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Energy efficiency in a channel model for the spiking axon

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Abstract

We examine the spiking axon as a communication channel. We develop a first principles channel model that encompasses the noise in the axon, which manifests itself as spike jitter, and the power consumption, which arises from the activity of the $\text{Na}^+–\text{K}^+$ pump. This model enables us to examine the trade-off between the information rate and power consumption. Using parameters from the frog myelinated axon, we determine the spike rate that corresponds to the maximum energy efficiency. This spike rate is consistent with experimental observations, which suggests that neural communication may have developed to maximize energy efficiency rather than information rate alone.

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1. Introduction

Recently, several researchers have suggested that energy efficiency is a guiding constraint in the evolution of neural systems [3,9,2,7]. In this paper, we examine the energy efficiency of spike communication over a myelinated axon. We determine the most energy efficient way to communicate information and compare this result to experimental observations. We also explore how fundamental biophysical parameters contribute to the energy efficiency by means of a scaling analysis.

Energy efficiency can be expressed as a function of *signal properties*, such as the interspike interval (ISI) distribution, and *channel properties*, such as the behavior of ion channels. In Section 2, we set up the optimization problem that yields the signal

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properties corresponding to optimal usage of the axon. In Section 3, we determine the channel properties by developing biophysical models of the spike jitter and power consumption. In Section 4, we describe the optimization results and the scaling analysis. In Section 5, we discuss the results and conclude the paper.

2. Optimizing signal properties for energy efficiency

In this work, we examine the myelinated axon as a communication channel. The input X is the spike train that is generated at the soma. The output Y is the spike train that emerges from the axon into the presynaptic region. Our energy efficiency metric \mathcal{E} (units of bits/ATP) is given by the ratio of the information rate through the axon \mathcal{R} (units of bits/s) and the power consumption of the axon P (units of ATP/s) [9]:

$$\mathcal{E} = \mathcal{R}/P. \quad (1)$$

We do not know a priori what aspect of the spike trains X and Y carry information. An upper bound on the amount of information a spike train can carry can be determined by considering solely the ISIs, as a list of successive ISIs is sufficient to reconstruct the spike train in its entirety [1]. Our work makes use of this upper bound, so the signal is the ISI, and the noise is anything that alters the ISI, which we term ISI jitter.

In this context, the mutual information (in bits/symbol) is given by

$$I(X; Y) = h(Y) - h(Y|X) = h(Y) - h(N) \quad (2)$$

where $h \cdot$ indicates differential entropy. To obtain the upper bound on the information rate, we make the assumption that the ISIs are independent. In this case, the information rate \mathcal{R} is simply the product of the mutual information and the spike rate λ (the number of symbols per second):

$$\mathcal{R} = \lambda[h(Y) - h(N)]. \quad (3)$$

The energy efficiency \mathcal{E} becomes

$$\mathcal{E} = \lambda[h(Y) - h(N)]/P(\lambda), \quad (4)$$

where we write $P(\lambda)$ to show that the power consumption is a function of spike rate.

The maximum energy efficiency \mathcal{E}^* is given by

$$\mathcal{E}^* = \max_{f_Y(\lambda)} \lambda[h(f_Y(\lambda)) - h(f_N)]/P(\lambda) = \lambda^*[h(f_Y^*(\lambda^*)) - h(f_N)]/P(\lambda^*), \quad (5)$$

where $f_Y^*(\cdot)$ and λ^* are respectively the ISI distribution and mean spike rate that realize the maximum energy efficiency. In order to maximize \mathcal{E} , $h(f_Y)$ must be as large as possible. Therefore, we choose the distribution that maximizes $h(f_Y)$ for a fixed spike rate λ . In the presence of a refractory period t_{ref} , f_Y^* is given by a shifted exponential interspike interval distribution with corresponding entropy [1]

$$h(f_Y^*) = \log_2[e(1 - \lambda^* t_{\text{ref}})/\lambda^*]. \quad (6)$$

The maximum energy efficiency becomes

$$\mathcal{E}^* = \lambda^* \{ \log_2[e(1 - \lambda^* t_{\text{ref}})/\lambda^*] - h(f_N) \}/P(\lambda^*). \quad (7)$$

Now, λ^* is the only remaining free parameter. In order to find its value, we need to fill in the (unknown) fixed parameters of Eq. (7). They are f_N , the distribution of the ISI jitter, and $P(\cdot)$, the relationship between the power consumption and the spike rate. To do this, we must examine a biophysical model of the axon.

