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

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Abstract

We define a biological communication system at the level of a single neuron and quantify the temporal variability of afferent and efferent impulse patterns by means of an interval entropy measure. Two signal transmission conditions which bound a physiologically plausible range of transmission possibilities are explored. The number of efferent synapses is predicted by matching estimates of the mean efferent entropy to the total afferent entropy.

Key words: Cerebellum; Purkinje Cell; Model; Timing; Entropy.

1 Introduction

The application of information theory to the analysis of neural communications systems is predicated on the mapping of theoretical components to the biological structures subserving neural function. Recently, several different definitions of signal source and destination have been employed, e.g. [6,8]. Here we present a communication system defined at the level of the single neuron. It extends from a source provided by active afferent fibers to a destination composed of the efferent synaptic terminals of a given cell. The input/output relations of this model system are explored by means of the temporal analytic-distribution interval method [9] which provides estimates of the entropy of afferent and efferent impulse activity.

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The interval methodology is based on the idea that by fitting observed interval data to a suitable continuous analytic distribution, extrapolations to long intervals and long data records are both effectively carried out in compliance with the observed impulse activity. The procedure provides a so-called "interval entropy" measure which can be used to quantify the temporal variability of afferent impulse activity and evoked cell discharge under the assumption that intervals in a sequence are uncorrelated. The approach is demonstrated by application to a composite cerebellar Purkinje cell model [4].

2 Methods

The relation between a theoretical communication system comprising five elements including a source, transmitter, channel, receiver, and destination [12] and the analyzed biological communication system is given in Figure 1. The messages in the biological system consist of the discrete temporal intervals which exist between successive impulses on individual afferent fibers.

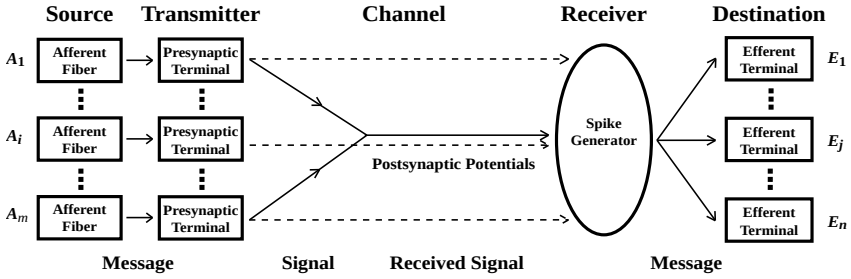

Fig. 1. Relation between the theoretical and the modeled biological communication system. Dashed lines indicate preservation of interval duration for impulse sequences occurring at individual afferent synapses as might occur when multiple dendrites attach independently to the soma (non-interleaved case). Solid lines indicate the interleaving of impulse times as might occur when dendritic branches converge to form a single dendritic trunk (interleaved case).

Calculation of the interval entropy, H_I, proceeds by assuming (i) the distribution of intervals in an arbitrarily long sample can be estimated by fitting a sum of one (Q, eq. 1) or more suitable continuous analytic probability distribution functions to an observed discrete cumulative interval probability distribution (O) by minimization of the RMS error (E, eq. 2) for a total of M intervals. For the case of a single incomplete gamma function

$$Q(x;a,s,\tau) = \gamma\left(\frac{x-s}{\tau}, a\right) \equiv \frac{1}{\Gamma(a)} \int_0^{\left(\frac{x-s}{\tau}\right)} t^{a-1}e^{-t}dt, \ (a,s>0) \qquad (1)$$

where a, s, and τ are the order, time axis shift, and time scaling parameters, respectively, and

$$E = \left\{ \frac{1}{M} \sum_{j=1}^{M} \left[O(x_j) - Q(x_j; a, s, \tau) \right]^2 \right\}^{1/2} \times 100\%. \tag{2}$$

The probabilities (p_i) that interspike intervals lie in the intervals $x = [i\Delta t, (i+1)\Delta t], i = 1, \ldots N$ can be calculated from the analytic distribution for an appropriate choice of temporal resolution (Δt) where

$$p_i = \Big[Q((i+1)\Delta t; a, s, \tau) - Q(i\Delta t; a, s, \tau) \Big]. \tag{3}$$

The interval entropy is obtained from the discrete formulation given by Shannon [12]

$$H_I = -\sum_{i=1}^{N} p_i \log_2 p_i. \tag{4}$$

The sum is truncated when $1 - \sum_i p_i < \epsilon$, where ϵ is the required tolerance.

