

Burst firing improves the detection of weak signals in spike trains

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Abstract

The detection of weak sensory signals is an important aspect of neuronal information processing. Behaviorally relevant signals are often encoded as perturbations of on-going spiking activity in primary afferents. Here, we show that a biologically plausible model, the leaky integrate-and-fire (LIAF) neuron, is capable of efficient and reliable detection of a single spike added to baseline activity. Detection performance is dependent on the statistical properties of the spike train. For the type of statistics considered here, a LIAF neuron can distinguish between a correct detection by means of burst firing, whereas false alarms tend to result in isolated spikes. The methods are illustrated by an application to electrosensory afferents of weakly electric fish.

Keywords: signal detection, integrate-and-fire neuron, electrosensory system, weakly electric fish.

1. Introduction

The sensory environment of an animal is in a state of constant flux. Behaviorally relevant signals often appear at unknown times and may be so weak that they are obscured by irrelevant background activity. The task of higher-order neurons is to filter out the irrelevant information and extract what can be a weak but relevant signal. This has to be done in real time, i.e., on the basis of a continuous online examination of the incoming spiking activity. The traditional framework for signal detection is trial based testing employing spike count windows and a binary hypothesis test [4]. This requires repeated sampling in order to make a decision and is not suitable for online detection.

In a companion study [8], we show that the performance of a model neuron, the leaky integrate and fire neuron (LIAF), can approach that of a theoretically optimal online signal processing algorithm (the CUSUM algorithm) for detecting an abrupt, sustained shift in the interspike interval (ISI) distribution. Here we explore the performance of the LIAF neuron for detecting weak, transient changes in spike activity. We show that the statistical structure of the spike train can enhance the detection performance by indicating the presence of a signal with a burst of activity, whereas a false alarm (false positive) results in isolated spiking events spaced relatively far apart in time. We apply these methods to the detection of weak signals in noisy electrosensory afferents of weakly electric fish [2,7].

2. Methods

Extracellular recordings of baseline (spontaneous) P-type afferent activity were made from afferents of *Apteronotus albifrons* (black ghost knife fish). The experimental procedures are described in Xu *et al.* [9]. *A. albifrons* has a stable and precise EOD with a fundamental frequency that ranges from 1000 to 1400 Hz. Neurons fire at most one spike per EOD period, on average once every three periods, making the EOD frequency a convenient sampling rate. Spike trains were thus discretized and represented as a string of 1's and 0's according to whether a spike was observed in an EOD period (see [7]). Recorded spike trains ranged from 200 to 450 seconds in duration. The baseline spike trains formed the “noise” data set for this study.

A weak signal was modeled by the random addition of a spike to the baseline data. The perturbed spike train was considered the “signal + noise” data set. To detect the added spike, the spike train was filtered using a leaky integrator, which simulates the LIAF neuron (Fig. 1). The integrator output was continuously compared to a fixed threshold. If a threshold crossing (hit) occurred, it was scored as a detection if the hit occurred within a time window (the signal window) following the added spike. The

duration of the signal window was set to the time constant T of the leaky integrator. Detection probability (P_d) was computed by dividing the number of detections by the number of added spikes. If the hit did not occur within the signal window it was considered a false alarm. False alarm rates were computed from the baseline data set by dividing the number of false alarms by the duration of the recorded spike train. By testing over a range of thresholds an operating characteristic (OC) curve can be constructed, showing the false alarm rate versus the detection probability P_d . After the threshold crossing, the integrator input can be reset to zero, which will result in an absolute and relative refractory period. If the integrator is reset to zero, this has the effect that for a time of the order of the time constant, no new hits are likely. Reset to other values is also possible [2,5]. The extreme case occurs when the integrator is not reset after a hit. Both cases were tested in this study to determine the effect on detection performance.

Detections with partial resets generate burst like activity in the LIAF neuron. We defined a burst as the presence of more than one hit within a time constant T of the leaky integrator. We evaluated the performance by considering only bursts of hits, i.e., single hits were ignored, and calculated the detection probabilities as a function of false alarm rate.

3. Results

In a simulated detection task, a P-type afferent spike train was perturbed by the addition of one spike at an arbitrary location. The goal of the detector was to determine *online* the presence of this added spike. Since such detection is presumably carried out at the next higher level of processing in the brainstem, the electrosensory lateral line lobe (ELL), we consider the IAF model to represent a neuron (pyramidal cell) in the ELL. Figure 2 shows the signal detection performance of an IAF neuron with input a P-type afferent spike train (mean baseline firing rate for the unit shown is 449 ± 3.4 Hz, EOD = 1061 Hz). Spike trains from the P-type unit were filtered using a leaky integrator with time constant $T = 10$ EOD cycles (about 10 ms) and passed through a threshold element to generate spikes. The mean firing rate of the

output (ELL) unit was adjusted by varying its threshold. In the absence of a signal in the input spike train, we call this the false alarm rate (see Fig. 2A). Detection performance of the IAF neuron was quantified using an operating characteristic (OC) curve (Fig. 2B), which measures detection probability as a function of the false alarm rate. It can be seen that the hypothetical ELL unit has near ideal detection performance ($P_d = 1$) even for low false alarm rates (about 1 Hz).

