Identification of a Free Energy Functional in an Integro-Differential Equation Model for Neuronal Network Activity

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Abstract

Neuronal activity in a synaptically coupled network of excitatory and inhibitory neurons can be modeled by an integro-differential equation. Solutions to this equation represent cellular activity and are dependent on the neuron's spatial location and time. One area of interest to researchers has been the identification and analysis of stationary bump solution which are steady states of the evolution problem. In this brief report we furnish an energy functional. It is expected that this energy will be useful in analyzing the dynamic behavior of the system, finding steady states, studying the stability of these stationary solutions, and developing numerical methods.

1. Introduction: Population activity in neuronal networks is an area of ongoing research interest. The models for this activity typically involve integro-differential equations and arise through a limiting argument from a discrete synaptically coupled network of excitatory and inhibitory neurons [1]. The dependent variables are the spatial location and time. Studies of these models focus on wave behavior obtained through numerical computations and traveling wave arguments [2]. There is also interest in stationary bump solutions (see [3], [4], or [5]). The wave behavior has been observed in various experimental studies involving retinal activity in the brain (see [6] or [7]) and the cortex when the inhibitory activity is pharmacologically blocked [2]. Bumps are thought to occur in working memory (see [3] or [8]) and in head direction cells that are found in the hippocampus [9].

We will study the following integro-differential equation model for neuronal activity:

$$u_t + u = w * P(u - \theta) \tag{1}$$

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Here $u = u(x,t)$ is a measure of the neuron activity at spatial location $x \in R^n$ where $n = 1, 2,$ or 3 and time t. The symbol $*$ is for convolution over the spatial domain; $(w*v)(x) = \int_{R^n} w(x-y)v(y)dy$. The weight function $w = w(z)$ represents the connectivity or coupling in the network. We assume that w is even, has compact support or decays quite quickly away from 0, and

$$\int_R w\ dx = 1. \tag{2}$$

Negative values of w represent inhibitory connections while positive values are excitatory. Sometimes w is defined to be a Gaussian [2] or a Mexican hat [3]. The nonlinear function $P(v)$ measures the firing rate. We assume P is nonnegative and monotone increasing. Sometimes P is close to a Heaviside function although it appears that our theory will be more applicable in cases where P is smoother. For example, in [4], $P(u-\theta) = \frac{1}{2}(1 + \tanh(\beta(u-\theta)))$ where $\beta > 0$. The constant θ is a firing threshold. The reader should consult [1] for a derivation, more references, and discussion of this model.

Energy functionals are useful in the analysis of evolution problems such as (1). In a generic situation the energy of a solution trajectory is decreasing as $t \to \infty$. Critical points of the energy are steady state solutions and minimums are stable. There are many examples of such energy functionals in the time-dependent partial differential equations literature (see, for instance, [10], [11], [12], or [13]).

In this short report we derive an energy functional for (1) which we anticipate will be useful in studies of the dynamic and equilibrium solutions. Much of our argument closely follows the work in Bates and Chmaj [14]. The key difference is that in our case there is a nonlinear function of u inside the convolution integral instead of just u. We also compare this energy to one obtained by Hopfield [15] that is derived in a related but spatially discrete model.

2. The Energy Functional: In this section we show that if u is a solution of (1) then

$$\frac{d}{dt}E(u) = -\int_{R^n} P'(u-\theta)u_t^2 dx \leq 0 \tag{3}$$

where E is the energy;

$$E(u) = \frac{1}{4}\int_{R^n}\int_{R^n} w(x-y)\left(P(u(x,t)-\theta) - P(u(y,t)-\theta)\right)^2\ dxdy + \int_{R^n} F(u)dx \tag{4}$$

and

$$F(u) = \int_0^u P'(s-\theta)\left(s - P(s-\theta)\right)ds.$$

Note that if w is positive then E will be bounded from below. Following [14], one can show that in the case the support of w is small the first term in (4) is close to an integral over R^n of the square of the spatial gradient of $P(u-\theta)$ (It is argued in [14] the first term in (3) is a natural generalization of the Cahn-Hilliard energies, see [11]).