3. A channel model for the myelinated axon

We formulate a model of the ISI jitter in the myelinated axon based on ion channel stochasticity at the node of Ranvier [12]. The stochastic behavior of the ion channel population can be described by binomial statistics: For N channels, each with a single channel current \bar{i} and probability of being open p , the coefficient of variation (CV) of the channel current is given by

$$\sigma_I/\mu_I = \sqrt{N\bar{i}^2 p(1-p)/N\bar{i}p} \approx 1/\sqrt{Np} \quad (p \ll 1). \quad (8)$$

Variability decreases as the number of ion channels increases, as the stochastic behavior of individual ion channels is averaged out.

Analysis of the mechanism of spiking at the node of Ranvier reveals that the spike time is vulnerable to the stochastic Na^+ current only during a very brief “stochastic interval” during the rising phase of the action potential (Fig. 1(a) and (b)). The duration of this interval is given by $T = C\theta/I$, where C is the node capacitance, θ is the range of voltages that delimit the interval, and I is the stochastic Na^+ current during the interval. Because the time constant of the channel noise is large compared to the threshold crossing time (Fig. 1(c)), we model I as constant during a particular interval but variable *between* intervals.

Because I is a binomial r.v. and N is large, we can approximate I as Gaussian. Then the distribution of T is given by the inverse of a Gaussian r.v. [8,13]. This yields a spike time distribution that is approximately Gaussian with standard deviation $\sigma_T = C\theta\sigma_I/\mu_I^2$ (derivation omitted) where μ_I and σ_I are the mean and standard deviation of the current during the rising phase of the action potential. The CV of the spike time is given by

$$\sigma_T/\mu_T = (C\theta\sigma_I/\mu_I^2)/(C\theta/\mu_I) = \sigma_I/\mu_I \approx 1/\sqrt{Np}. \quad (9)$$

This means that the CV of the spike time is equal to the CV of the ion channel noise, implying that the scaling behavior of ion channel noise extends to spike time variability.

We can relate the spike jitter at a single node to the ISI jitter for the entire fiber by $\sigma_{\text{ISI}} = (2M)^{1/2}\sigma_T$ where M is the number of nodes in the fiber. The factor of 2 arises because the interspike interval is made up of two spikes. The entropy of the ISI jitter distribution, $h(f_N)$, is given by the entropy of a Gaussian distribution with variance σ_{ISI}^2 .

We can test the validity of the spike jitter model by comparing it to measured values of ISI jitter in the frog myelinated axon. Using values of θ , μ_I , and σ_I^2 from Hodgkin–Huxley simulations of the node of Ranvier, we obtain $\sigma_{\text{ISI}} = 35 \mu\text{s}$. The only measurement of ISI jitter in this system was made by Lass and Abeles [6], who

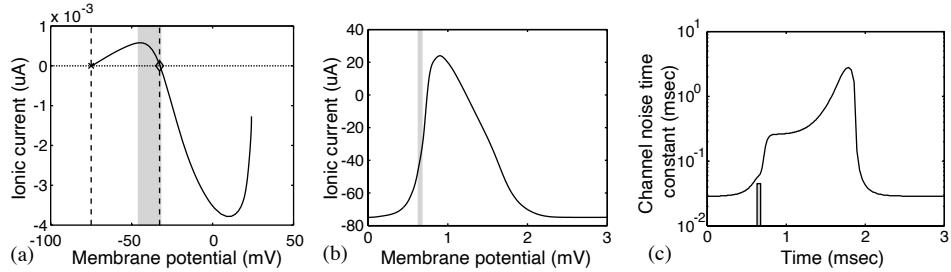


Fig. 1. The stochastic behavior of Na^+ channels is only relevant during a brief interval. Data generated by a Hodgkin–Huxley simulation. (a) I – V curve of the rising phase of the action potential. The \times denotes a stable equilibrium point, corresponding to the resting state, and the \diamond denotes an unstable equilibrium point, corresponding to the spiking threshold [10]. The region of negative conductance is indicative of the positive feedback action of the Na^+ channels. We model the spike time as vulnerable to Na^+ channel noise only during the “stochastic interval” defined from the start of the positive feedback to the spiking threshold (shaded area). (b) The action potential with the stochastic interval (shaded region) superimposed. (c) The Na^+ channel noise time constant during the action potential (derived from a kinetic model [5]). The gray box represents the duration of the stochastic interval.

obtained $\sigma_{\text{ISI}} = 6 \mu\text{s}$. There are many reasons for the discrepancy, including uncertainty in the number of ion channels and variability across different frog species.

In the myelinated axon, there are two sources of power consumption: the energy expended by the $\text{Na}^+–\text{K}^+$ to counteract the passive leak of ions across the membrane (resting cost) and the energy used by the pumps to restore the concentration gradients following an action potential (signaling cost). Power consumption can be expressed as

$$P = a\lambda + b, \quad (10)$$

where a is the ATP expended per spike, λ is the spike rate, and b is the ATP expended per second due to resting costs. The values of these constants can be determined by considering the stoichiometry of the $\text{Na}^+–\text{K}^+$ pump [14].

