

# Energy coding in biological neural networks

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**Abstract** According to the experimental result of signal transmission and neuronal energetic demands being tightly coupled to information coding in the cerebral cortex, we present a brand new scientific theory that offers an unique mechanism for brain information processing. We demonstrate that the neural coding produced by the activity of the brain is well described by our theory of energy coding. Due to the energy coding model's ability to reveal mechanisms of brain information processing based upon known biophysical properties, we can not only reproduce various experimental results of neuro-electrophysiology, but also quantitatively explain the recent experimental results from neuroscientists at Yale University by means of the principle of energy coding. Due to the theory of energy coding to bridge the gap between functional connections within a biological neural network and energetic consumption, we estimate that the theory has very important consequences for quantitative research of cognitive function.

## Introduction

Due to the limitations in current biophysical models of neural coding, research into the mechanisms of neural information processing remain very difficult (Quiroga et al. 2005; Stein et al. 2005; Wang and Zhang 2003,

2005; Wang and Jiao 2006; Jiao and Wang 2005). Because of these limitations, currently, the principles of neural information processing underlying cognitive processes within the brain are not completely understood (Arbib 2002; Wilson and Keil 1999; Freeman 2000; Crotty and Levy 2005; Jiao and Wang 2006). William B Levy and Robert A. Baxter studied the relationship between neural coding and energy consumption, and gave a description of the average energy consumption required for a given level of neural network activity according to Shannon's principle (Levy and Baxter 1996; Levy and Baxter 2002). Here the role of energy efficiency was detected in the process of neural coding (Levy and Baxter 1996; Levy and Baxter 2002). Recently, Simon B. Laughlin and Terrence J. Sejnowski have posited that networks of neurons increase efficiency by distributing signals sparsely in space and time (Laughlin and Sejnowski 2003). It was already recognized that sparse coding improves energy efficiency. However, the functional relationship between information coding and energy consumption for neurons is not known. Does the energy-efficient cortical neuron select signals from synapses that are most informative? This question draws energy efficiency into one of the most active and important areas of neuroscience: synaptic plasticity (Laughlin and Sejnowski 2003). The research in this paper is relevant to this kind of question and we will focus upon this question in a series of papers to follow (Wang and Zhang 2006).

Here we show that principle of the energy coding can reveal intrinsic property of brain information processing by way of a biophysically plausible model. We bring a new perspective upon global brain information processing. We will demonstrate that this perspective provides us a great comprehension of the role of information coding in neural networks.

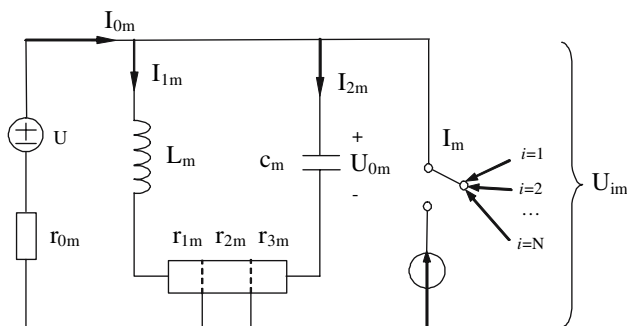
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## Biophysical model

Analysis of both neuro-electrophysiological experimental data and the biophysical properties of neurons suggest the following equivalent electric circuit model or the biophysical model that reflects the essential electronic properties of neuronal activity as in Fig. 1.

This physical model describes the interaction between a single neuron and all other neurons connected to the single neuron. Interaction and mutual coupling among neurons is achieved through the total electrical current formed by the input of  $N$  neurons to the  $m$ th neuron to generate the sub-threshold current level. The  $m$ th neuron in the coupling relationship under the state of firing action potential does not react to external stimulation, hence, the stimulation-induced electric current  $I_m$  becomes a fixed constant (i.e. constant-current source). Similar to the model in reference (John et al. 2000), for the separation of positive and negative ions inside and outside of the cellular membrane we use  $C_m$  to denote this membranous capacitance. For the voltage formed by charges of positive and negative ions at the cellular membrane we use  $U_{0m}$  to express this corresponding potential difference. In the resting membrane state the intensity of the magnetic field produced by the motion of the ionic charges upon neuronal activity is very weak, therefore, it can be neglected. However, the magnetic field formed by the violent motion of ionic charges during action potential is much stronger than during the resting state, and can not be ignored. This is because the influx of sodium ions and efflux of potassium ions achieve extremely high rates. Motion charges formed in this case have to produce the self-induction phenomenon. Hence, we use the inductance  $L_m$  to denote the intensity of the magnetic field is not only important but also reasonable in a physical sense. And the physical phenomenon of membrane current depending on membrane potential has been confirmed by many experiments (Arbib 2002; Freeman 2000). Therefore taking into



**Fig. 1** Physical model of  $m$ th neuron under case of coupling

account the effect of inductance in electricity during the neuronal action potential follows naturally. The site of the inductance is designed to parallel the membranous capacitance as in Fig. 1. Although this is a hypothesis, the computational results obtained from the biophysical model in this paper show that introduction of inductance into the model agrees well with the experimental results of neuro-electrophysiology.

