Upper limit on the thermodynamic information content of an action potential

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Abstract

In computational neuroscience, spiking neurons are often analyzed as computing devices that register bits of information, with each action potential carrying at most one bit of Shannon entropy. Here, I question this interpretation by using Landauer's principle to estimate an upper limit for the quantity of thermodynamic information that can be dissipated by a single action potential in a typical mammalian neuron. I show that an action potential in a typical mammalian cortical pyramidal cell can carry up to approximately $3.4 \cdot 10^{11}$ natural units of thermodynamic information, or about $4.9 \cdot 10^{11}$ bits of Shannon entropy. This result suggests that an action potential can process much more information than a single bit of Shannon entropy.

1 Introduction

> *"The fundamental constraint on brain design emerges from a law of physics. This law governs the costs of capturing, sending, and storing information. This law, embodied in a family of equations developed by Claude Shannon, applies equally to a telephone line and a neural cable, equally to a silicon circuit and a neural circuit."* – Peter Sterling and Simon Laughlin [1]

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Many hypotheses and theories analyze spiking neurons as binary electrochemical switches [1-3]. At this level of abstraction, a spiking neuron can be treated as a physical memory system with two stable positions. The neuron may be firing, in which case its state is typically labeled as a one, or the neuron may be resting, in which case its state is typically labeled as a zero. Since the probability that a neuron will fire an action potential is influenced by many different unknown factors (such as the neuron's temperature, its firing threshold, its degree of connectivity with presynaptic inputs, and so forth), the distinction between a firing state and a resting state can be treated as a random variable in Shannon's theory of communication. Thus, in many models of neuronal information processing, a single action potential carries a Shannon entropy of

$$H = p\,\log_2\left(\frac{1}{p}\right) + (1-p)\,\log_2\left(\frac{1}{1-p}\right) \tag{1}$$

where H is the number of bits of Shannon entropy in an action potential, and p is the action potential's initial probability. At a maximum, $H = 1$ bit.

Many hypotheses and theories in information-theoretic neuroscience use the assumption that each action potential carries a quantity on the order of one bit of Shannon entropy to study information in the brain. For example, as one insightful analysis [1] writes about spike trains, "Using a standard currency (bits) we can ask like good engineers: how fast does a neuron send information (bits per second) and how efficiently (bits per spike)?" Another example of this assumption can be found in efforts to use action potentials to estimate the quantities of information processed in brain networks [4]. As a third example, it is commonly argued that laws of physics which place ultimate limits on the information storage capacity of physical systems, such as the Bekenstein bound [5] or the Bekenstein-Hawking area law [6], place such high limits on information content that they are irrelevant to the study of neuronal signaling.

The common assumption that an action potential can carry at most one bit of Shannon entropy from the initial segment of an axon to its terminal is certainly useful in many contexts. For this reason, the goal of this paper is not to argue that this assumption is necessarily erroneous or unjustified. Rather, I hope to explain why this interpretation of the action potential as a simple 1 or 0 may be misleading, at least from the perspective of fundamental physics. The next section discusses how the physical information content of an action potential is limited by the laws of thermodynamics.

2 Landauer's principle

> *"Thermodynamics is a mysterious subject. Powerful conclusions can materialize out of scant inputs, and it is forgiving of fundamental misconceptions about the underlying details. [...] Radical insights into new physics can come about through the study of thermodynamics."* – Ted Jacobson [7]

A profound development in the history of classical thermodynamics was the discovery of Landauer's principle, a form of information-energy equivalence [8]. Amazingly, this simple equation imposes a universal lower limit on the quantity of energy that must enter an environment when information is dissipated from any physical memory [9]. Landauer's principle states that, at approximately constant ambient temperature, the quantity of energy dissipated from a memory system into an environment increases linearly with respect to the quantity of thermodynamic information dissipated from the system:

$$\Delta E_{\text{env}} = -k_B T \Delta I_{\text{sys}} \tag{2}$$

where ΔE_{env} is energy dissipated into the environment, k_B is Boltzmann's constant, T is ambient temperature in Kelvin, and $-\Delta I_{\text{sys}}$ is information erased from a physical memory system. Here, $k_B = 1.38064852 \cdot 10^{-23}$ J/K. In physical neuroscience, it is convenient to follow Brillouin, Szilard, Maxwell, and others in defining a decrease in relative thermodynamic information to be an increase in relative thermodynamic entropy, so that $-\Delta I_{\text{sys}} = \Delta S_{\text{sys}}$ [10]. Thus, Landauer's principle can also be written

$$\Delta E_{\text{env}} = k_B T \Delta S_{\text{sys}} \tag{3}$$

where $\Delta S_{sys} = -\Delta I_{sys}$, since an observer's loss of relative thermodynamic information is equivalent to the generation of relative thermodynamic entropy. Because the removal of each natural unit of thermodynamic information from an observer's memory leads to a relative entropy increase of $\Delta S_{sys} = \mathit{ln\ 2}$ [8], a physical system erasing N natural units of thermodynamic information from its memory must dissipate at least

$$\Delta E_{\text{env}} = N k_B T \ \mathit{ln2} \tag{4}$$

units of energy, where N is the number of natural units of information dissipated into the environment, and *ln2* is the natural logarithm of 2. To find an upper limit on the number of natural units of information that a system can process irreversibly, we can simply divide an empirically measured value of energy dissipation from a system ΔE_{env} by the Landauer limit. A brain system can process at most

$$N = \frac{\Delta E_{\text{env}}}{k_B T \; ln2} \tag{5}$$

natural units of information. By imposing fundamental physical limits on energy and information dissipation, these equations provide convenient ways to measure the energetic efficiency of brain systems processing information. The next section provides a realistic estimate for N in equation (5) as applied to action potentials in typical neurons in mammalian brains.

