

大脑皮层内神经元集团的能量演变*

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摘要 在能量编码原理的基础上,利用哈密顿函数得到了大脑皮层内大规模神经元集群在阈下和阈上互相耦合时神经元电位变化的能量函数.根据神经电生理的实验数据得到了高斯白噪声条件下神经元电位活动的膜电位运动方程.研究表明:本文得到的膜电位的均值恰是先前已发表的膜电位运动方程的精确解.在这个基础上,还得到了神经元集群编码的哈密顿函数随时间的演变过程,即神经元集群随时间的能量演化过程的定量表达式.

关键词 神经元集群, 能量编码, 哈密顿函数, 生物学神经网络

引言

用能量的方法研究神经信息处理已得到越来越多的神经科学家的关注,并得到了大量的神经电生理学实验结果的支持^[1-10].在这项研究中基于大脑运作过程中的能量消耗和神经信号处理之间有紧密的耦合关系的实验结果,我们提出了能量编码的概念.利用这样一个理论,能够证明能量编码的概念可以得到与 Hodgkin - Huxley 方程的数值解近似相同的结果^[1-3].最近的一个研究表明在改进了神经元的生物物理模型以后,用能量编码的概念可以得到与 Hodgkin - Huxley 方程的数值解更逼近的结果.这就表明用能量原理研究神经信息处理的确是十分有效的.关于能量编码研究成果的一个详细的扩展可参阅文献[4].

然而,上述研究成果的主要问题是神经元的阈下和阈上活动被分别考虑并进行了分别的描述.但是神经元集群的阈下和阈上活动是耦合在一起的,分别描述显然不符合实际情况.因此,在本论文中我们将神经元的阈下和阈上活动耦合在一起加以考虑和计算,得到了该耦合条件下神经元能量动态编码的量化表达式.再一个主要问题是以前给出的能量函数仅仅与单个神经元的活动有关,这对于研究大脑局部神经网络的信息编码没有太大的实际意义.

因此,在本论文中我们得到了阈下活动和阈上

活动时神经元相互作用的神经元集群随时间变化的哈密顿能量函数.这个哈密顿能量函数反映了局部脑活动时神经元集群的总能量,可以预测这个总能量今后可能是生物学神经网络稳定性计算的基础.因此本文的得到的研究结果具有更大的普遍性,也更具有实际意义.

1 运动方程和哈密顿能量函数

根据文献[2,3],神经元集群中处于阈下和阈上活动时神经元的哈密顿函数可分别用下式表示,阈下活动时:

$$H_{1m} = \frac{(p_m - a_2 - a_3 q_m)^2}{4a_1} - (a_4 q_m^2 + a_5 q_m + a_6)$$

阈上活动时:

$$H_{2m} = \frac{(p_m - d_2 - d_3 q_m)^2}{4d_1} - (d_4 q_m^2 + d_5 q_m + d_6)$$

(1)

其中上述方程中的参数表达可在文献[4]中查阅.

由于 $q_m = U_{0m}$,根据文献[2,3]可知

当第 m 个神经元处于阈下状态时

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

当第 m 个神经元处于阈上状态时

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

由 N 个神经元组成的集团,哈密顿函数可构造为:

$$H = \sum_{m=1}^N [(1-k_m)H_{1m} + k_m H_{2m}] \quad (2)$$

当第 m 个神经元处于阈下状态时 $k_m = 0$, 当第 m 个神经元处于阈上状态时 $k_m = 1$.

方程(2)表示阈上和阈下神经元是互相耦合在一起的. 根据文献[11,12], 含有高斯白噪声的哈密尔顿运动方程为

$$\begin{cases} \dot{p}_m = -\frac{\partial H}{\partial q_m} + \xi_m(t) \\ \dot{q}_m = \frac{\partial H}{\partial p_m} \end{cases} \quad m = 1 \cdots N \quad (3)$$

$$E\xi_m(t) = 0$$

$$E(\xi_m(t)E\xi_l(t+\tau)) = \begin{cases} 2D_m & (m=l) \\ 0 & (m \neq l) \end{cases} \quad (4)$$

由(1)式求出:

$$\begin{aligned} \frac{\partial H_{1m}}{\partial p_m} &= \frac{p_m - a_2 - a_3 q_m}{2a_1} = A_1 p_m + A_2 q_m + A_3 \\ \frac{\partial H_{2m}}{\partial p_m} &= \frac{p_m - d_2 - d_3 q_m}{2d_1} = B_1 p_m + B_2 q_m + B_3 \\ \frac{\partial H_{1m}}{\partial q_m} &= -\frac{a_3}{2a_1}(p_m - a_2 - a_3 q_m) - 2a_4 q_m - a_5 = \\ & A_2 p_m + A_4 q_m + A_5 \\ \frac{\partial H_{2m}}{\partial q_m} &= B_2 p_m + B_4 q_m + B_5 \end{aligned} \quad (5)$$