The neuronal action potential requires energy for activity, and voltage source  $U$  denotes the total energy supplied by both the sodium-potassium pump, through the production of charge separation and thermal noise energy generated by water molecules having undergone ATP hydrolysis (Wang et al. 2003). In addition, that a neuron can maintain its resting membrane potential shows that there exists a current source  $E$  of energy within the cell body. The electric resistance  $r_{0m}$  models the loss of energy, and the electric resistance  $r_{1m} + r_{2m} + r_{3m}$  as in Fig. 1, is equivalent to the electrical resistance in reference (John et al. 2000). Neurophysiologists pay great attention to these sites in neuronal activities because the highest energetic demand in the brain is centralized to sites of synaptic input (Schwartz et al. 1979; Mata et al. 1980). Therefore the internal energy source  $E$  for the  $m$ th neuron and the site of total temporal-spatial input from  $N$  neurons to the  $m$ th neuron is designed to different points in the physical model as in Fig. 1, i.e. the site of internal energy generation and the site of total synaptic current have associated resistances  $r_{1m}$  and  $r_{3m}$ , respectively, and the electric resistance between  $r_{1m}$  and  $r_{3m}$  is denoted by  $r_{2m}$ . The physical quantities can be observed as the membrane potential  $U_{im}$  and the membrane electric current  $I_{0m}$  in the physical model, as in Fig. 1. The work of investigators at Yale University indicates that most of the energy used in brain is for the propagation of the action potential and for the restoring postsynaptic ion fluxes after the receptors have been stimulated by neurotransmitters (Raichle and Gusnard 2002). The symbol  $I_m$  denotes the total synaptic current formed after temporal-spatial integration of numerous synaptic inputs on the  $m$ th neuron—this interaction among neurons in the cerebral cortex is orderable and obeys a self-organizing rule (Haken 1996). Hence, the stimulation induced free motion of electric currents does not take arbitrary values. This is because the dynamic mechanism of the ionic channel can greatly restrict the form of the electric current  $I_m$  (Koch and Segev 1998). According to this point of view, the numerical computational results given in the later section of the paper confirmed that the concrete form of energy consumption for neurons is just the Hamiltonian energy function presented below.

**Circuit equations**

We obtain the following equations in Fig. 1

$$U_{im} = C_m r_{3m} \dot{U}_{0m} + U_{0m} \tag{1}$$

$$I_{2m} = C_m \dot{U}_{0m} \tag{2}$$

$$U_{im} = L_m \dot{I}_{0m} + r_{1m} I_{1m} + r_{2m} (I_m - I_{2m}) \tag{3}$$

$$I_{0m} = I_{1m} + I_{2m} - I_m \tag{4}$$

$$U = r_{0m} I_{0m} + r_{1m} I_{1m} + L_m \dot{I}_{1m} \tag{5}$$

Combination Eqs. (1)–(5) yields the model equations:

$$L_m \dot{I}_{1m} + r_{1m} I_{1m} = C_m (r_{2m} + r_{3m}) \dot{U}_{0m} + U_{0m} - r_{2m} I_m \tag{6}$$

$$I_m = \frac{1}{r_{0m}} (C_m r_{0m} \dot{U}_{0m} - U + (r_{0m} + r_{1m}) I_{1m} + L_m \dot{I}_{1m}) \tag{7}$$

At sub-threshold state the intensity of the magnetic field produced by the motion of the ionic charges upon neuronal activity is very weak, therefore, it can be ignored, i.e.

$$L_m = 0 \tag{8}$$

The electric current  $I_{1m}$  is eliminated from (6, 7) we obtain

$$C_m R_2 \dot{U}_{0m} + (r_{0m} + r_{1m}) U_{0m} = R_1 I_m + r_{1m} U \tag{9}$$

Where  $R_1 = r_{0m} r_{1m} + r_{0m} r_{2m} + r_{1m} r_{2m}$  (10)

$$R_2 = r_{0m} r_{1m} + r_{0m} r_{2m} + r_{0m} r_{3m} + r_{1m} r_{2m} + r_{1m} r_{3m} \tag{11}$$

The electric current  $\dot{I}_{1m}$  is eliminated from (6, 7) we obtain

$$I_{1m} = \frac{1}{R_1} (C_m r_{0m} r_{3m} \dot{U}_{0m} + r_{0m} U_{0m} + r_{2m} U) \tag{12}$$

At supra-threshold level, we set

$$I_m = i_0 \tag{13}$$

The  $m$ th neuron in the coupling relationship under the state of firing action potential does not react to external stimulation, hence, stimulation's the electric current  $I_m$  becomes a fixed constant  $i_0$  (i.e. constant-current source).

**The numerical analysis of the biophysical model and comparison of neuro-electrophysiological results**

(1) The membrane potential at sub-threshold stimulation  
The experimental condition is the following

$$I_m = i_0 \tag{14}$$

One obtains the following result from (9)

$$U_{0m} = U_{0m}(\infty) + (U_{0m}(0) - U_{0m}(\infty)) e^{-\frac{t}{\tau}} \tag{15}$$

$$U_{im} = U_{0m}(\infty) + \left(1 - \frac{C_m r_{3m}}{\tau}\right) (U_{0m}(0) - U_{0m}(\infty)) e^{-\frac{t}{\tau}} \tag{16}$$