To determine the effect of resetting the integrator, we measured detection performance by changing the reset value. This is shown in Fig. 2B for two extreme values: complete reset to 0 after firing (circles) and no reset (lozenge). The reset value affects signal detection ability only at high false alarm rates, but for the rates shown here (< 10 Hz) it does not make much difference on the performance of the IAF unit. It should be noted that a good detector aims for a high probability of detection ($= 1$) while keeping its false alarm rate as small as possible. For the unit shown in Figure 2, the added spike can be detected easily with very high reliability and very low false alarm rate. Almost all units performed at comparable levels.

Raising the threshold level to reduce the false alarm rate has the undesirable effect of simultaneously lowering the detection probability (Fig. 2). One way to overcome this problem is to use bursting activity to distinguish between true detections and false alarms. This is illustrated in Fig. 3 by employing partial integrator resets (to illustrate, we consider the case of no reset). In Fig. 3A, it can be seen that for reasonably low thresholds, the number of multiple hits (i.e., bursts, lozenge) forms a significant proportion of the total number of detections (circles). However, at such low thresholds, the false alarm rate is high (see Fig. 2). On the other hand, the number of bursts during a false alarm are uniformly low over a wide range of false alarm rates (Fig. 3B, filled symbols). If we were to calculate performance based on all hits (single spikes or bursts), then at a threshold of 5.22 (false alarm rate of 9.3 Hz, Fig. 2A) the detection probability is almost 1 (Fig. 3A, circles). If only bursts are accepted, then the detection probability is only marginally lowered to 0.98 (Fig. 3A, lozenge), whereas the false alarm rate drops by a

factor of 6 to 1.5 Hz (Fig. 3B). Thus, bursts provide a convenient way to distinguish between correct detections and false alarms with a large increase in performance.

4. Discussion

This main findings of this work are that: 1) a simple leaky integrator with a threshold mechanism can function as an efficient online detector, and 2) high false alarm rates are acceptable if correct detections occur in small bursts of spikes whereas false alarms occur as isolated spikes. In this case, isolated hits can be ignored with little penalty on detection performance. Gabbiani *et al.* [3] and Metzner *et al.* [6] showed that bursts of ELL neurons encode more features than isolated spikes and carry more useful information. Our finding from the viewpoint of signal detection also supports this.

The principal mechanism by which detections trigger bursts whereas false alarms generate only isolated spikes is based on the strong anti-correlations between adjacent ISIs in the baseline spike train [7]. Briefly, anti-correlations provide a firing rate stabilizing mechanism whereby fluctuations away from the mean rate are strongly resisted. Thus a threshold crossing is brief with a quick return to mean firing rate. This tends to generate isolated spikes. On the other hand, adding a signal elevates the overall firing rate and so threshold crossings persist for longer duration, thus generating bursts.

Weak signals at the limit of sensory threshold may cause barely noticeable changes in the baseline firing activity of a neuron. To counter this, selection pressure may have evolved mechanisms to enhance detection performance. Among such mechanisms may be rate stabilization by anti-correlated ISIs, and consequently, the presence of bursting activity to emphasize presence of a signal. Since the nervous system processes information in stages, a hierarchy of neurons can successively filter information and refine the decision making scheme, and thereby achieve very high detection performance.

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Figure captions

Fig. 1. A leaky integrate-and-fire (LIAF) neuron can function as a signal detector. *A.* Baseline spike train (left panel) is filtered by a leaky integrator (right). A threshold crossing (dashed line) results in an output spike, and the LIAF neuron is reset to the mean value of the input (dotted line). In this case, output spikes are false alarms and represent spontaneous firing of the LIAF detector. *B.* A signal spike is added at an arbitrary location (triangle) to the baseline spike train (left panel); the task for the LIAF neuron is to detect the presence of this added spike. The LIAF neuron (right) generates an output spike within a few milliseconds of the added input spike (compare right panels in *A* and *B*). This particular output spike represents a correct detection.

Fig. 2. Performance characterization of a leaky integrate-and-fire neuron (LIAF) as a detector. *A.* False alarm rate versus threshold level of the LIAF model. *B.* Operating characteristic (OC) curve shows the probability of correct detection as a function of false alarm rate, when a single spike is added to an afferent spike train of *A. albifrons*. The detection probability for small false alarm rates (< 1 Hz) is nearly 1, indicating that these neurons are extremely reliable detectors. The reset value of the integrator makes little difference (circles: reset to 0; lozenge: no reset).