其中

$$A_1 = \frac{1}{2a_1}; A_2 = \frac{a_3}{2a_1}$$

$$A_3 = A_{31} + A_{32}e^{-ht}$$

$$A_{31} = -\frac{a_{21}}{2a_1}; A_{32} = -\frac{a_{22}}{2a_1}$$

$$A_4 = \frac{a_3^2}{2a_1} - 2a_4, A_5 = A_{51} + A_{52}e^{-ht}$$

$$A_{51} = \frac{a_{21}a_2}{2a_1} - a_{51}, A_{52} = \frac{a_{22}a_3}{2a_1} - a_{52}$$

$$B_1 = \frac{1}{2d_1}, B_2 = -\frac{d_3}{2d_1}$$

$$B_3 = B_{31} + B_{32}e^{-at} + B_{33}e^{p_1 t} + B_{34}e^{p_2 t}$$

$$B_{31} = -\frac{d_{21}}{2d_1}; B_{32} = -\frac{d_{22}}{2d_1}$$

$$B_{33} = -\frac{d_{23}}{2d_1}; B_{34} = -\frac{d_{24}}{2d_1}$$

$$B_4 = \frac{d_3^2}{2d_1} - 2d_4$$

$$B_5 = B_{51} + B_{52}e^{-at} + B_{53}e^{p_1 t} + B_{54}e^{p_2 t}$$

$$B_{51} = \frac{d_{21}d_3}{2d_1} - d_{51}; B_{52} = -\frac{d_{22}d_3}{2d_1} - d_{52}$$

$$B_{53} = \frac{d_{23}d_3}{2d_1} - d_{53}; B_{54} = \frac{d_{24}d_3}{2d_1} - d_{54} \quad (6)$$

将(5)式代入(3)式得到

$$\frac{\partial H}{\partial p_m} = (1-k_m)(A_1 p_m + A_2 q_m + A_3) + k_m(B_1 p_m + B_2 q_m + B_3) = C_{1m} p_m + C_{2m} q_m + C_{3m} \quad (7)$$

其中

$$C_{1m} = (1-k_m)A_1 + k_mB_1$$

$$C_{2m} = (1-k_m)A_2 + k_mB_2$$

$$C_{3m} = (1-k_m)A_3 + k_mB_3 \quad (8)$$

同样可得

$$\frac{\partial H}{\partial q_m} = C_{2m} p_m + C_{4m} q_m + C_{5m} \quad (9)$$

其中

$$C_{4m} = (1-k_m)A_4 + k_mB_4$$

$$C_{5m} = (1-k_m)A_5 + k_mB_5 \quad (10)$$

运动方程(3)对应的 FPK 方程为:

$$\begin{aligned} \frac{\partial p}{\partial t} &= \sum_{m=1}^N \left[\frac{\partial H}{\partial q_m} \frac{\partial H}{\partial p_m} - \frac{\partial H}{\partial p_m} \frac{\partial H}{\partial q_m} + D_m \frac{\partial^2 p}{\partial p_m^2} \right] = \\ & \sum_{m=1}^N \left[(C_{2m} p_m + C_{4m} q_m + C_{5m}) \frac{\partial p}{\partial p_m} - (C_{1m} p_m + \right. \\ & \left. C_{2m} q_m + C_{3m}) \frac{\partial p}{\partial q_m} + D_m \frac{\partial^2 p}{\partial p_m^2} \right] \end{aligned} \quad (11)$$

其中概率密度的形式是 $P = P(p_1, q_1, p_2, q_2, \dots, p_N, q_N, t)$, 设概率密度是互相独立的, 则

$$p = \prod_{m=1}^N [(1-k_m)P_{1m}(p_m, q_m, t) + k_m P_{2m}(p_m, q_m, t)] \quad (12)$$

将(12)式代入(11)式, 得到

$$\begin{aligned} (1-k_m) \frac{\partial P_{1m}}{\partial t} + k_m \frac{\partial P_{2m}}{\partial t} &= (1-k_m) [(A_2 p_m + A_4 q_m + \\ & A_5) \frac{\partial P_{1m}}{\partial p_m} - (A_1 p_m + A_2 q_m + A_3) \frac{\partial P_{1m}}{\partial q_m} + D_m \frac{\partial^2 P_{1m}}{\partial p_m^2}] + \\ & k_m [(B_2 p_m + B_4 q_m + B_5) \frac{\partial P_{2m}}{\partial p_m} - (B_1 p_m + B_2 q_m + \\ & B_3) \frac{\partial P_{2m}}{\partial q_m} + D_m \frac{\partial^2 P_{2m}}{\partial p_m^2}] \quad (m = 1 \cdots N) \end{aligned} \quad (13)$$