The mean afferent interval entropy, H_{A}, may be calculated by assuming the received signal is a temporally interleaved composite of the transmitted signal (Fig. 1, converged unbroken lines). This treatment is justified when impulses received at presynaptic terminals have equivalent effects at the soma, as for the one-compartment case studied here. Other treatments may be required when synapses are not equivalent. An alternative non-interleaved case is illustrated in Figure 1 (dashed lines) and described in the figure caption. If it is assumed neuronal activity is reliable [3,7,1,13,11] and that each transmitted signal always gives the same received signal with no two transmitted signals producing the same received signal, any distortion introduced by signal mismatch may be corrected at the receiver and the channel is noise free [12].

Simulated spike trains were obtained from a model cerebellar Purkinje neuron (PC) [4] in response to two extensively investigated activation paradigms [5]. In the stochastic or 'Poissonian' case, the impulse activity across afferent fibers is temporally uncorrelated. Alternatively, in the 'pulsed' case the stimulus is composed of pulse 'packets' delivered with a fixed interpulse interval. The impulses within each packet are distributed as a truncated Gaussian in time across the afferent fibers and their temporal correlation is determined by the coefficient of variation (CV = standard deviation/mean) of the Gaussian. Each afferent fiber contributes a single impulse to a packet. In both paradigms the number of active fibers controls cell discharge rate. Neither afferent transmission failure nor quantal variation is included [6], but the amplitude of each postsynaptic potential is modulated by paired pulse facilitation according to the model of Atluri [2]. The impulse rate is identical

for all fibers, held constant for the duration of a simulation, and given as the mean rate/s per fiber.

3 Results

The total afferent interval entropy per second is given by

$$H_{A(\mathrm{tot})} = H_{\mathrm{A}} \times N_{\mathrm{aff}} \times \text{impulse rate},$$

where N_{aff} is the afferent fiber number. For the interleaved case under Poissonian stimulation, $H_{A(\mathrm{tot})}$ increases as the afferent stimulation rate is raised. However, doubling the stimulus rate from 64 to 128 impulses/s has little effect (Fig. 2A). Alternatively, under pulsed stimulation $H_{A(\mathrm{tot})}$ is effectively independent of the stimulus rate (Fig. 2B).

In the absence of knowledge about efferent synapse number, the mean efferent interval entropy rate per second is given by

$$H_{\mathrm{E(r)}} = H_{\mathrm{E}} \times \text{discharge rate}.$$

Under Poissonian stimulation $H_{\mathrm{E(r)}}$ is little influenced by the stimulation rate and is maximal at a discharge rate of about 100–120 spikes/s (Fig. 2C). Alternatively, changing the rate of pulsed stimulation has little effect on $H_{\mathrm{E(r)}}$ for discharge rates below about 100 spikes/s (Fig. 2D). However, as the discharge rate increases, the magnitude of $H_{\mathrm{E(r)}}$ becomes increasingly sensitive to stimulation rates in the range of 64–128 impulses/s.

When the total number of efferent synapses made by a single neuron is unknown, by assuming that entropy equivalence is maintained throughout the system, it can be estimated as

$$E_{\mathrm{syn}} = H_{A(\mathrm{tot})} / H_{\mathrm{E(r)}},$$

where E_{syn} gives the number of efferent synapses required to match $H_{\mathrm{E(r)}}$ to $H_{A(\mathrm{tot})}$. In the Possionan interleaved case, there is a range of discharge rates for which less than one efferent synapse is sufficient to maintain entropy equivalence (Fig. 3A). This operating regime may be associated with the somewhat puzzling observation that transmitter release probabilities in many neurons are significantly less than the naively expected 1.0 [10]. Alternatively, in the interleaved case under pulsed stimulation, approximately 10 synapses are sufficient for entropy equivalence at a discharge rate of 40 spikes/s. At higher stimulation (64–128 Hz) and discharge rates (125–265 spikes/s) the number falls to 2.5–5.5 synapses (Fig. 3B).

