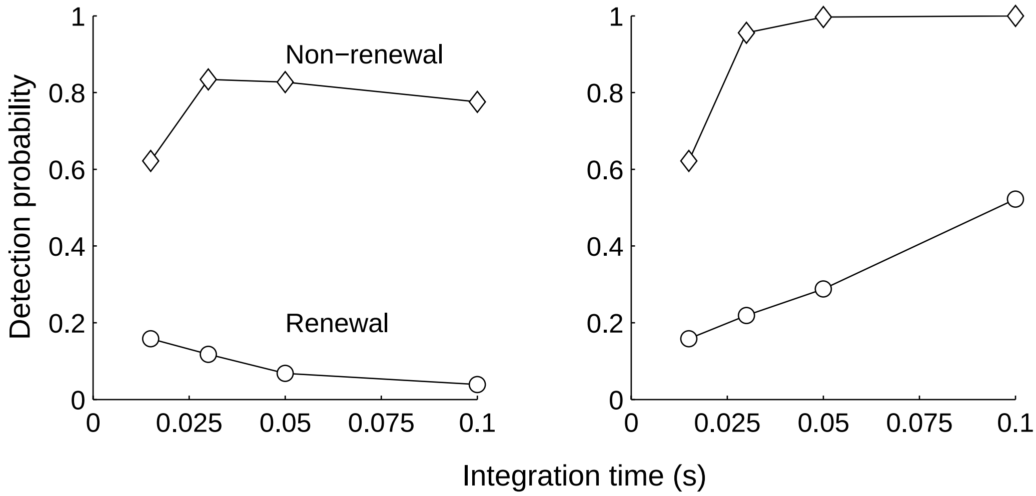


Figure 2: Speed of detection and effect of signal duration on detection probability. Panels show the probability of obtaining a hit following the change point as a function of the integrator time constant (abscissa). Left panel: probability of detecting the signal within 15 ms following the change point. Right panel: probability of detection in a window of the same duration as the integrator time-constant. For renewal spike trains reliable signal detection requires long integration times and a long signal duration (right panel). Non-renewal spike trains with anti-correlated ISIs provide speedy detections that are robust to changes in integration time.

range of time constants even within a pool of homogenous neurons. If the input is renewal, the optimal integration time to achieve reliable detection differs from the optimal time constant to achieve quick detection.

## 3.3 Variance stabilization provides robust signal detection performance

For renewal spike trains, it can be easily shown that the mean and variance of the integrator output increase linearly with increasing integrator time-constants [4]. Anti-correlated spike trains however, have the intriguing property of keeping their variance nearly constant over long integration time periods [1, 5, 7, 9]. This multi-scale regularity increases the signal detection ability of post-synaptic detector neurons, and is a powerful mechanism for detecting weak signals [5, 7].

The utility of anti-correlations in the ISIs of spike trains can be explained using the asymptotic properties of serially correlated ISIs. Let $\sigma_k^2$ denote the variance of the $k^{th}$ order interval. This is simply the variance of the sum of $k$ consecutive ISIs (with $\sigma_1^2$ being the variance of the ISI). Further, if the serial correlation coefficients (SCCs) exhibited by the sequence of ISIs are $\rho_k$, where

$k$ is the lag (the $k^{th}$ following ISI), then the variance of the $k^{th}$ order intervals is related to the variance of the ISI $\sigma_1^2$ by [4]

$$\sigma_k^2 = k\sigma_1^2\{1 + 2\sum_{l=1}^{k-1}(1 - \frac{l}{k})\rho_l\}. \tag{1}$$