从(13)可以分离出两个等式:

$$\begin{aligned} \frac{\partial P_{1m}}{\partial t} &= (A_2 p_m + A_4 q_m + A_5) \frac{\partial P_{1m}}{\partial p_m} - (A_1 p_m + \\ & A_2 q_m + A_3) \frac{\partial P_{1m}}{\partial q_m} + D_m \frac{\partial^2 P_{1m}}{\partial p_m^2} \end{aligned}$$

$$\frac{\partial P_{2m}}{\partial t} = (B_2 p_m + B_4 q_m + B_5) \frac{\partial P_{2m}}{\partial p_m} - (B_1 p_m + B_2 q_m + B_3) \frac{\partial P_{2m}}{\partial q_m} + D_m \frac{\partial^2 P_{2m}}{\partial p_m^2} \quad (14)$$

根据文献[11],取 $P_{1m}(p_m, q_m, t)$ 的特征函数 $\phi(u, v, t)$,则(14)第一式对应的特征方程为:

$$\frac{\partial \phi}{\partial t} = (A_1 v - A_2 u) \phi'_u + (A_2 v - A_4 u) \phi'_v + [j(A_3 v - A_5 u) - D_m u^2] \phi \quad (15)$$

偏微分方程(15)可化为常微分方程组:

$$\frac{dt}{1} = \frac{du}{A_2 u - A_1 v} = \frac{dv}{A_4 u - A_2 v} = \frac{d\phi}{\phi [j(A_3 v - A_5 u) - D_m u^2]} \quad (16)$$

从(16)前三式得出:

$$\begin{cases} \dot{u} = A_2 u - A_1 v \\ \dot{v} = A_4 u - A_2 v \end{cases} \quad (17)$$

通解为:

$$\begin{cases} u = l_1 e^{\lambda_1 t} + l_2 e^{-\lambda_1 t} \\ v = \frac{1}{A_1} [(A_2 - \lambda_1) l_1 e^{\lambda_1 t} + (A_2 + \lambda_1) l_2 e^{-\lambda_1 t}] \end{cases} \quad (18)$$

从(18)求出:

$$\begin{cases} l_1 = \frac{A_1}{2\lambda_1} e^{-\lambda_1 t} \left(\frac{A_2 + \lambda_1}{A_1} u - v \right) \\ l_2 = \frac{A_1}{2\lambda_1} e^{\lambda_1 t} \left(\frac{\lambda_1 - A_2}{A_1} u + v \right) \end{cases} \quad (19)$$

利用(18)(19)关系式,可以求出:

$$\int u_m dt = \frac{1}{\lambda} (l_1 e^{\lambda t} - l_2 e^{-\lambda t}) = \frac{1}{\lambda^2} (C_{2m} u_m - C_{1m} v_m)$$

$$\int v_m dt = \frac{1}{C_{1m} \lambda} ((C_{2m} - \lambda) l_1 e^{\lambda t} - (C_{2m} + \lambda) l_2 e^{-\lambda t}) = \frac{1}{\lambda^2} (C_{4m} u_m - C_{2m} v_m)$$

$$\int e^{-at} u_m dt = \frac{l_1}{\lambda - a} e^{(\lambda-a)t} - \frac{l_2}{\lambda + a} e^{-(\lambda+a)t} = \frac{e^{-at}}{\lambda^2 - a^2} ((C_{2m} + a) u_m - C_{1m} v_m)$$

$$\int e^{-at} v_m dt = \frac{C_{2m} - \lambda}{C_{1m}(\lambda - a)} l_1 e^{(\lambda-a)t} - \frac{C_{2m} + \lambda}{C_{1m}(\lambda + a)} l_2 e^{-(\lambda+a)t} = \frac{e^{-at}}{\lambda^2 - a^2} (C_{4m} u_m - (C_{2m} - a) v_m)$$

$$\int u_m^2 dt = \frac{l_1^2}{2\lambda} e^{2\lambda t} - \frac{l_2^2}{2\lambda} e^{-2\lambda t} + 2l_1 l_2 t =$$

$$\frac{1}{2\lambda^2} ((-C_{1m} C_{4m} t + C_{2m}) u_m^2 - A_1^2 t v_m^2 +$$

$$(2C_{1m} C_{2m} t - C_{1m}) u_m v_m) \quad (20)$$

从常微分方程组(16)第一、四式得出:

$$\begin{aligned} \varphi = l_3 e^{[j(A_3 v - A_5 u) - D_m u^2]t} = l_3 \exp \{ j [\frac{A_{31}}{A_1 \lambda_1} ((A_2 - \lambda_1) l_1 e^{\lambda_1 t} - (A_2 + \lambda_1) l_2 e^{-\lambda_1 t}) + A_{32} (\frac{A_2 - \lambda_1}{A_1 (\lambda - h)} l_1 e^{\lambda_1 - ht} - \frac{A_2 + \lambda_1}{A_1 (\lambda + h)} l_2 e^{(\lambda_1 + h)t}) - \frac{A_{51}}{\lambda_1} (l_1 e^{\lambda_1 t} - l_2 e^{-\lambda_1 t}) - A_{52} (\frac{l_1}{\lambda_1 - h} e^{(\lambda_1 - h)t} - \frac{l_2}{\lambda_1 + h} e^{-(\lambda_1 + h)t})] - D_m (\frac{l_1^2}{2\lambda_1} e^{2\lambda_1 t} - \frac{l_2^2}{2\lambda_1} e^{-2\lambda_1 t} + 2l_1 l_2 t) \} = l_3 \exp \{ j ((\frac{A_{31} A_4 - A_2 A_{51}}{\lambda_1^2} + \frac{A_{32} A_4 - (A_2 + h) A_{52}}{\lambda_1^2 - h^2} e^{-ht}) u + (\frac{A_1 A_{51} - A_2 A_{31}}{\lambda_1^2} + \frac{A_1 A_{52} - (A_2 - h) A_{32}}{\lambda_1^2 - h^2} e^{-ht}) v) - \frac{D_m}{2\lambda_1^2} ((A_2 - A_1 A_4 t) u^2 - A_1^2 t v^2 + A_1 (2A_2 t - 1) uv) \} \end{aligned} \quad (21)$$

设初始条件

$$\begin{aligned} P_{1m}(p_m, q_m, t/p_{m1}, q_{m1}, 0) = \delta(p_m - p_{m1}) \delta(q_m - q_{m1}) \end{aligned} \quad (22)$$

代入特征函数定义式,可得到:

$$\begin{aligned} \varphi(u, v, 0) = \exp [j (up_{m1} + vq_{m1})] = \exp [j (l_1 + l_2) p_{m1} + \frac{q_{m1}}{A_1} ((A_2 - \lambda) l_1 + (A_2 + \lambda) l_2)] \end{aligned} \quad (23)$$

代入 Φ 表达式(21),可得:

$$\begin{aligned} \varphi(u, v, 0) = l_3 \exp \{ j [\frac{A_{31}}{A_1 \lambda} ((A_2 - \lambda_1) l_1 - (A_2 + \lambda_1) l_2) + A_{32} (\frac{A_2 - \lambda_1}{A_1 (\lambda_1 - h)} l_1 - \frac{A_2 + \lambda_1}{A_1 (\lambda_1 + h)} l_2) - \frac{A_{51}}{\lambda_1} (l_1 - l_2) - A_{52} (\frac{l_1}{\lambda_1 - h} - \frac{l_2}{\lambda_1 + h})] - \frac{D_m}{2\lambda_1} (l_1^2 - l_2^2) \} \end{aligned} \quad (24)$$

结合(23)(24),可以得到

$$\begin{aligned} l_3 = \exp \{ j [\frac{A_1}{\lambda_1} (\frac{A_2 + \lambda_1}{A_1} u - v) [- \frac{\lambda_1 q_{m1}}{A_1} - \frac{A_2 A_{31}}{A_1 \lambda_1} - \frac{A_{32} \lambda_1 (A_2 - h)}{A_1 (\lambda_1^2 - h^2)} + \frac{A_{51}}{\lambda_1} + \frac{\lambda_1 A_{52}}{(\lambda^2 - h^2)}] e^{-\lambda_1 t} + \frac{D_m A_1^2}{8\lambda_1^3} [(\frac{A_2 + \lambda_1}{A_1} u - v)^2 e^{-2\lambda_1 t} - (\frac{\lambda_1 - A_2}{A_1} u + v)^2 e^{2\lambda_1 t}] \} \end{aligned} \quad (25)$$

将(25)代入(23)得到

$$\begin{aligned} \varphi(u, v, t) = \exp [j (M_{1m} u + M_{2m} v) + R_{1m} u^2 + R_{2m} v^2 + R_{3m} uv] \end{aligned} \quad (26)$$