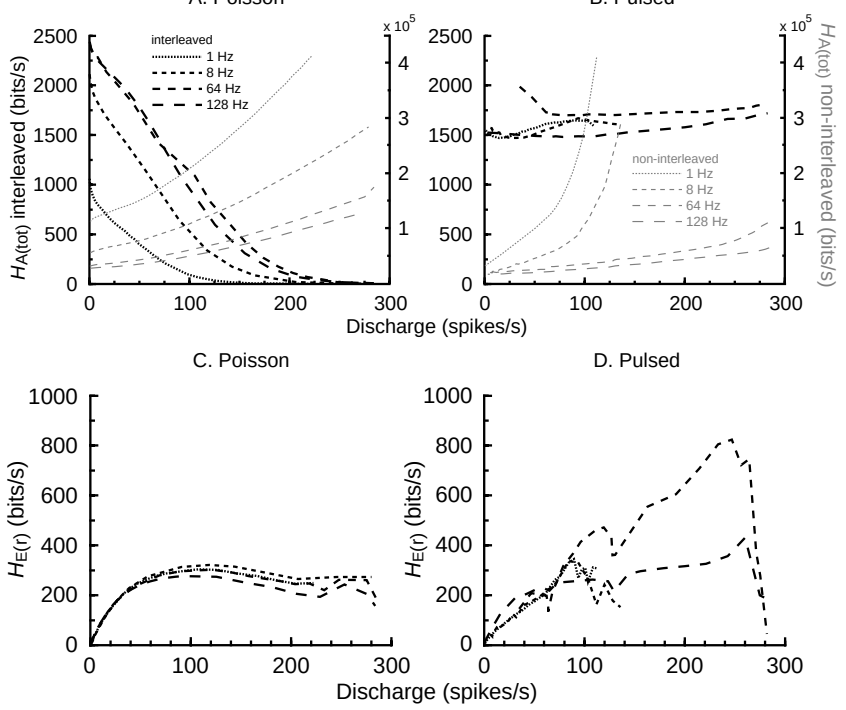

Fig. 2. Total afferent interval entropy, $H_{A(\mathrm{tot})}$ for the interleaved case under A: Poissonian and B: pulsed stimulation. Magnitude given by left axes. The equivalent non-interleaved cases (see Fig. 1) are also given (gray, magnitude given by right axes). Mean efferent entropy rate per second, $H_{\mathrm{E(r)}}$, for C: Poissonian and D: pulsed stimulation. Legends give stimulation rate. The legend in A applies to all panels. Legend in B applies to panels A and B.

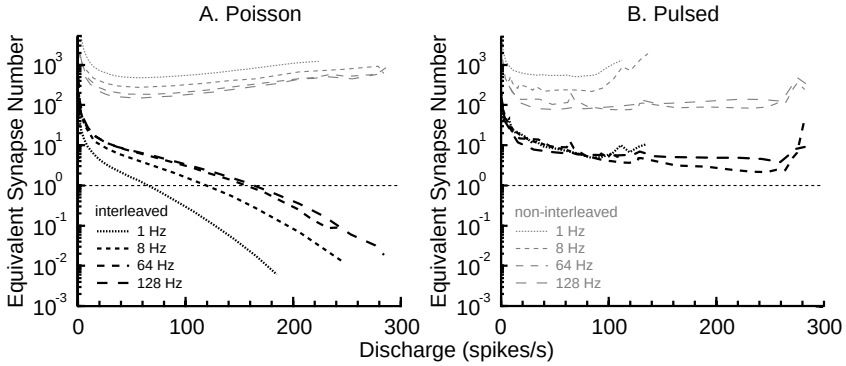

Fig. 3. Equivalent synapse number, E_{syn}, gives the number of efferent synapses required to match the mean efferent entropy rate per second, $H_{\mathrm{E(r)}}$, to the total afferent entropy, $H_{A(\mathrm{tot})}$, for the interleaved case (see Fig. 1). A: Poissonian, and B: pulsed stimulation Horizontal line indicates 1 efferent synapse. Also given are the equivalent non-interleaved cases (gray). Legends give stimulation rates, each applies to both panels.

4 Conclusions

The entropy of signal transmission within a neuronal communication system may be determined by synaptic connectivity. Conditions are identified for

which, under Poissonian stimulation, the total afferent ($H_{A(\mathrm{tot})}$) and efferent ($H_{E(\mathrm{tot})}$) entropies are matched with less than one efferent synapse. It is unlikely that this would occur under conditions of near-synchronous pulsed activation.

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