3 Physical information in an action potential

To find an upper limit for the quantity of physical information that can be carried by each action potential in a typical mammalian cortical pyramidal cell, we begin by estimating the energy use of an action potential. Depending on species and specific cell subtype, a typical mammalian cortical pyramidal cell uses between about 10^6 and 10^{10} molecules of ATP per action potential, with each ATP molecule providing about 10^{-19} joules of useful energy [11-13]. Thus, a realistic upper bound for the numerator in equation (5) is

$$\Delta E_{\text{env}} \approx 10^{10} \; ATP \cdot 10^{-19} \; J/ATP \approx 10^{-9} \; J \tag{6}$$

joules of useful energy dissipated into the environment per action potential (not including initial heat dissipated during the conversion of ATP to ADP). Our next step is to find an empirically realistic value for the denominator in equation (5). For a neuron whose internal temperature is about $T = 310$ K, a realistic lower bound for the denominator of equation (5) is

$$k_B T \; ln2 \approx 1.38064852 \cdot 10^{-23} \; J/K \cdot 310 \; K \; ln2 \approx 2.97 \cdot 10^{-21} \; J \tag{7}$$

joules of energy dissipated into the environment per natural unit of information carried by an action potential. We can now divide the upper limit on energy dissipation by the lower limit on energy dissipation to find the greatest possible number of natural units of information that can be carried by an action potential. We find that an action potential can carry up to

$$N \approx \frac{10^{-9} \; J}{2.97 \cdot 10^{-21} \; J} \approx 3.37 \cdot 10^{11} \tag{8}$$

natural units of thermodynamic information. If we would prefer to measure these distinctions using Shannon entropy, we can also use the conversion factor 1 Shannon bit = $1/ln2$ natural units to find that an action potential can carry up to about $N \approx 4.86 \cdot 10^{11}$ bits of Shannon entropy.

In summary, we have arrived at an estimate for the ultimate thermodynamic limit on the quantity of information that can be carried by an action potential in a typical mammalian spiking neuron. By incorporating empirically realistic values of energy dissipation and temperature into the equation for Landauer's principle, we find that a single action potential in a typical mammalian pyramidal cell can carry up to about $N \approx 3.4 \cdot 10^{11}$ natural units of information, or about $4.9 \cdot 10^{11}$ bits of Shannon entropy.

4 Discussion

While a typical neuronal action potential is commonly treated as carrying no more than a single bit of Shannon entropy, simple thermodynamic arguments suggest that this interpretation is too oversimplified to be consistent with known laws of physics. Combining realistic values for neuronal temperature and energy dissipation with the equation for Landauer's principle shows that a single action potential in a typical mammalian cortical pyramidal cell can carry up to approximately $3.4 \cdot 10^{11}$ natural units of thermodynamic information, or approximately $4.9 \cdot 10^{11}$ bits of Shannon entropy. To put these numbers into perspective, consider the following. If a typical action potential carried information at an efficiency of only a billionth of the maximum efficiency allowed by known laws of thermodynamics, this action potential could still carry hundreds of bits of Shannon entropy. Clearly, this result challenges the notion that a typical mammalian spiking neuron can be conceptualized as a binary computing element.

Many questions naturally arise from these calculations. For example, if we make the reasonable assumption that spiking neurons are at least somewhat energy-efficient, we are led to conclude that a typical action potential must process many bits of thermodynamic information. What physical degrees of freedom are being used to store all of these bits? Certainly, a spiking neuron stores many bits of information by recording distinctions about the locations of ions and electrons relative to its axonal membrane. But might the information contained in each action potential also include the degrees of freedom stored in larger physical particles, such as phospholipid molecules or various proteins? Given that thermodynamics allows a single action potential to carry such a large number of bits of information, and that evolution has had hundreds of millions of years to optimize the dynamics of action potentials, how close to the thermodynamic limit do spiking neurons operate? How many bits of relevant information are carried by an action potential?

These results also have broader implications for areas of neuroscience beyond the biophysics of cellular computation. From molecular biology to the neuropsychology of consciousness, the concept of neuronal information processing is a central component of a wide range of models and theories in contemporary neuroscience. By showing that a typical action potential can hold a very large quantity of information, these calculations suggest that it would be wise to assume that neurons process information in ways that are more nuanced and sophisticated than we often suppose. How will the assumption that an action potential carries at most one bit of information impede our progress in understanding neuronal information processing?

Conflict of Interest Statement

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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