

Estimating the Afferent and Efferent Temporal Interval Entropy of Neuronal Discharge for Single Spike Trains

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Introduction:

Several approaches exist for estimating the signaling capacities of spike trains. These approaches are typically limited either by reliance on explicit coding and decoding models or by the type of noise assumed (reviewed by Borst & Theunissen, 1999). A recent development, that of the ‘direct’ method (de Ruyter van Steveninck et al., 1997; Strong et al., 1998), relies on counting the number of different temporal patterns in a neuronal spike train evoked by a range of stimuli to estimate signal entropy. Unfortunately, its practical application may be significantly limited by the ‘sampling’ problem associated with finite data sets, i.e. the impracticality of collecting the large data sets required to accurately estimate the occurrence probability of activity patterns, particularly long ones; and the ‘binning’ problem, i.e. how to make a principled choice for the temporal resolution at which an analysis should be performed. These problems are likely to become increasingly acute as the application of such methodologies moves from primary sensory pathways and areas to post-sensory associational or poly-modal, supra-modal, and motor areas.

To circumvent the problems associated with the direct method we have proposed (ms. in preparation) the analytic-distribution interval method (for convenience referred to as the temporal interval method, or just the interval method when application to temporal data is unambiguous). It is based on the idea that extrapolation to infinitely long data sets can best be carried out at the level of interspike interval data rather than at the level of the computed entropy. By fitting the observed interval data to a suitable continuous theoretical distribution, extrapolation to long intervals and long data records are both effectively carried out in compliance with the observed impulse behavior of the cell type under consideration. The procedure provides a so-called ‘interval’ entropy measure which is distinguished from previous entropy measures by the emphasis on the distribution of intervals observed for either afferent or efferent impulse activity.

Methods

The Temporal Interval Method: The steps are now described for calculation of the efferent, H_e , and afferent, H_a , entropies of spike discharge and activation for a single neuron. They are illustrated in Figure 1. H_e is obtained by assuming that (i) a spike train consists of a sequence of symbols composed of interval-spike pairs where each temporal interval following an initial spike is terminated by spike occurrence, (ii) the distribution of spike intervals in an arbitrarily long spike train can be estimated by fitting (by minimization of the RMS error) a sum of one or more suitable continuous analytic probability distribution functions to the observed discrete cumulative spike interval distribution, and (iii) the entropy contributed by spike timing can be calculated from the continuous probability distribution for an appropriate choice of temporal resolution, Δt , by dividing the continuous distribution into bins of width Δt , calculating the probability of each bin as a definite integral of the underlying continuous distribution over the width of the bin, and then

calculating the Shannon (1948) entropy

$$H = -\sum p_i \log_2 p_i \quad (1)$$

from the resulting bin probabilities p_i . To keep the set of possible messages finite, the sum is truncated after N terms, when the p_i have become sufficiently small to achieve numerical convergence, i.e. $\sum p_i \approx 1$.

A similar procedure is used to calculate the afferent entropy, H_a . Here, the discrete interval probability distribution of step (ii) is provided by the set of intervals obtained by merging the impulse patterns conveyed by each afferent fiber during a given spike train into a single impulse stream. (This procedure may need to be modified depending on the integrative properties of the neurons' dendritic tree, for a detailed treatment of signals in noisy cable structures see Manwani & Koch, 1999). The interval methodology gives the entropy in bits/event where for H_a the event is a single afferent impulse and for H_e it is a single spike. Thus, the total afferent entropy is

$$H_{a(\text{tot})} = H_a (\text{bits/impulse}) \times N_{\text{aff}} \times \text{impulses/s per fiber}$$

where N_{aff} is the number of afferent fibers converged at the neuron.

Similarly, the total efferent entropy is

$$H_{e(\text{tot})} = H_e (\text{bits/spike}) \times N_{\text{eff}} \times \text{neuronal discharge rate (spikes/s)}$$

where for simplicity N_{eff} is assumed to be unity and represents a single axon.

