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 sensory neuronal processing. Behaviorally relevant signals from the environment are often encoded as perturbations of on-going spiking activity in primary afferents, but little is known about how they are detected when embedded in noisy neural activity. Here, we show that a biologically plausible neuron, 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 a false alarm (or false positive) results in isolated spikes. The methods are illustrated by an application to primary 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 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.

Weakly electric fish are nocturnal teleosts that navigate and hunt in the dark muddy waters of tropical rivers in Africa and South America. They use a weak self-generated electric organ discharge (EOD) to generate a short-range field for locating objects. Distortions induced by

objects cause amplitude modulations in the field, which are then transduced by electroreceptors on the skin of the fish, and transmitted by P-type afferent neurons to higher brain centers. These modulations cause changes in baseline firing rates of the afferents and provide cues for detecting objects such as small prey. Earlier we have shown that the afferents have very high firing rates and are very regular, allowing the detection of weak signals with high sensitivity [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 in the spike train 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

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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

The baseline activity of P-type afferent units in *Apteronotus albifrons* have statistical properties that are similar to those of a related species *Apteronotus leptorhynchus* [7]. In particular, *A. albifrons* has the same rather remarkable regularity as *A. leptorhynchus* as demonstrated by the strong anti-correlations between adjacent interspike intervals (ISIs). The main differences between the P-type units of the two species are that *A. albifrons* shows somewhat higher regularity and higher firing rates measured across a population.

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). When the afferent spike train was perturbed by the addition of a spike, the IAF neuron had to detect this added spike by generating a hit (i.e., a threshold crossing) within 10 EOD cycles. 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. To obtain an understanding of the actual number of false alarms, it should be noted, that for thresholds larger than 5.6, less than 11 false alarms were generated in about 280000 EOD cycles (264 s, false alarm rate about 0.04 Hz)

It is not possible to simultaneously increase the probability of detection while decreasing the false alarm rate. Thus, raising the threshold can reduce the false alarm rate but also lower detection probability (Fig. 2). One way to overcome this problem is to use bursting activity to distinguish between detection 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). This provides a convenient mechanism for distinguishing a true detection from a false alarm. 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. It should be noted that output spikes within a burst are typically one mean (afferent) ISI or less apart.

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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.

Acknowledgements

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Figure captions

Fig. 1. An integrate-and-fire (IAF) neuron can function as a signal detector. *A*. Baseline spike train (noise, left panel) is filtered by a leaky integrator (right). A threshold crossing (dashed line) results in a spike, and the neuron resets to the mean value of the input (dotted line). This is the spontaneous firing activity of a downstream neuron and signals a false alarm. *B*. A spike, denoting the signal, is added at an arbitrary location (triangle), and the task for the downstream IAF neuron is to detect the presence of this added spike. The IAF neuron (right) generates a spike within a few milliseconds of the added spike (compare right panels in *A* and *B*). This is a correct hit, i.e., a detection. The number and locations of false alarms are unchanged. Detection performance is measured as the proportion of detections for a given rate of false alarms (see text).

