Comment on ”Energy and information in Hodgkin-Huxley neurons”

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Abstract

In a recent paper [A. Moujahid, A. d’Anjou, F. J. Torrealdea and F. Torrealdea, Phys. Rev. E 83, 031912 (2011)], the authors have calculated the energy consumed in firing neurons by using the Hodgkin-Huxley (HH) model. The energy consumption rate adopted for the HH model yields a negative energy consumption meaning an energy transfer from an HH neuron to a source which is physically strange, although they have interpreted it as a biochemical energy cost. I propose an alternative expression for the power consumption which leads to a positive energy consumed in an HH neuron, presenting some model calculations which are compared to those in their paper.

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It has been controversial how to experimentally and theoretically evaluate the energy consumption in firing neurons. Recently Moujahid, d’Anjou, Torrealdea and Torrealdea [1] have proposed such a theoretical method by using the Hodgkin-Huxley (HH) model given by

\[
\begin{align*}
CV' & = -I_{Na} - I_{K} - I_{L} + I, \\
\dot{m} & = -(a_m + b_m)m + a_m, \\
\dot{h} & = -(a_h + b_h)h + a_h, \\
\dot{n} & = -(a_n + b_n)n + a_n.
\end{align*}
\]

Here \( V \) denotes the membrane potential in mV, \( I \) stands for the total current in \( \mu A/cm^2 \), the membrane capacitance is \( C = 1 \mu F/cm^2 \), and \( m, h \) and \( n \) are dimensionless gating variables of Na, K and leakage (L) channels, respectively. Currents in respective channels are expressed by

\[
\begin{align*}
I_{Na} & = g_{Na}m^3h(V - V_{Na}), \\
I_{K} & = g_{K}n^4(V - V_{K}), \\
I_{L} & = g_{L}(V - V_{L}),
\end{align*}
\]

where reversal potentials of Na, K and L channels are \( V_{Na} = 50 \) mV, \( V_{K} = -77 \) mV and \( V_{L} = -54.5 \) mV, respectively, in the conventional absolute unit [2, 3], and the maximum values of corresponding conductances are \( g_{Na} = 120 \) mS/cm\(^2\), \( g_{K} = 36 \) mS/cm\(^2\) and \( g_{L} = 0.3 \) mS/cm\(^2\) [2, 3]. Coefficients of \( a_m \) and \( b_m \) et. al. are given in the absolute unit by [2, 3]

\[
\begin{align*}
a_m & = 0.1(V + 40)/[1 - e^{-(V+40)/10}], \\
b_m & = 4 e^{-(V+65)/18}, \\
a_h & = 0.07 e^{-(V+65)/20}, \\
b_h & = 1/[1 + e^{-(V+35)/10}], \\
a_n & = 0.01 (V + 55)/[1 - e^{-(V+55)/10}], \\
b_n & = 0.125 e^{-(V+65)/80}.
\end{align*}
\]

In Ref. [1] the total energy \( H \) is expressed by

\[
H = \frac{1}{2}CE^2 + H_{Na} + H_{K} + H_{L}.
\]
where the first term expresses the energy stored in the capacitor and $H_i$ denotes the energy in the channel $i$ ( = Na, K and L). Based on a biochemical consideration, the authors in Ref. [1] have derived a derivative of $H$ with respect to time given by

$$\dot{H} \equiv P' = CE\dot{E} + I_{Na}E_{Na} + I_{K}E_{K} + I_{L}E_{L},$$

(9)

where $E$ (= $V - V_{\text{res}}$) and $E_i$ (= $V_i - V_{\text{res}}$) are action potential and reversal potentials, respectively, in the reduced unit with $V_{\text{res}}$ (= −65 mV) [3]. The four terms in Eq. (9) stand for energy consumption rates in respective channels. By using Eq. (9), the authors in Ref. [1] have studied the energy consumption rate against firing rate in an HH neuron. Equation (9), however, yields a negative energy consumption [Fig. 2(b) in Ref. [1]], for which alternative methods are studied as will be explained in the following.