其中

$$\begin{aligned}
 M_{1m} &= \frac{A_{31}A_4 - A_2A_{51}}{\lambda_1^2} + \frac{A_{32}A_4 - (A_2 + h)A_{52}}{\lambda_1^2 - h^2} e^{-ht} + \\
 &\frac{A_2 + \lambda_1}{\lambda_1} \left(-\frac{\lambda_1 U_{0m}(0)}{A_1} - \frac{A_2 A_{31}}{A_1 \lambda_1} - \right. \\
 &\left. \frac{\lambda_1 A_{32}(A_2 - h)}{A_1(\lambda_1^2 - h^2)} + \frac{A_{51}}{\lambda_1} + \frac{\lambda_1 A_{52}}{\lambda_1^2 - h^2} \right) e^{-\lambda_1 t} \\
 M_{2m} &= \frac{A_1 A_{51} - A_2 A_{31}}{\lambda_1^2} + \frac{A_1 A_{52} - (A_2 - h) A_{32}}{\lambda_1^2 - h^2} e^{-ht} + (U_{0m}(0)) + \\
 &\frac{A_2 A_{31}}{\lambda_1^2} + \frac{A_{32}(A_2 - h)}{(\lambda_1^2 - h^2)} - \frac{A_1 A_{51}}{\lambda_1^2} + \frac{A_1 A_{52}}{\lambda_1^2 - h^2} e^{-\lambda_1 t} \\
 R_{1m} &= -\frac{D_m}{2\lambda_1^2} (A_2 - A_1 A_4 t - \frac{1}{4\lambda_1} ((A_2 + \lambda_1)^2 e^{-2\lambda_1 t} - \\
 &(\lambda_1 - A_2)^2 e^{2\lambda_1 t})) \\
 R_{2m} &= \frac{A_1^2 D_m}{2\lambda_1^2} (t + \frac{(e^{-2\lambda_1 t} - e^{2\lambda_1 t})}{4\lambda_1}) \\
 R_{3m} &= -\frac{A_1 D_m}{2\lambda_1^2} (2A_2 t - 1 + \\
 &\frac{(A_2 + \lambda_1)e^{-2\lambda_1 t} + (\lambda_1 - A_2)e^{2\lambda_1 t}}{2\lambda_1}) \quad (27)
 \end{aligned}$$

令

$$\Lambda = \begin{pmatrix} -2R_{1m} & -R_{3m} \\ -R_{3m} & -2R_{2m} \end{pmatrix},$$

则

$$\begin{aligned}
 \Lambda^{-1} &= \begin{pmatrix} \frac{2R_{2m}}{R_{3m}^2 - 4R_{1m}R_{2m}} & -\frac{R_{3m}}{R_{3m}^2 - 4R_{1m}R_{2m}} \\ -\frac{R_{3m}}{R_{3m}^2 - 4R_{1m}R_{2m}} & \frac{2R_{1m}}{R_{2m}^2 - 4R_{1m}R_{2m}} \end{pmatrix} \\
 |\Lambda| &= 4R_{1m}R_{2m} - R_{3m}^2 = \frac{D_m^2}{\lambda_1^4} \left[-A_1^2(\lambda_1^2 t^2 + \frac{1}{2}) - \right. \\
 &\frac{A_1 A_4 (\lambda_1^2 - 1)t + (A_2 - A_1^2(\lambda_1 - A_2))}{4\lambda_1} e^{-2\lambda_1 t} + \\
 &\left. \frac{A_1 A_4 (A_2^2 - 1)t + (A_2 - A_1^2(\lambda_1 - A_2))}{4\lambda_1} e^{2\lambda_1 t} \right] \quad (28)
 \end{aligned}$$

可以看出,特征函数表示的是二元联合高斯分布,其概率密度为:

$$\begin{aligned}
 P_{1m}(p_m, q_m, t) &= \frac{1}{2\pi\sqrt{|\Lambda|}} \exp\left[-\frac{1}{2}(p_m - M_{1m}, \right. \\
 &\left. q_m - M_{2m})\Lambda^{-1} \begin{pmatrix} p_m - M_{1m} \\ q_m - M_{2m} \end{pmatrix}\right] \quad (29)
 \end{aligned}$$

由概率论可以很容易的看出,上述概率密度中的广义动量 p_m 和广义位移 q_m 在均值 M_{1m} 和 M_{2m} 处形成高峰.当 D_m 越小,高峰越陡峭,可以认为 p_m 和 q_m

分别位于 M_{1m} 和 M_{2m} 处.