Fig. 2. Performance characterization of a leaky integrate-and-fire neuron (LIAF) as a detector. *A.* The false alarm rate (ordinate) is the number of threshold crossings in the absence of a signal, per unit time and is uniquely determined by the threshold (abscissa) of the LIAF. At high thresholds, the number of false alarms is small. *B*. Operating characteristic (OC) curve measures the probability of correct detection (ordinate) as a function of false alarm rate (abscissa) when a single spike is added to an afferent spike train of *A. albifrons* (see Fig. 1). The detection probability for small false alarm rates (< 1 Hz) is nearly 1, indicating that these neurons are extremely reliable detectors. The resetting value of the integrator makes little difference to the performance except at high false alarm rates (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.
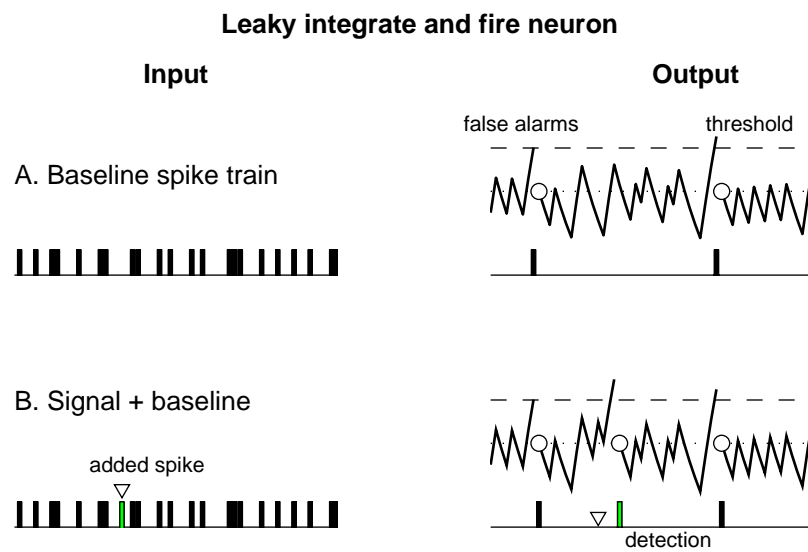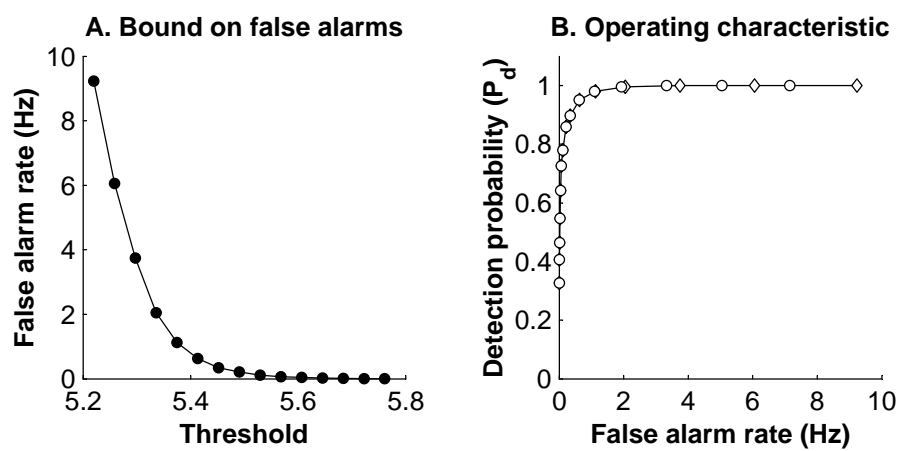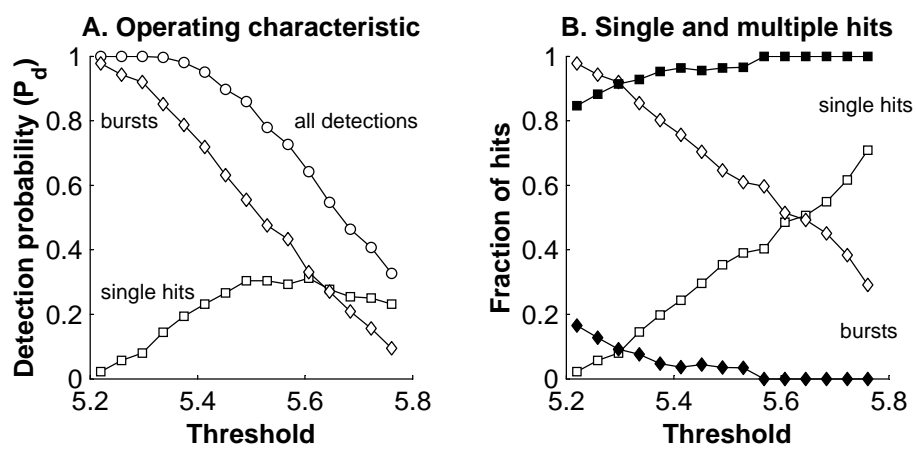
Leaky integrate and fire neuron

Input   **Output**

A. Baseline spike train

false alarms   threshold

B. Signal + baseline

added spike

detection

Figure 1

A. Bound on false alarms

B. Operating characteristic

Figure 2

A. Operating characteristic

B. Single and multiple hits

Figure 3