It is well known that the HH equation given by Eq. (1) expresses an electric circuit (see Fig. 1 in Ref. [2]) consisting of capacitor $C$ and three Na, K and L ion channels, which are connected in parallel. The channel $i$ ( = Na, K and L) includes a resistor $R_i$ and a battery $V_i$, through which a current $I_i$ flows. The total current $I$ flows when these components are connected to a source battery $V$. Applying Kirchhoff’s law to the circuit, we obtain

$$I = CV\dot{E} + \sum_i I_i,$$

(10)

$$I_iR_i = V - V_i \quad (i = \text{Na, K and L}).$$

(11)

Equation (10) is nothing but Eq. (1). Total consumed energy rate (power) in the circuit is given by

$$P = CV\dot{E} + \sum_i (P_{Ji} + P_{Ri}),$$

(12)

$$= CV\dot{E} + \sum_i P_i,$$

(13)

with

$$P_{Ji} = I_i^2R_i = I_i(V - V_i),$$

(14)

$$P_{Ri} = I_iV_i,$$

(15)

where $I_i^2R_i$ and $I_iV_i$ signify contributions from Joule heat and reversal potential, respectively, in the channel $i$. 3
Now we consider three methods A, B and C for a calculation of the power consumed in an HH neuron, depending on which contributions are taken into account,

\[ P_A = CV \dot{V} + \sum_i P_{Ri} \]  
(method A),

\[ P_B = CV \dot{V} + \sum_i P_{Ji} \]  
(method B),

\[ P_C = CV \dot{V} + \sum_i (P_{Ri} + P_{Ji}) = VI \]  
(method C).

Methods A, B and C take into account contributions from the reversal potential \((P_{Ri})\), Joule heat \((P_{Ji})\), and the reversal potential plus Joule heat \((P_{Ri} + P_{Ji})\), respectively, besides that from the capacitor \((CV \dot{V})\). The \(VI\) term in Eq. (18) expresses a total power supplied from a source. By a simple calculation, the total power adopted in Ref.[1] becomes [Eq. (9)]

\[ P' = P_A - V_{res} I, \]  
(19)

which does not include a contribution from Joule heat.

The inset of Fig. 1(a) shows the time course of an action potential for an external current of \(I = 6.9 \mu A/cm^2\), for which a neuron fires with a period of 17.36 ms[1]. Properties of the consumed power depend on which method among the three is adopted. Figure 1(a), 1(b) and 1(c) show time courses of power consumption in four channels and total power for a single firing calculated in the methods A, B and C, respectively. We note that total power \(P_A\) in Fig. 1(a) is negative, \(P_B\) in Fig. 1(b) is positive, and \(P_C\) in Fig. 1(c) is oscillating because \(P_C = IV\).

From the total power \(P\), we may evaluate the mean total power \(\bar{P}\), which is given by \(\bar{P}_A < 0, \bar{P}_B > 0\) and \(\bar{P}_C < 0\) for methods A, B and C, respectively, a bar denoting an average over a period. Absolute mean powers \(|\bar{P}_\kappa|\) (\(\kappa = A, B\) and \(C\)) calculated in the methods A, B and C are plotted by solid, dashed and chain curves, respectively, as a function of external current \(I\) in Fig. 2, whose inset shows the \(I\) dependence of firing frequency \(f\) of an HH neuron. The mean power of firing state in the method A is about 10000 ∼ 15000 nJ/s for \(I = 7 ∼ 30 \mu A/cm^2\) while that of the quiescent state without firings is much smaller (300 ∼ 900 nJ/s). \(|\bar{P}_A|\) shown by the solid curve is similar to the result presented in Fig. 3(b) of Ref.[1]. The mean power in the method B is almost the same as that in the method A,

\[ \bar{P}_B \simeq |\bar{P}_A|, \]  
(20)