同理,取 $P_{2m}(p_m, q_m, t)$ 的特征函数 $\phi(u, v, t)$, 则特征方程为

$$\frac{\partial \phi}{\partial t} = (B_1 v - B_2 u)\phi'_u + (B_2 v - B_4 u)\phi'_v + [j(B_3 v - B_5 u) - D_m u^2]\phi \quad (30)$$

上述偏微分方程可化为下列常微分方程组:

$$\begin{aligned}
 \frac{dt}{1} &= \frac{du}{B_2 u - B_1 v} = \frac{dv}{B_4 u - B_2 v} = \\
 &\frac{d\phi}{\phi[j(B_3 v - B_5 u) - D_m u^2]} \quad (31)
 \end{aligned}$$

从(31)前三式得出:

$$\begin{cases} \dot{u} = B_2 u - B_1 v \\ \dot{v} = B_4 u - B_2 v \end{cases} \quad (32)$$

上述方程的通解为:

$$\begin{cases} u = l_1 e^{\lambda_2 t} + l_2 e^{-\lambda_2 t} \\ v = \frac{1}{B_1} [(B_2 - \lambda_1)l_1 e^{\lambda_2 t} + (B_2 + \lambda_1)l_2 e^{-\lambda_2 t}] \end{cases} \quad (33)$$

从上式求出:

$$\begin{cases} l_1 = \frac{B_1}{2\lambda_1} e^{-\lambda_2 t} (\frac{B_2 + \lambda_1}{B_1} u - v) \\ l_2 = \frac{B_1}{2\lambda_1} e^{\lambda_2 t} (\frac{\lambda_1 - B_2}{B_1} u + v) \end{cases} \quad (34)$$

从常微分方程组(31)第一和第四式可求得:

$$\begin{aligned}
 \phi &= l_3 \exp\{ \int [j(B_3 v - B_5 u) - D_m u^2] dt \} = \\
 &l_3 \exp\{ j \left[\frac{B_{31}}{B_1 \lambda_2} ((B_2 - \lambda_2)l_1 e^{\lambda_2 t} - (B_2 + \lambda_2)l_2 e^{-\lambda_2 t}) + \right. \\
 &\frac{B_{32}}{B_1} \left[\frac{B_2 - \lambda_2}{\lambda_2 - a} l_1 e^{(\lambda_2 - a)t} - \frac{B_2 + \lambda_2}{\lambda_2 + a} l_2 e^{-(\lambda_2 + a)t} \right] + \\
 &\frac{B_{33}}{B_1} \left[\frac{B_2 - \lambda_2}{\lambda_2 + p_1} l_1 e^{(\lambda_2 + p_1)t} - \frac{B_2 + \lambda_2}{\lambda_2 - p_1} l_2 e^{-(\lambda_2 - p_1)t} \right] + \\
 &\frac{B_{34}}{B_1} \left[\frac{B_2 - \lambda_2}{\lambda_2 + p_2} l_1 e^{(\lambda_2 + p_2)t} - \frac{B_2 + \lambda_2}{\lambda_2 - p_2} l_2 e^{-(\lambda_2 - p_2)t} \right] - \frac{B_{51}}{\lambda_2} (l_1 e^{\lambda_2 t} - \\
 &l_2 e^{-\lambda_2 t}) - B_{52} \left(\frac{l_1 e^{(\lambda_2 - a)t}}{\lambda_2 - a} - \frac{l_2 e^{-(\lambda_2 + a)t}}{\lambda_2 + a} \right) - B_{53} \left(\frac{l_1 e^{(\lambda_2 + p_1)t}}{\lambda_2 + p_1} - \right. \\
 &\left. \frac{l_2 e^{-(\lambda_2 - p_1)t}}{\lambda_2 - p_1} \right) - B_{54} \left(\frac{l_1 e^{(\lambda_2 + p_2)t}}{\lambda_2 + p_2} - \frac{l_2 e^{-(\lambda_2 - p_2)t}}{\lambda_2 - p_2} \right) \left. \right\} - D_m \left(\frac{l_1^2 e^{2\lambda_2 t}}{2\lambda_2} - \right. \\
 &\left. \frac{l_2^2 e^{-2\lambda_2 t}}{2\lambda_2} + 2l_1 l_2 t \right) \} = l_3 \exp\{ j \left[\frac{B_{31} B_4 - B_2 B_{51}}{\lambda_2^2} + \right. \\
 &\frac{B_{32} B_4 - (B_2 + a) B_{52}}{\lambda_2^2 - a^2} e^{-at} + \frac{B_{33} B_4 - (B_2 - p_1) B_{53}}{\lambda_2^2 - p_1^2} e^{p_1 t} + \\
 &\left. \frac{B_{34} B_4 - (B_2 - p_2) B_{54}}{\lambda_2^2 - p_2^2} e^{p_2 t} \right] u + \left[\frac{B_1 B_{51} - B_2 B_{31}}{\lambda_2^2} + \right.
 \end{aligned}$$

$$\frac{B_1 B_{32} - (B_2 - a) B_{32}}{\lambda_1^2 - a^2} e^{-at} + \frac{B_{33} B_1 - (B_2 + p_1) B_{33}}{\lambda_2^2 - p_1^2} e^{p_1 t} + \frac{B_{34} B_1 - (B_2 + p_2) B_{34}}{\lambda_2^2 - p_2^2} e^{p_2 t} \} v \} - D_m \left[\frac{B_2 - B_1 B_4 t}{2\lambda_2^2} u^2 - \frac{B_1^2 t}{2\lambda_2^2} v^2 + \frac{B_1 (2B_2 t - 1)}{2\lambda_2^2} uv \right] \} \quad (35)$$