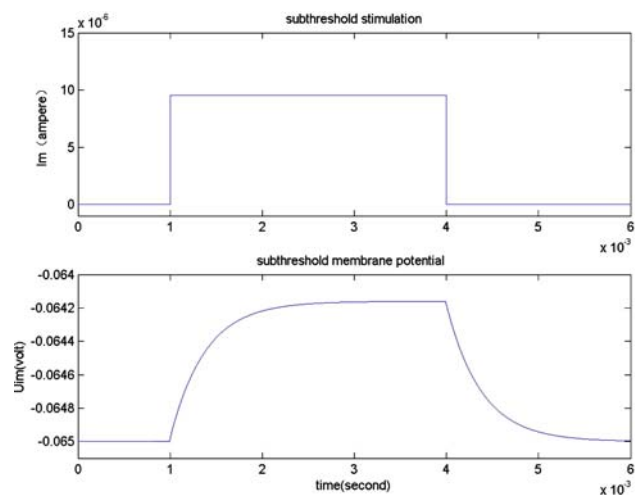
where

$$\tau = \frac{C_m R_2}{r_{0m} + r_{1m}} \tag{17}$$

$$U_{0m}(\infty) = \frac{R_1 i_0 + r_{1m} U}{r_{0m} + r_{1m}} \tag{18}$$

Using Eqs. (14, 16), one obtains the following numerical results in Fig. 2.  $i_0 = 0.954 \times 10^{-5} A$ ,  $r_{0m} = 0.004 \Omega$ ,  $r_{1m} = 5 \Omega$ ,  $r_{2m} = 88 \Omega$ ,  $r_{3m} = 2.2 \Omega$ ,  $U_{0m}(0) = -65 \times 10^{-3} V$ .

The above result proved that membrane potential at sub-threshold stimulation agrees astonishingly with result given in Figure 7.3 in reference (John et al. 2000). This biophysical model can reproduce all kind of membrane potentials given in Figure 3 in reference (John et al. 2000) as long as parameters are chosen. Therefore the biophysical model can be used to describe the basic



**Fig. 2** Plot of the subthreshold membrane potential

characteristic of neuron’s electric activity under condition of various different stimulations. In order to demonstrate the validity of the biophysical model, an example is given again in the below.

(2) The action current at supra-threshold level  
The experimental condition is the following

$$U_{im} = Au(t) + U_{0m}(0) \tag{19}$$

Where  $u(t)$  is a step function.

Substituting  $U_{0m}$  into (2) one obtains

$$I_{2m} = C_m \dot{U}_{0m} = \frac{A}{r_{3m}} e^{-\frac{t}{C_m r_{3m}}} \tag{20}$$

Using above conditions, one obtains solution from Eq. (6) as follows

$$I_{1m} = I_{1m}(0)e^{-\frac{r_{1m}t}{L_m}} + \frac{A + U_{0m}(0) - r_{2m}i_0}{r_{1m}} \left( 1 - e^{-\frac{r_{1m}t}{L_m}} \right) + \frac{r_{2m}A}{L_m r_{3m}} \frac{e^{-\frac{t}{C_m r_{3m}}} - e^{-\frac{r_{1m}t}{L_m}}}{\frac{1}{C_m r_{3m}} - \frac{r_{1m}}{L_m}} \tag{21}$$

Inserting (20, 21) into (4) yields the action current

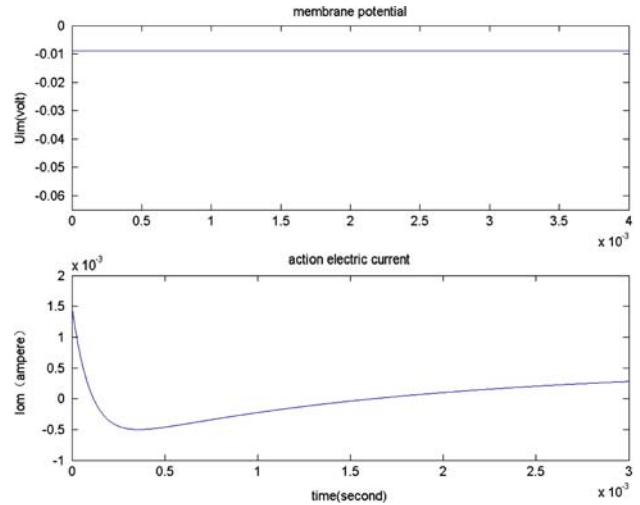
$$I_{0m} = \frac{A - (r_{1m} + r_{2m})i_0 + U_{0m}(0)}{r_{1m}} + \frac{A}{r_{3m}} \left( 1 - \frac{\frac{r_{2m}}{L_m}}{\frac{1}{C_m r_{3m}} - \frac{r_{1m}}{L_m}} \right) e^{-\frac{t}{C_m r_{3m}}} - \left( \frac{A + U_{0m}(0) - r_{2m}i_0}{r_{1m}} - \frac{Ar_{2m}}{L_m r_{3m} \left( \frac{1}{C_m r_{3m}} - \frac{r_{1m}}{L_m} \right)} - I_{1m}(0) \right) e^{-\frac{r_{1m}t}{L_m}} \tag{22}$$

Using Eqs. (19, 22), one obtains the following numerical results in Fig. 3.  $L_m = 10.9 \times 10^{-3}$  H,  $C_m = 8 \times 10^{-6}$  F,  $r_{1m} = 6.5\Omega$ ,  $r_{2m} = 52.8524 \Omega$ ,  $r_{3m} = 12.5167\Omega$ ,  $i_0 = -2.0639 \times 10^{-4}$  A,  $U_{0m}(0) = -69 \times 10^{-3}$  V,  $I_{1m}(0) = -3.5$  mA.