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FIG. 1: (Color online) Time courses of powers consumed in a capacitor (C), Na, K and L channels and total powers calculated in (a) the method A, (b) method B and (c) method C with $I = 6.9 \, \mu A/cm^2$, a total power in (c) being multiplied by a factor of ten. The inset in (a) shows the time course of an action potential $V$.

which arises from the relation,

$$\sum_i P_{ji} = - \sum_i P_{Ri} + V I \simeq - \sum_i P_{Ri}, \quad (21)$$

because $VI \ll |\sum_i P_{Ri}|$ (Fig. 1). The mean power in the method C is smaller than those in the methods A and B, and it is almost linearly increased with increasing $I$. The positive mean power implies that energy is supplied from an external source to a neuron while the negative power means the opposite in which a neuron plays a role of a power generator. The authors in Ref. [1] have interpreted an obtained negative energy consumption rate ($P' < 0$)
FIG. 2: (Color online) Absolute mean total power $|\bar{P}|$ as a function of input current $I$ calculated in the method A (solid curve), method B (dashed curve) and method C (chain curve), result of the method C being multiplied by a factor of ten. The $I$ dependence of firing rate $f$ is shown in the inset where a firing occurs at $I > 6.2 \mu A/cm^2$.

as a loss in electrochemical energy which is expected to correspond to consumed power because it has to be recharged by adenosine triphosphatase (ATPase) activity. Equation (21) shows that the energy consumption assumed in the method A (also in Ref.[1]) may be related to Joule heat consumed in conductors of ion channels in the model B.

The authors in Ref.[1] have extended their analysis to two-electrically coupled HH neurons and also to a collection of uncoupled HH neurons, for which expressions for energy consumption rates similar to Eq. (9) have been derived (e.g. Eq. (8) in Ref.[1] for two-HH neurons). They have the same deficit as in the case of a single HH neuron having been mentioned above.

To summarize, the calculation in Ref.[1] based on Eq. (9) yields a negative mean power consumption in an HH neuron, which is physically inappropriate, although its biochemical interpretation is reasonable. We have proposed an alternative method, considering three methods A, B and C given by Eqs. (16)-(18). The method B which takes into account a contribution from Joule heat consumed in conductors, leads to a positive mean power in the HH model. Energies calculated in the reduced unit adopted in Ref. [1] are different from those in the absolute unit [3]. For example, the mean value of $\bar{E}$ in the reduced unit is
positive \[1\] while its counterpart \(\overrightarrow{V I}\) in the absolute unit is negative. By using the method B, we may study nonequilibrium properties of an HH neuron from a viewpoint adopted in Ref.\[4\] where an analogy between an electric RC circuit and a damped Brownian particle is employed.

\[\text{[1] A. Moujahid, A. d’Anjou, F. J. Torrealdea and F. Torrealdea, Phys. Rev. E 83, 031912 (2011).}\]

\[\text{[2] A. L. Hodgkin and A. F. Huxley, J. Physiol. 117, 500 (1952).}\]

\[\text{[3] Ref. \[1\] has adopted the reduced unit in which the membrane potential } E \text{ and reversal potentials } E_i (i = \text{Na, K and L}) \text{ are given by } E = V - V_{\text{res}} \text{ and } E_i = V_i - V_{\text{res}} (i = \text{Na, K and L}) \text{ where } V_{\text{res}} (= -65 \text{ mV}) \text{ denotes the resting action potential in the absolute unit. In the reduced unit, the resting action potential vanishes and reversal potentials are } E_{\text{Na}} = 115 \text{ mV, } E_{\text{K}} = -12 \text{ mV and } E_{\text{L}} = 106 \text{ mV \[1\].}\]

\[\text{[4] R. van Zon, S. Ciliberto, and E. G. D. Cohen, Phys. Rev. Lett. 92, 130601 (2004).}\]