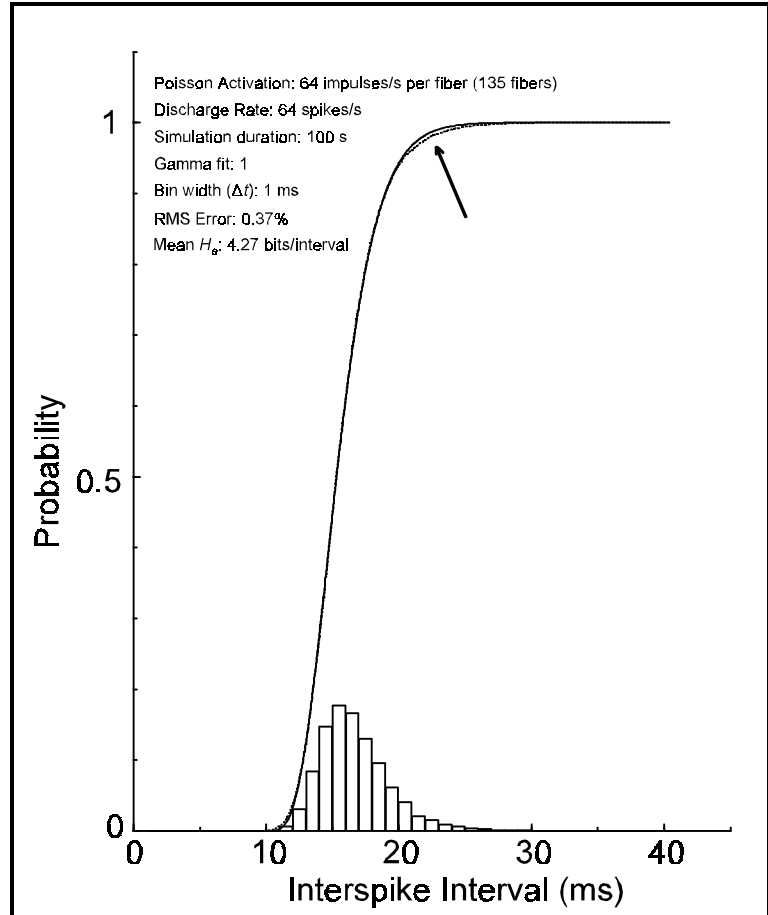


Figure 1: Fit of a theoretical distribution (solid line) to the observed interval data (dashed line) for a simulated spike train. Details given in legend. The cumulative interval histogram was well fit with a single incomplete gamma function. The arrow indicates the increased probability of longer intervals obtained with the theoretical interval distribution. The histogrammed data are given for comparison.

Source Data: Simulated spike trains were obtained from a model cerebellar Purkinje neuron (PC) (Coop & Reeke, 2001a) in response to two activation paradigms that have already been extensively investigated (Coop & Reeke, 2001b). In the stochastic or ‘Poissonian’ case, impulse activity on each afferent fiber is generated as a Poisson point process with impulses temporally uncorrelated across fibers. In the ‘pulsed’ case, the stimulus is composed of pulse ‘packets’ delivered with a fixed interpulse interval. Each packet is composed of a given number of impulses

distributed as a Gaussian in time across the afferent fibers (Coop & Redman, 1995; Coop & Reeke, 2001b). The temporal jitter of impulses within each pulse is controlled by the coefficient of variation (CV=standard deviation/mean) of the Gaussian. The number of fibers contributing impulses to the pulse packet controls the discharge rate.

Results

As an example of the interval entropy method Figure 2 shows $H_{a(tot)}$ and $H_{e(tot)}$ calculated for a simulated 100 s spike train generated by either Poissonian (filled circles) or pulsed (unfilled circles) stimulation at a rate of 64 impulses/s per fiber and a temporal resolution, Δt , of 0.5 ms. We have previously shown that for pulsed stimulation when the model PC is contacted by an appropriate number of afferent fibers the mean discharge rate becomes frequency locked to the stimulus rate (given in impulses/fiber) and one spike is emitted in response to a single impulse on all afferent fibers (Coop & Reeke, 2001b). At this equivalence frequency (here 64 impulses/s) the cell discharge CV drops