Fig. 3. Bursting activity is a reliable indicator of the presence of a weak signal. *A.* Detection probability versus threshold, showing the total number of detections (circles) when there is no integrator reset. This is further partitioned into probabilities of single hits (squares) and bursts of hits (lozenge). *B.* Fraction of single hits (squares) and bursts (lozenge) for detections (open symbols) and false alarms (closed symbols). The proportion of bursts during false alarms is significantly lower than single hit false alarms, whereas for detections, the opposite is true for a wide range of thresholds. This indicates that bursts are reliable indicators of a true hit, whereas false alarms are more likely to be single hits.

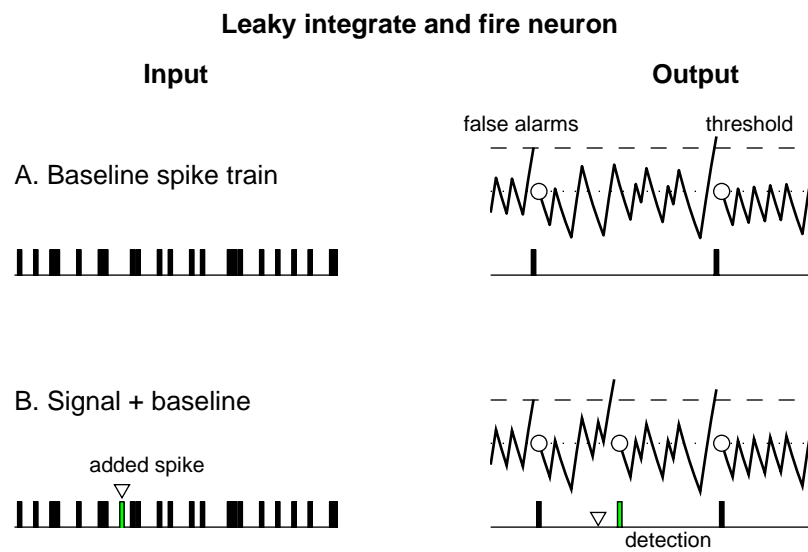


Figure 1

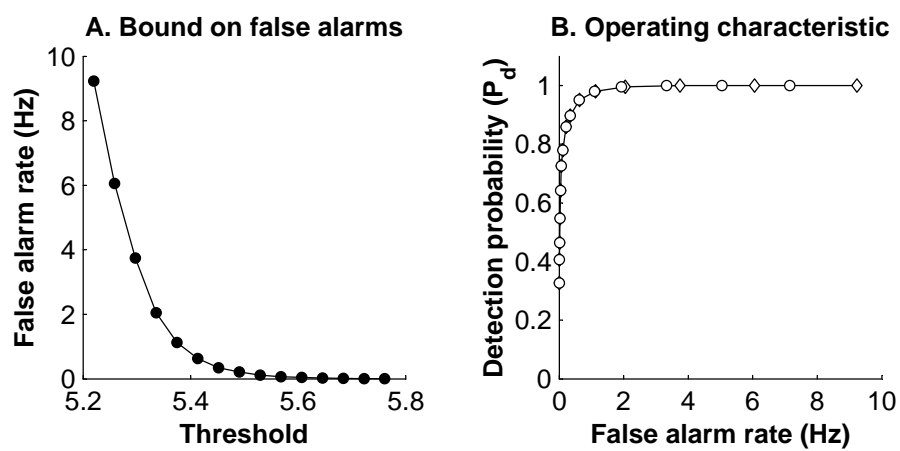


Figure 2

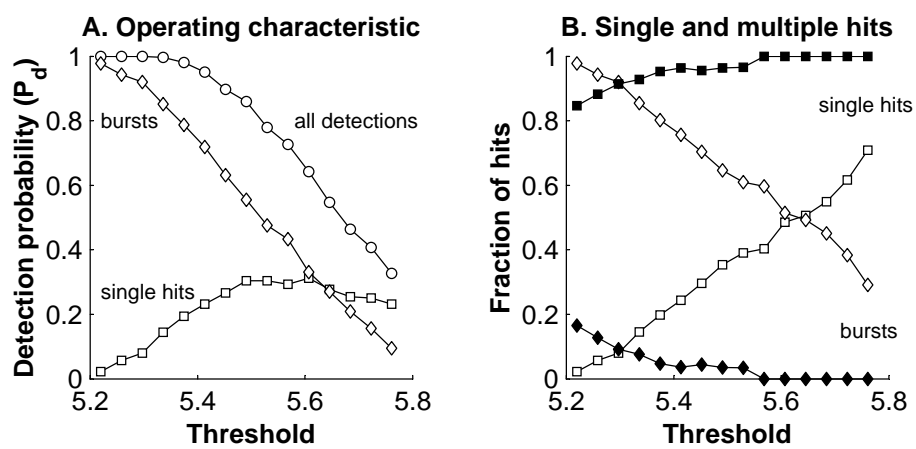


Figure 3