The above result demonstrates that the biophysical model given in Fig. 1 can reproduce a depolarizing membrane current. This membrane current is completely in accordance with figure 6.3 in reference [John et al. 2000].

**The numerical simulation of EPSP and IPSP**

We know that output of the model is neuronal membrane current from Fig. 1. The symbol  $I_m$  denotes the total synaptic current formed after temporal-spatial integration of numerous synaptic inputs on the  $m$ th neuron. Hence, output of the membrane current obtained from the biophysical model is actually a result of interacting coupled neurons, and energy method is used from starting dynamic theory to discuss relationship between input and output of among  $N$



**Fig. 3** Plot of the depolarizing membrane electric current at supra-threshold stimulation

neurons to the  $m$ th neuron. According to the biophysical model in Fig. 1, the following result can be read at sub-threshold level

$$L_m = 0$$

The  $I_m$  is result of stimulation of  $N$  neurons to the  $m$ th neuron. This stimulation will be strictly mastered under action of mechanism of neurodynamics, so it does not take arbitrary values. However, the membrane current seems to be able to take arbitrary values in the biophysical model, but the microscopic mechanism of neuron shows that dynamic rule of the convergence of positive and negative ions inside and outside of the cellular membrane can restrain membrane current  $I_m$ ’s motion form. A reasonable assumption is that choose  $U_{0m}$  to be the generalized displacement, and the power provided by  $U$  and  $I_m$  to the system is a Lagrange function or Hamiltonian function. Accordingly, the form of  $I_m$  is dominated by Hamiltonian motion equation.

One obtains the power of the membranous capacitance from Fig. 1

$$w_{1m} = C_m U_{0m} \dot{U}_{0m} \tag{23}$$

and the power of resistances

$$w_{2m} = C_m^2 r_{3m} \dot{U}_{0m}^2 + r_{1m} I_{1m}^2 + r_{2m} (I_m - C_m \dot{U}_{0m})^2 + r_{0m} (I_{1m} - I_m + C_m \dot{U}_{0m})^2$$

Lagrange function is structured according to Fig. 1 as follows

$$L(U_{0m}, \dot{U}_{0m}) = w_{1m} + w_{2m} \tag{24}$$

Inserting (9–12) into (23–25) yields

$$L(U_{0m}, \dot{U}_{0m}) = a_1 \dot{U}_{0m}^2 + a_2 \dot{U}_{0m} + a_3 U_{0m} \dot{U}_{0m} + a_4 U_{0m}^2 + a_5 U_{0m} + a_6 \tag{25}$$

where

$$a_1 = C_m^2 r_{3m} \left( 1 + \frac{r_{3m}(r_{0m} + r_{1m})}{R_1} \right) \tag{26}$$

$$a_2 = -\frac{2C_m r_{1m} r_{3m}}{R_1} U \tag{27}$$

$$a_3 = C_m \left( 1 + \frac{2r_{3m}(r_{0m} + r_{1m})}{R_1} \right) \tag{28}$$

$$a_4 = \frac{r_{0m} + r_{1m}}{R_1} \tag{29}$$

$$a_5 = -\frac{2r_{1m}U}{R_1} \tag{30}$$

$$a_6 = \frac{r_{1m} + r_{2m}}{R_1} U^2 \tag{31}$$

We define that the generalized displacement is denoted as

$$q_m = U_{0m} \tag{32}$$

and the generalized momentum is denoted as

$$p_m = 2a_1 \dot{U}_{0m} + a_2 + a_3 U_{0m} \tag{33}$$

According to the above generalized displacement and generalized momentum, Hamiltonian energy function from the power function of the electric resistance and the capacitance can be easily obtained as follows:

$$H(p_m, q_m) = \frac{(p_m - a_2 - a_3 q_m)^2}{4a_1} - (a_4 q_m^2 + a_5 q_m + a_6) \tag{34}$$

then motion equation which corresponds to the above Hamiltonian energy function is given by

$$\begin{cases} \dot{q} = \frac{p_m - a_2 - a_3 q_m}{2a_1} \\ \dot{p}_m = 2a_4 q_m + a_5 + \frac{a_3}{2a_1} (p_m - a_2 - a_3 q_m) \end{cases} \tag{35}$$

Let

$$U = -E + Ae^{-ht} \tag{36}$$

Combination of circuit equation, as in Fig. 1, and the computational results of electronic current stimulation allow us to obtain an exact solution for the membrane potential from motion Eq. (35).

$$U_{0m} = -\frac{r_{1m}E}{r_{0m} + r_{1m}} + \frac{Ar_{1m}(1 - C_m r_{3m}h)}{C_m^2 r_{3m} R_2 (\lambda^2 - h^2)} e^{-ht} + \frac{r_{1m}}{2(r_{0m} + r_{1m})} \left( E - \frac{A\lambda(1 - C_m r_{3m}h)}{\lambda - h} + \frac{2k_2(r_{0m} + r_{1m})}{r_{1m}} \right) e^{-\lambda t} \tag{37}$$

$$\text{Where } \lambda = \sqrt{\frac{a_4}{a_1}} \tag{38}$$

$$h = \lambda \frac{A - E - \frac{2k_1(r_{0m} + r_{1m})}{r_{1m}}}{C_m r_{3m} \lambda A + E + \frac{2k_1(r_{0m} + r_{1m})}{r_{1m}}} \tag{39}$$