We seek the condition $\sigma_k^2 = \sigma_1^2$ for large $k$, as this would stabilize the variance over long time scales. Asymptotically, when $k >> 1$, the term $\frac{l}{k}\rho_l$ will be small for $l << k$. For large $l$ also, $\rho_l \to 0$. This is because of the limited memory of real processes, where any pair of intervals becomes increasingly decorrelated as their separation increases. By applying these conditions to Eq. (1), we have the asymptotic formula for $k \to \infty$ given by

$$\sum_{l=1}^{\infty}\rho_l = -\frac{1}{2}. \tag{2}$$

When the sum of the SCCs approaches $-0.5$, the variance of intervals of all orders remains constant over all time scales. In Fig. 3 the mean of the partial sum $\sum_{l=1}^{k}\rho_k$, over the population, is shown as a function of $k$ (left panel). If variance is stabilized then all such partial sums should tend to $-0.5$ for large $k$. The observed mean was $0.48 \pm 0.02$ for $k = 20$. In Fig. 3 (right panel) the sum for $k = 20$ is shown for individuals in the population (each bar represents one afferent). All afferents closely approach the limit of stable variance. A consequence of the anti-correlation structure is that post-synaptic neurons can exhibit a range of time-constants. Because the variance of the process over multiple time scales is simply the variance of the ISI, post-synaptic neurons can flexibly integrate such inputs over a range of time scales without loss of performance.

# 4 Conclusions

We showed that the statistical properties of spike trains play a vital role in the speed and reliability of signal detection by higher-order neurons. Anti-correlations in the ISI sequence stabilize the variance of the input, thereby relaxing the constraint of optimizing the integration time in post-synaptic detector neurons. Thus, variability in integration time can be tolerated and robust detection performance can be achieved over a range of integration times. Additionally, it is of significance that correct detections can be made quickly even when the integration time is long,

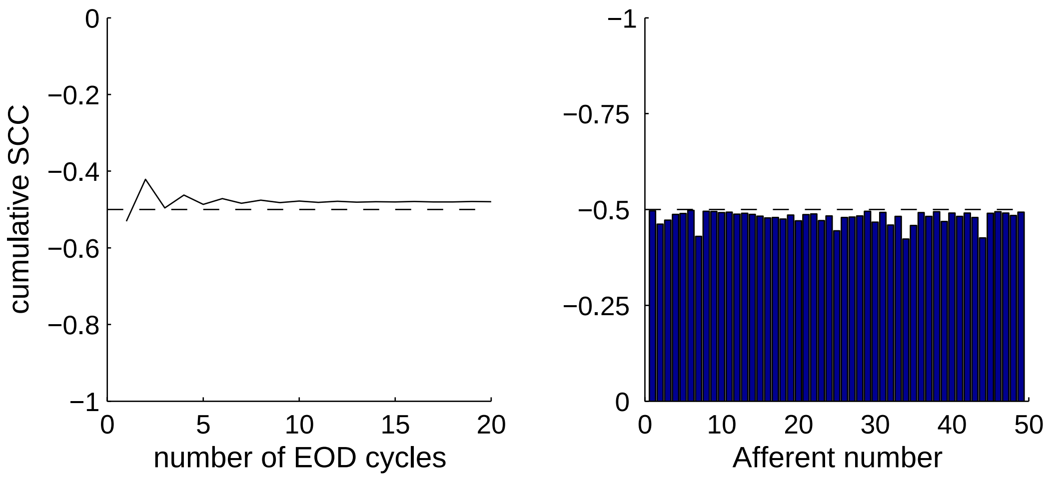


Figure 3: Variance stabilization over multiple time-scales makes it possible to detect weak signals reliably and quickly. Left panel: partial sums of the ISI serial correlation coefficients of the input spike train as a function of the correlation lag (average over 49 afferent spike trains). When the sum tends to -0.5 at infinite lags, the variance of the sum of any number of intervening ISIs is the same as the variance of a single interval (see text). The afferents closely approximate this property. Right panel: sum of the serial correlations over 20 lags (each bar representing the value for one afferent). Almost all afferents approach the limit of constant variance.

i.e., integrating inputs for long periods does not rule out the possibility of detecting signals quickly and reliably. When the input is renewal, these benefits are not available. Reliability increases with increasing integration time, but speed is sacrificed. The study points to the need to consider the statistics of the input when examining decision making in the nervous system.

## Acknowledgement

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