设初始条件

$$P_{2m}(p_m, q_m, t/p_{m2}, q_{m2}, 0) = \delta(p_m - p_{m2}) \delta(q_m - q_{m2}) \quad (36)$$

代入特征函数定义式,可得到:

$$\varphi(u, v, 0) = \exp[j(up_{m2} + vq_{m2})] = \exp[j(l_1 + l_2)p_{m2} + \frac{q_{m2}}{B_1}((B_2 - \lambda_2)l_1 + (B_2 + \lambda_2)l_2)] \quad (37)$$

代入 Φ 表达式,可得

$$\begin{aligned} \varphi(u, v, 0) = & l_3 \exp \{ j \left[\frac{B_{31}}{B_1 \lambda_2} ((B_2 - \lambda_2)l_1 - (B_2 + \lambda_2)l_2) + \frac{B_{32}}{B_1} \left(\frac{B_2 - \lambda_2}{(\lambda_2 - a)} l_1 - \frac{B_2 + \lambda_2}{(\lambda_1 + a)} l_2 \right) + \frac{B_{33}}{B_1} \left(\frac{B_2 - \lambda_2}{\lambda_2 + p_1} l_1 - \frac{B_2 + \lambda_2}{\lambda_1 - p_1} l_2 \right) + \frac{B_{34}}{B_1} \left(\frac{B_2 - \lambda_2}{\lambda_2 + p_2} l_1 - \frac{B_2 + \lambda_2}{\lambda_1 - p_2} l_2 \right) - \frac{B_{51}}{\lambda_2} (l_1 - l_2) - B_{52} \left(\frac{l_1}{\lambda_2 - a} - \frac{l_2}{\lambda_2 + a} \right) - B_{53} \left(\frac{\lambda_1}{\lambda_2 + \pi_1} - \frac{\lambda_2}{\lambda_2 - \pi_1} \right) - B_{54} \left(\frac{\lambda_1}{\lambda_2 + \pi_2} - \frac{\lambda_2}{\lambda_2 - \pi_2} \right) \right] - \frac{\Delta u}{2\lambda_2} (\lambda_1^2 - \lambda_2^2) \} \end{aligned} \quad (38)$$

结合(37)(38),可以得到 l_3

$$\begin{aligned} l_3 = & \exp \{ j B_1 \left(\frac{B_2 + \lambda_2}{B_1} u - v \right) \left[-\frac{q_{m1}}{B_1} - \frac{B_2 B_{31}}{B_1 \lambda_2^2} - \frac{B_{32}}{B_1} \frac{B_{32} (B_2 - a)}{\lambda_2^2 - a^2} - \frac{B_{33} (B_2 + p_1)}{B_1 (\lambda_2^2 - p_1^2)} - \frac{B_{34} (B_2 + p_2)}{B_1 (\lambda_2^2 - p_2^2)} + \frac{B_{51}}{\lambda_2^2} + \frac{B_{52}}{\lambda_2^2 - a^2} + \frac{B_{53}}{\lambda_2^2 - p_1^2} + \frac{B_{54}}{\lambda_2^2 - p_2^2} \right] e^{-\lambda_2 t} + \frac{D_m B_1^2}{8\lambda_2^3} \left[\left(\frac{B_2 + \lambda_2}{B_1} u - v \right)^2 e^{-2\lambda_2 t} - \left(\frac{\lambda_2 - B_2}{B_1} u + v \right)^2 e^{2\lambda_2 t} \right] \} \end{aligned} \quad (39)$$

将上式代入(35)

$$\varphi(u, v, t) = \exp \left[j (M_{1m} u + M_{2m} v) + R_{1m} u^2 + R_{2m} v^2 + R_{3m} uv \right] \quad (40)$$