Substituting (37–39) into (1) we obtain the following membrane potential

$$U_{im} = -\frac{r_{1m}E}{r_{0m} + r_{1m}} + \frac{Ar_{1m}(1 - C_m r_{3m}h)^2}{C_m^2 r_{3m} R_2 (\lambda^2 - h^2)} e^{-ht} + \frac{r_{1m}(1 - C_m r_{3m}\lambda)}{2(r_{0m} + r_{1m})} \left( E - \frac{A\lambda(1 - C_m r_{3m}h)}{\lambda - h} + \frac{2k_2(r_{0m} + r_{1m})}{r_{1m}} \right) e^{-\lambda t} \tag{40}$$

Substituting (36, 37) into (9), we obtain stimulation current as follows:

$$I_m = \frac{I_1 e^{-ht} + I_2 e^{-\lambda t}}{R_1} \tag{41}$$

where

$$I_1 = Ar_{1m} \left( \frac{(r_{0m} + r_{1m} - C_m R_2 h)(1 - C_m r_{3m}h)}{C_m^2 r_{3m} R_2 (\lambda^2 - h^2)} - 1 \right) \tag{42}$$

$$I_2 = \frac{r_{1m}(r_{0m} + r_{1m} - C_m R_2 \lambda)}{2(r_{0m} + r_{1m})} \times \left( E - \frac{A\lambda(1 - C_m r_{3m}h)}{\lambda - h} + \frac{2k_2(r_{0m} + r_{1m})}{r_{1m}} \right) \tag{43}$$

The exact solution describes the excitatory postsynaptic potentials (EPSP) and the inhibitory postsynaptic potentials (IPSP) in Fig. 4.  $C_m = 4.2 \times 10^{-6}$  F,  $r_{0m} = 0.004 \Omega$ ,  $r_{1m} = 5 \Omega$ ,  $r_{2m} = 88 \Omega$ ,  $r_{3m} = 2.2 \Omega$ ,  $U_{0m}(0) = -69 \times 10^{-3}$  V,  $-71 \times 10^{-3}$  V,  $\dot{U}_{0m}(0) = \pm 50$  V/t.

From the above numerical results we can clearly show that the Hamiltonian energy function can effectively reproduce both EPSP and IPSP obtained by means of experimental methods. In addition, we have proved that the biophysical model given in Fig. 1 is both very effective and accurate in Figs. 2 and 3.

**The numerical simulation of action potential at supra-threshold level**

The membrane potential  $U_{im}$  is achieved to threshold value due to  $I_m = i_0$  under situation of supra-threshold stimulation and the action potential is produced. After the action potential is achieved to peak value, the membrane potential  $U_{im}$  is dominated by rule of sub-threshold activities. Therefore, one obtains the powers of the membranous capacitance and the inductance from Fig. 1 as follows:

$$w_{1m} = C_m U_{0m} \dot{U}_{0m} + L_m I_{1m} \dot{I}_{1m} \tag{44}$$

And power of resistances is the following

$$w_{2m} = r_{0m}(I_{1m} + C_m \dot{U}_{0m} - i_0)^2 + r_{1m} I_{1m}^2 + r_{2m}(i_0 - C_m \dot{U}_{0m})^2 + C_m^2 r_{3m} \dot{U}_{0m}^2 \tag{45}$$

One obtains the result from (6)

$$I_{1m} = ke^{-at} - \frac{r_{2m}i_0}{r_{1m}} + \frac{C_m(r_{2m} + r_{3m})U_{0m}}{L_m} + e^{-at} \int \frac{\left(1 - \frac{C_m r_{1m}(r_{2m} + r_{3m})}{L_m}\right)U_{0m}}{L_m} e^{at} dt \tag{46}$$

Where  $a = \frac{r_{1m}}{L_m}$  (47)

Inserting the following Eq. (48) into integral term in Eq. (46)

$$U_{0m} = k_0 + k_1 e^{p_1 t} + k_2 e^{p_2 t} \tag{48}$$

Where  $k_0, k_1, k_2, p_1, p_2$  are adjustable parameters. Combining (46) and (48) one obtains

$$I_{1m} = ke^{-at} - \frac{r_{2m}i_0}{r_{1m}} + \frac{C_m(r_{2m} + r_{3m})U_{0m}}{L_m} + g(t) \tag{49}$$