4. Results

The expression for the maximum energy efficiency becomes

$$\mathcal{E}^* = \lambda^* \{ \log_2 [e(1 - \lambda^* t_{\text{ref}})/\lambda^*] - (1/2) \log_2 (2\pi e \sigma_{\text{ISI}}^2) \} / M(a\lambda^* + b). \quad (11)$$

The models of Section 3 enable us to derive the values for all of the channel parameters in Eq. (11) (given in the caption of Fig. 2). The only remaining free parameter is the optimal spike rate, which is found numerically. The information rate and energy efficiency are plotted as functions of spike rate in Fig. 2(a) and (b), respectively. The maximum information rate, i.e. the information capacity, is given by the peak of the curve in Fig. 2(a), whereas the maximum energy efficiency is given by the peak of the curve in Fig. 2(b). It is clear that spike rates corresponding to the two maxima are distinct.

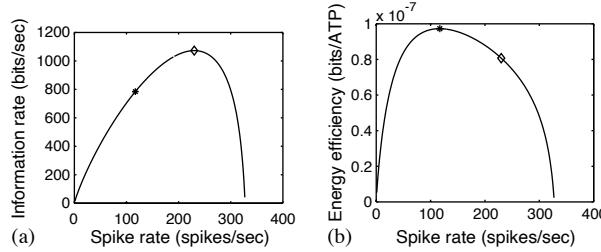


Fig. 2. Information rate and energy efficiency as a function of spike rate. Parameters as follows: $\sigma_{\text{ISI}} = 35 \mu\text{s}$, $t_{\text{ref}} = 3 \text{ ms}$, $a = 6.42 \times 10^5 \text{ ATP/spike}$, $b = 3.69 \times 10^7 \text{ ATP/s}$, $M = 72$ nodes. The point corresponding to the maximum energy efficiency is denoted by the * (117 Hz), and the point corresponding to the information capacity is denoted by the ◇ (230 Hz). (a) Information rate as a function of spike rate. (b) Energy efficiency as a function of spike rate.

We are also interested in understanding of how fundamental biophysical parameters affect the energy efficiency. We must perform this analysis with caution; we cannot vary parameters at will because the kinetics of the Hodgkin–Huxley equations are voltage-dependent. Therefore, the membrane potential of the axon must remain constant while the parameters are varied. Rushton's *principle of corresponding states* provides us with a way to do this: we scale the fiber diameter, nodal area, and inter-node distance by a factor S , while keeping all of the *specific* properties of the fiber constant [11].

The absolute number of ion channels increases with S , so ISI jitter goes as $S^{-1/2}$ (Eq. (9)). This gives rise to a logarithmic increase in the information rate. The power consumption is proportional to the number of ions displaced, which increases proportionally with the nodal area and in turn S . These trends alone are not a priori sufficient to establish the scaling behavior of \mathcal{E}^* because the spike rate λ is a free parameter. Therefore, for each value of S , we numerically determined \mathcal{E}^* and λ^* . Over the scales we examined ($S = [0.1, 10]$), λ^* had the relatively narrow range of 95 and 135 Hz. If we approximate λ as constant, then it becomes clear that as S increases, the denominator P^* grows faster (linearly) than the numerator \mathcal{R}^* (logarithmically), causing \mathcal{E}^* to decrease. These trends were verified numerically.

5. Discussion and conclusions

We have found that energy efficient use of the spiking axon corresponds to a shifted exponential ISI distribution with a mean spike rate of 117 Hz. In order to compare the form of the distribution with neurophysiological data, we need to consider the spiking statistics of the frog myelinated axon over the ensemble of natural behaviors. While this may prove difficult, the mean spike rate is much easier to measure. Indeed, spike rates of 100 Hz are typical of the frog myelinated axon [4], suggesting that this system may have developed to maximum energy efficiency rather than information rate alone.

We examined the scaling behavior of this system and found that despite the fact that jitter is reduced by increasing the number of ion channels participating in spike

generation, the benefits of having more ion channels does not outweigh the accompanying power consumption cost. Our results can be interpreted to mean that for transmitting information over proportional distances, smaller axons are more energy efficient.

In this work, we examined axonal communication only. Spike communication entails the transformation of analog information to and from spikes, and the noise and power consumption associated with these processes can considerably affect the energy efficiency. In order to gain a more complete understanding of spike communication, we are currently performing similar analyses of spike encoding and decoding.

Acknowledgements

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