其中

$$\begin{aligned} M_{1m} = & \frac{B_{31} B_4 - B_2 B_{51}}{\lambda_2^2} + \frac{B_{32} B_4 - (B_2 + a) B_{52}}{\lambda_2^2 - a^2} e^{-at} + \frac{B_{33} B_4 - (B_2 - p_1) B_{53}}{\lambda_2^2 - p_1^2} e^{p_1 t} + \frac{B_{34} B_4 - (B_2 - p_2) B_{54}}{\lambda_2^2 - p_2^2} e^{p_2 t} + \end{aligned}$$

$$\frac{B_2 + \lambda_2}{\lambda_2 - a} \left[\frac{a d_{51}}{\lambda_2^2} + \frac{(p_1 + a)(d_{33} - p_1 d_{23})}{\lambda_2^2 - p_1^2} + \frac{(p_2 + a)(d_{34} - p_2 d_{24})}{\lambda_2^2 - p_2^2} + 2d(K_1(\lambda_2 + a) - K_2(\lambda_2 - a)) \right] e^{-\lambda_2 t}$$

$$M_{2m} = \frac{B_1 B_{51} - B_2 B_{51}}{\lambda_2^2} + \frac{B_1 B_{52} - (B_2 - a) B_{52}}{\lambda_2^2 - a^2} e^{-at} + \frac{B_{53} B_1 - (B_2 + p_1) B_{53}}{\lambda_2^2 - p_1^2} e^{p_1 t} + \frac{B_{54} B_1 - (B_2 + p_2) B_{54}}{\lambda_2^2 - p_2^2} e^{p_2 t} +$$

$$\frac{B_2}{\lambda_2 - a} \left[\frac{a d_{51}}{\lambda_2^2} + \frac{(p_1 + a)(d_{33} - p_1 d_{23})}{\lambda_2^2 - p_1^2} + \frac{(p_2 + a)(d_{34} - p_2 d_{24})}{\lambda_2^2 - p_2^2} + 2d_1(K_1(\lambda_2 + a) - K_2(\lambda_2 - a)) \right] e^{-\lambda_2 t}$$

$$R_{1m} = -\frac{D_m}{2\lambda_2^2} (B_2 - B_1 B_4 t - \frac{1}{4\lambda_2} ((B_2 + \lambda_2)^2 e^{-2\lambda_2 t} - (\lambda_2 - B_2)^2 e^{2\lambda_2 t}))$$

$$R_{2m} = \frac{D_m B_1^2}{2\lambda_2^2} \left(t + \frac{(e^{-2\lambda_2 t} - e^{2\lambda_2 t})}{4\lambda_2} \right)$$

$$R_{3m} = -\frac{D_m B_1}{2\lambda_2^2} (2B_2 t - 1 + \frac{(B_2 + \lambda_2) e^{-2\lambda_2 t} + (\lambda_2 - B_2) e^{2\lambda_2 t}}{2\lambda_2}) \quad (41)$$

可以证明, $P_{2m}(p_m, q_m, t)$ 也同样服从二元高斯分布, 广义动量 p_m 和广义位移 q_m 也分别在均值 M_{1m} 和 M_{2m} 处形成峰值.

2 初步讨论

1. 本文的结论得到均值为 $p_m = M_{1m}, q_m = M_{2m}$, 且在均值处为概率密度的最高峰. 而且广义位移 $q_m = U_{0m}$ 正好就是膜电位.

2. 与前一篇文章[2]比较, 均值 M_{2m} 就是膜电位运动方程的精确解. 说明在白噪声影响下, 膜电位还是以精确解为中心, 同时向两边扩散.

3. 将均值代入 H 表达式, $H = \sum_{m=1}^N [(1 - k_m) H_{1m}(M_{1m}, M_{2m}, t) + k_m H_{2m}(M_{1m}, M_{2m}, t)]$ 表示 N 个神经元组成的神经元集团的哈密顿函数的最可能的结果. 随着时间的推移, 可以得到哈密顿函数的演变过程, 也就是能量的演变过程.

4. 阈下时, 膜电位精确解含有参数 A , 其实是其他神经元对第 m 个神经元的作用, 它决定了神经元活动是否从阈下跃迁到阈上活动. 所以 A 含有

两层意思:一是耦合作用,二是决定了 k_m 的数值.

5. 由于阈上神经元只能维持 $2ms$ 左右,所以密度分布的时间范围最多也只能保持在 $2ms$ 之内,然后重新选择 k_m 和初始条件,再次用相同的公式计算,可得到神经元集群的新的能量演变.

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ENERGY EVOLUTION OF NEURAL POPULATION IN CEREBRAL CORTEX*

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Abstract Based on the principle of energy coding, an energy function of variety of electric potential of neural population in cerebral cortex was proposed. The energy function can reflect the energy evolution of neural population with time, and the coupling relationship at sub-threshold and at supra-threshold stimulation. The Hamiltonian motion equation of the membrane potential was obtained under the condition of Gaussian white noise according to neuro-electrophysiological data. The results show that the mean of the membrane potential obtained is just the exact solution of the motion equation of the membrane potential in the previously published paper.

Key words neural population, energy coding, Hamiltonian function, biological neural network