where

$$g(t) = g_0 + g_1 e^{p_1 t} + g_2 e^{p_2 t} \tag{50}$$

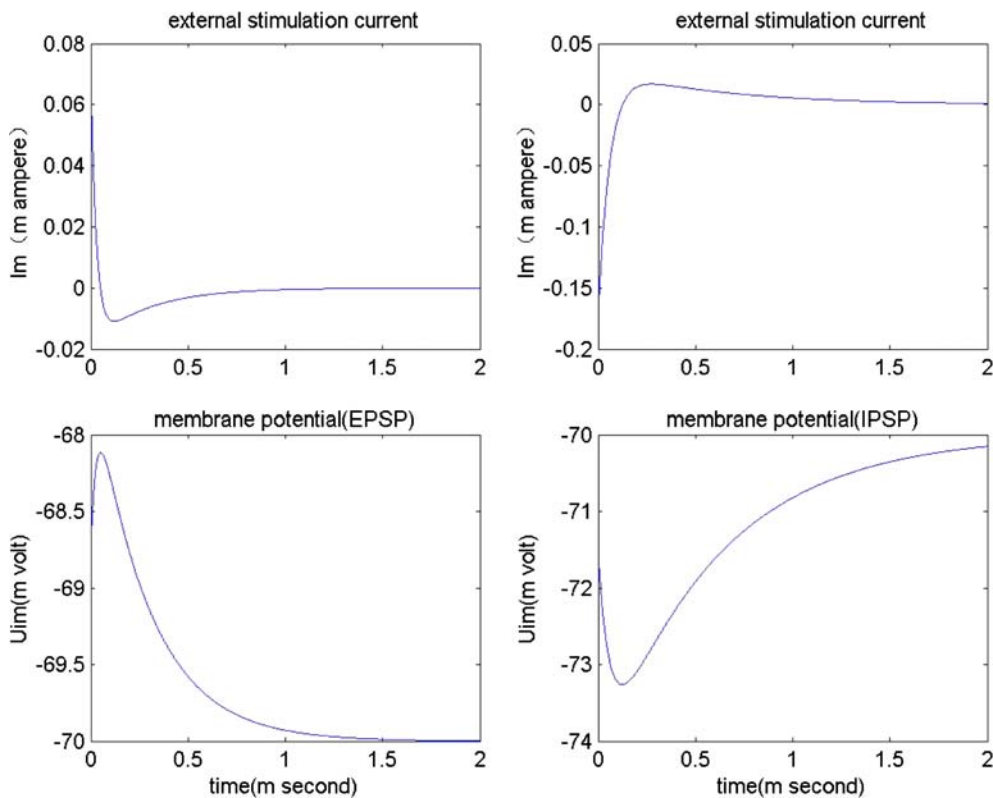


Fig. 4 EPSP and IPSP described by Hamiltonian energetic function

$$g_0 = \frac{1}{r_{1m}} \left( 1 - \frac{C_m r_{1m} (r_{2m} + r_{3m})}{L_m} \right) k_0 \tag{51}$$

$$g_1 = \frac{1}{L_m} \left( 1 - \frac{C_m r_{1m} (r_{2m} + r_{3m})}{L_m} \right) \frac{k_1}{p_1 + a} \tag{52}$$

$$g_2 = \frac{1}{L_m} \left( 1 - \frac{C_m r_{1m} (r_{2m} + r_{3m})}{L_m} \right) \frac{k_2}{p_2 + a} \tag{53}$$

Lagrange function is structured as follows

$$L(U_{0m}, \dot{U}_{0m}) = w_{1m} + w_{2m} \tag{54}$$

Substituting (6), (46–53) into (54) yields the following Lagrange function

$$L(U_{0m}, \dot{U}_{0m}) = d_1 \dot{U}_{0m}^2 + d_2 \dot{U}_{0m} + d_3 U_{0m} \dot{U}_{0m} + d_4 U_{0m}^2 + d_5 U_{0m} + d_6 \tag{55}$$

where

$$d_1 = C_m^2 (r_{0m} + r_{2m} + r_{3m}) \tag{56}$$

$$d_2 = d_{21} + d_{22} e^{-at} + d_{23} e^{p_1 t} + d_{24} e^{p_2 t} \tag{57}$$

$$d_{21} = -C_m i_0 \left( 2r_{0m} + 2r_{2m} + \frac{r_{2m}(2r_{0m} + r_{2m} + r_{3m})}{r_{1m}} \right) + C_m \left( 2r_{0m} + r_{2m} + r_{3m} + \frac{2r_{0m}(r_{2m} + r_{3m})}{L_m} \right) g_0 \tag{58}$$

The symbols  $d_1, d_2, d_3, d_4, d_5, d_6$  are adjustable parameters of induction, electric resistance, and capacitance in the following:.

$$d_{22} = k C_m (2r_{0m} + r_{2m} + r_{3m}) \tag{59}$$

$$d_{23} = C_m \left( 2r_{0m} + r_{2m} + r_{3m} + \frac{2r_{0m}(r_{2m} + r_{3m})}{L_m} \right) g_1 \tag{60}$$

$$d_{24} = C_m \left( 2r_{0m} + r_{2m} + r_{3m} + \frac{2r_{0m}(r_{2m} + r_{3m})}{L_m} \right) g_2 \tag{61}$$

$$d_3 = \frac{C_m}{L_m} (L_m + C_m (r_{2m} + r_{3m}) (2r_{0m} + r_{2m} + r_{3m})) \tag{62}$$

$$d_4 = \frac{c_m}{L_m} \left( 1 + \frac{c_m r_{0m} (r_{2m} + r_{3m})}{L_m} \right) (r_{2m} + r_{3m}) \tag{63}$$

$$d_5 = d_{51} + d_{52} e^{-at} + d_{53} e^{p_1 t} + d_{54} e^{p_2 t} \tag{64}$$

$$d_{51} = -i_0 \left( \frac{r_{2m}}{r_{1m}} + \frac{c_m (r_{2m} + r_{3m}) (2r_{0m} r_{1m} + 2r_{0m} r_{2m} + r_{1m} r_{2m})}{L_m r_{1m}} \right) + g_0 \tag{65}$$

$$d_{52} = k \left( 1 + \frac{2C_m r_{0m} (r_{2m} + r_{3m})}{L_m} \right) \tag{66}$$

$$d_{53} = g_1 \tag{67}$$

$$d_{54} = g_2 \tag{68}$$

$$d_6 = i_0^2 \left( r_{0m} + r_{2m} + \frac{r_{2m}(2r_{0m} + r_{2m})}{r_{1m}} + \frac{r_{0m} r_{2m}^2}{r_{1m}^2} \right) - \left( 2r_{0m} + r_{2m} + \frac{2r_{0m} r_{2m}}{r_{1m}} \right) i_0 k e^{-at} + r_{0m} k^2 e^{-2at} + r_{0m}^2 g^2(t) - \left( 2r_{0m} + r_{2m} + \frac{2r_{0m} r_{2m}}{r_{1m}} \right) i_0 g(t) + 2r_{0m} k g(t) e^{-at} \tag{69}$$