dramatically. Figure 2A shows that, as the number of afferent fibers is increased above that required to achieve frequency locking (95 fibers), $H_{a(tot)}$ is reduced from about 1708 ± 39 to 1241 ± 30 bits/s and is effectively independent of fiber number. This is clearly not the case for Poissonian stimulation where $H_{a(tot)}$ shows a monotonic decline to zero with increased PC discharge rate. Alternatively, Figure 2B shows $H_{e(tot)}$ to asymptote at a value of approximately 270 ± 25 bits/s for discharge rates above the equivalence frequency for Poissonian stimulation (64 spikes/s at 135 afferent fibers). However, $H_{e(tot)}$ for the pulsed case does not reach a maximum until a discharge rate of approximately 250 spikes/s is reached. Also notable is the frequency locking evidenced by the drop in $H_{e(tot)}$ at cell discharge rates of 64, 128 and 256 spikes/s (the equivalent discharge rates in the Poissonian case were obtained with 135, 210, and 415 fibers, respectively). These drops were not evident when the direct method was applied to the same data (not shown). We are currently analyzing data for other stimulation rates and expect to present these results at the time of the conference.

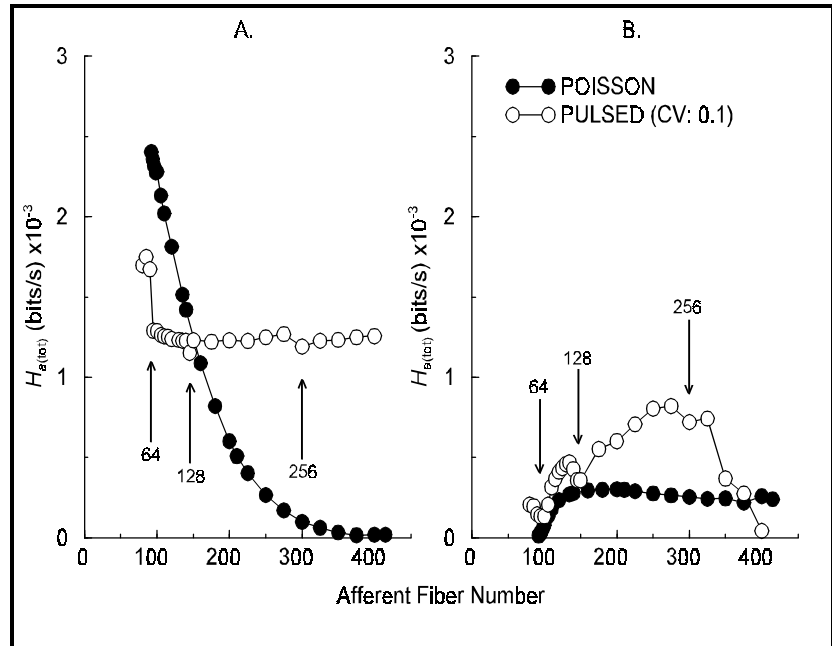


Figure 2: Total afferent, $H_{a(tot)}$, and efferent, $H_{e(tot)}$, interval entropies for a simulated spike train generated by stimulation of a model Purkinje cell at a mean rate of 64 impulses/s per fiber with either a Poissonian or pulsed activation process. Arrows indicate discharge rates of 64, 128, or 256 spikes/s for the pulsed case. See text for details.

Discussion

We have previously shown (ms. in preparation) that the entropy estimates obtained with the direct method are stimulus dependent in a way that may not accurately reflect the timing properties of neuronal discharge. The disparity between the entropy estimated for neuronal discharge by the direct method and the interval method may be attributed to the fact that the estimate provided by the former is based on an extrapolation to infinite word length which may incorrectly estimate the number of long words. We have shown this to be particularly likely to occur when neuronal discharge variability changes from random and Poisson-like to the more periodic activity associated with increased discharge rates or entry into regimes of periodic bursting.

Here, we have extended the interval method and illustrated its value for estimation of the entropy of the activation process for a single model cell. We expect this methodology will provide a valuable tool for exploration of the entropy fluxes and information transmitted by simulated cells and circuits. The simplification of treating all the inputs to a neuron as a single impulse stream interleaved onto one afferent fiber may be particularly useful in the treatment of real neurons, either *in vivo*, or in culture or slice preparations.

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