We define that the generalized displacement is denoted as

$$q_m = U_{0m} \tag{70}$$

and the generalized momentum is denoted as

$$p_m = 2d_1 \dot{U}_{0m} + d_2 + d_3 U_{0m} \tag{71}$$

We obtain the following Hamiltonian energy function according to the power function of induction electric resistance and capacitance in Fig. 1.

$$H(p_m, q_m) = \frac{(p_m - d_2 - d_3 q_m)^2}{4d_1} - (d_4 q_m^2 + d_5 q_m + d_6) \tag{72}$$

n, electric resistance and capacitance in Fig. 1. With the motion equation which corresponds to the above Hamiltonian energy function given by

$$\dot{q}_m = \frac{p_m - d_2 - d_3 q_m}{2d_1} \tag{73}$$

$$\dot{p}_m = 2d_4 q_m + d_5 + \frac{d_3}{2d_1} (p_m - d_2 - d_3 q_m)$$

According to Eq. (74) we obtain

$$\ddot{q}_m - \lambda^2 q_m = \frac{d_5 - d_2'}{2d_1} \tag{74}$$

$$\lambda = \sqrt{\frac{d_4}{d_1}}$$

According to the circuit equations in the physical model, we can obtain an exact solution for the action potential from the Hamiltonian motion Eq. (74),

$$\begin{aligned}
 U_{0m} = & -\frac{d_{51}}{2d_4} + \frac{1}{2d_1} \\
 & \left[ \frac{1}{\lambda-a} \left( \frac{d_{51}}{\lambda} + \frac{d_{53}-p_1d_{23}}{\lambda-p_1} + \frac{d_{54}-p_2d_{24}}{\lambda-p_2} + 4\lambda d_1 l_1 \right) e^{-at} \right. \\
 & \left. - \frac{d_{53}-p_1d_{23}}{\lambda^2-p_1^2} e^{p_1t} + \frac{d_{54}-p_2d_{24}}{\lambda^2-p_2^2} e^{p_2t} \right] \\
 & - \frac{1}{2d_1(\lambda-a)} \left( \frac{ad_{51}}{\lambda^2} + \frac{(p_1+a)(d_{53}-p_1d_{23})}{(\lambda^2-p_1^2)} \right. \\
 & \left. + \frac{(p_2+a)(d_{54}-p_2d_{24})}{(\lambda^2-p_2^2)} + 2d_1(l_1(\lambda+a) - l_2(\lambda-a)) \right) e^{-\lambda t}
 \end{aligned} \tag{75}$$

Where  $l_1 = \frac{1}{2} \left( U_{0m}(0) + \frac{\dot{U}_{0m}(0)}{\lambda} \right)$  (76)

$l_2 = \frac{1}{2} \left( U_{0m}(0) - \frac{\dot{U}_{0m}(0)}{\lambda} \right)$  (77)

$$\begin{aligned}
 U_{im} = & -\frac{d_{51}}{2d_4} \\
 & + \frac{1}{2d_1} \left[ \frac{1-C_m r_{3m} a}{\lambda-a} \left( \frac{d_{51}}{\lambda} + \frac{d_{53}-p_1d_{23}}{\lambda-p_1} + \frac{d_{54}-p_2d_{24}}{\lambda-p_2} + 4\lambda d_1 l_1 \right) e^{-at} \right. \\
 & - (1 + C_m r_{3m} p_1) \frac{d_{53}-p_1d_{23}}{\lambda^2-p_1^2} e^{p_1t} - (1 + C_m r_{3m} p_2) \\
 & \left. \frac{d_{54}-p_2d_{24}}{\lambda^2-p_2^2} e^{p_2t} \right] - \frac{1-C_m r_{3m} \lambda}{2d_1(\lambda-a)} \left( \frac{ad_{51}}{\lambda^2} + \frac{(p_1+a)(d_{53}-p_1d_{23})}{(\lambda^2-p_1^2)} \right. \\
 & \left. + \frac{(p_2+a)(d_{54}-p_2d_{24})}{(\lambda^2-p_2^2)} + 2d_1(l_1(\lambda+a) - l_2(\lambda-a)) \right) e^{-\lambda t}
 \end{aligned} \tag{78}$$

and the numerical simulation derived from Eq. (79) is shown in Fig. 5.  $L_m = 3.1 \times 10^{-3}$  H,  $C_m = 2.2 \times 10^{-6}$  F,  $r_{0m} = 0.004 \Omega$ ;  $r_{1m} = 5 \Omega$ ;  $r_{2m} = 88 \Omega$ ;  $r_{3m} = 2.2 \Omega$ ;  $i_0 = -0.78 \times 10^{-3}$  A,  $U_{0m}(0) = -67 \times 10^{-3}$  V,  $\dot{U}_{0m}(0) = 14463$  V/t.

The numerical result clearly shows that the energy function can elegantly reproduce the action potential taken from neuro-electrophysiological data. In other words, the result in Fig. 5 agrees with the numerical computational result obtained by means of the Hodgkin–Huxley equation. The difference lies in the fact that function used here to produce the action potential is different from the Hodgkin–Huxley equation. The difference is that motion Eq. (4) is linear, and the Hodgkin–Huxley equation is nonlinear. This simplification of the biophysical model of the action potential is significant because it models more complex neural network modeling formerly, limited by the nonlinear in the H–H model, possible. For this reason, the idea of energy coding can provide a brand new research method for understanding mechanisms of neural information processing, as well as a scientific description of the quantitative relationship between functional connections within a biological neural network and energy consumption.

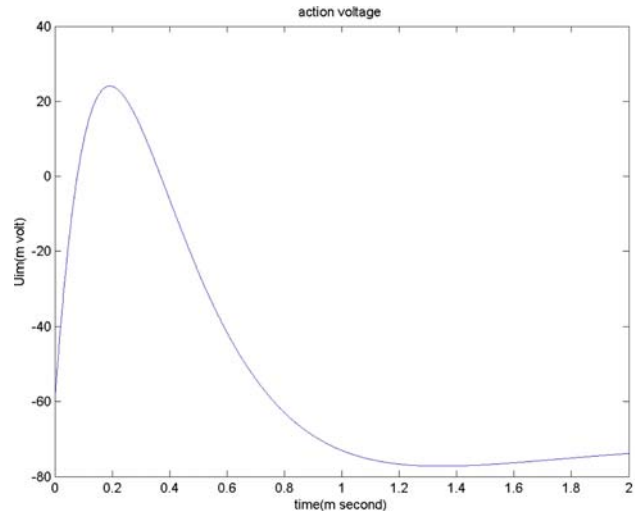


Fig. 5 Action potential described by Hamiltonian energetic function

According to the results mentioned above, the main conclusions are the following:

- (1) We found that the Hamiltonian function of energy consumption may be derived from a biophysical model of the electrical properties of the neuron. The computational results show that EPSP, IPSP and action potential obtained by numerical simulation agree with the experimental results of neuro-electrophysiology. Note that value of the membranous capacitance  $C_m$  and values of the electric resistance  $r_{1m}$ ,  $r_{2m}$  and  $r_{3m}$  in Figs. 2 and 3 are the same, respectively.
- (2) We emphasize that the results of our numerical simulation based upon the exact solution for the membrane potential expressed by the Hamiltonian energy function is the same as the result of numerical computation of the Hodgkin–Huxley equations. This discovery reveals an important phenomenon, i.e. although the Hodgkin–Huxley equation is nonlinear in nature, the linear element in the equation is actually the main function.
- (3) Another important consequence of our research results is that we quantitatively accessed the qualitative relationship between the energetic consumption associated with neural activities and neural information processing found by means of (BOLD) fMRI (blood oxygen level-dependent functional magnetic resonance imaging), as observed by neuroscientists at Yale University (Raichle and Gusnard 2002; Hyder et al. 2002; Smith et al. 2002).
- (4) The Hodgkin–Huxley equation and signal transmission with energetic coupling can be unified in the Hamiltonian energy function by means of the energy method presented in this paper.



According to the results mentioned above, we discovered that a possible dynamic mechanism of brain information processing is just a method of the energy coding. Due to the energy coding model's ability to describe mechanisms of brain information processing in biophysical terms, this idea and method can be applied to future research of information encoding in neural ensembles as well as cognitive functioning. In subsequent work many quantitative neural models and analytic results will be given by means of principle of energy coding. For example, using the principle of energetic superposition, we have obtained an evolution of the energy coding principle by observing neuronal ensembles as we varied the intensity of external stimulation continuously, which results in subsets of neurons firing action potentials at supra-threshold and others simultaneously perform activities at sub-threshold level in neural ensembles (Wang and Zhang 2006). It should be pointed out that the main difficulty and defect of phase encoding is that a lot of useful neural information will be lost for a population of low-dimension nonlinear mutually coupled neurons (Wang 2003; Wang et al. 2006), but in the frame of energy coding we can use the principle of energetic superposition for high-dimension nonlinear mutual coupled dynamic system (Zhu 2003). An advantage of the energy principle is that this loss of information does not occur for the dynamic system. Frequency coding and the energy coding also share a corresponding relationship. This is because the energy coding can be used to describe the intensity of frequency coding; however, frequency coding is only an interpretation of experimental results (Purushothman and Bradley 2005), and energy coding can describe a rule for neural information processing in terms of a biophysically reasonable model. By means of the principle of the energy coding, we can understand how some neurons to fire action potentials at supra-threshold and simultaneously other neurons perform activities at sub-threshold in neural ensembles. For each mode of activity the members continuously change in a stochastic dynamic way, so that this kind of neural model constructed with the energy principle can completely describe an evolutionary process of neural coding (Wang and Zhang 2006). We are going to further study the effects of distribution functions of the energy coding model on neuronal populations in temporal and spatial variation states. These distribution functions can express a direct relationship between the functional connection within biological neural networks and energy consumption. Hence, these distribution functions possess very important consequences by providing a sound biophysical framework for metabolic studies of neural activity, fMRI and PET (Mayhew 2003; Taylor 2003). We are aware of no other theory that provides such a theoretical basis for these studies.

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