The first step is to derive (3) is the following key identity which was shown in [14]:

$$\int_{R^n} (w*v)\, v_t\, dx = \int_{R^n} v v_t\, dx - \frac{1}{4}\frac{d}{dt}\int_{R^n}\int_{R^n} w(x-y)\,(v(x,t)-v(y,t))^2\ dxdy. \tag{5}$$

For completeness we present the derivation. We start with the double-integral term;

$$\frac{d}{dt}\int_{R^n}\int_{R^n} w(x-y)\,(v(x,t)-v(y,t))^2\ dxdy = 2\int_{R^n}\int_{R^n} w(x-y)\,(v(x,t)-v(y,t))\,(v_t(x,t)-v_t(y,t))\ dxdy$$

Multiplying out the terms in parentheses and using the assumption that w is even we have

$$\begin{aligned}\frac{d}{dt}\int_{R^n}\int_{R^n} w(x-y)\,(v(x,t)-v(y,t))^2\ dxdy \;\; = \;\; & 2[\int_{R^n}(\int_{R^n} w(y-x)dy)v(x,t)v_t(x,t)dx \\ & + \int_{R^n}(\int_{R^n} w(x-y)dx)v(y,t)v_t(y,t)dy \\ & - \int_{R^n}\int_{R^n} w(x-y)v(x,t)v_t(y,t)dxdy \\ & - \int_{R^n}\int_{R^n} w(y-x)v(y,t)v_t(x,t)dxdy]\end{aligned}$$

Using the assumption (2) we obtain

$$\frac{d}{dt}\int_{R^n}\int_{R^n} w(x-y)\,(v(x,t)-v(y,t))^2\ dxdy = 4\left[\int_{R^n} v(x,t)v_t(x,t)dx - \int_{R^n}(w*v)(x,t)\ v_t(x,t)\ dx\right]$$

which proves the identity (5).

To derive our free energy functional we let $v(x,t) = P(u(x,t)-\theta)$. Multiplying (1) by $v_t = \frac{d}{dt}P(u-\theta)$ and integrating over R^n we obtain

$$\int_{R^n} u_t\ \frac{d}{dt}P(u-\theta)\ dx + \int_{R^n} u\ \frac{d}{dt}P(u-\theta)\ dx = \int_{R^n}(w*v)\ v_t\ dx.$$

So, using the identity (5),

$$\int_{R^n} P'(u-\theta)u_t^2\ dx = -\int_{R^n} P'(u-\theta)u\ u_t\ dx + \int_{R^n} v\ v_t dx - \frac{1}{4}\frac{d}{dt}\int_{R^n}\int_{R^n} w(x-y)\,(v(x,t)-v(y,t))^2\ dxdy$$

or

$$\frac{1}{4}\frac{d}{dt}\int_{R^n}\int_{R^n} w(x-y)\,(v(x,t)-v(y,t))^2\ dxdy + \int_{R^n} P'(u-\theta)\,(u-P(u-\theta))\ u_t\ dx = -\int_{R^n} P'(u-\theta)u_t^2\ dx.$$

which verifies (3) once the assignments for F and E are made.

3. Comparison to Hopfield's Energy: If we identify sums with integrals the free energy (3) is the same as one derived previously but in a different form. We now proceed to show that (3) is the same as the one introduced in [15]. To assist in this matching let $v = g(u) = P(u-\theta)$ and recall that $(g^{-1})'(v) = 1/g'(u)$. We furthur assume $g(0) = 0$ as in [15] and then rewrite the first term in our energy;

$$\frac{1}{4}\int_{R^n}\int_{R^n} w(x-y)\left(v(x,t)-v(y,t)\right)^2\ dxdy = \frac{1}{2}\int_{R^n}\int_{R^n} w(x-y)\left(v(x,t)^2 - v(x,t)v(y,t)\right)\ dxdy$$

where we used the fact that w is even. From (2) we have

$$\int_{R^n}\int_{R^n} w(x-y)v(x,t)^2\ dxdy = \int_{R^n} v(x,t)^2 dx = \int_{R^n} g(u(x,t))^2\ dx.$$

Note also that

$$g(u(x,t))^2 = 2\int_0^{u(x,t)} g(s)g'(s)\ ds.$$

So,

$$\frac{1}{4}\int_{R^n}\int_{R^n} w(x-y)\left(v(x,t)-v(y,t)\right)^2\ dxdy = -\frac{1}{2}\int_{R^n}\int_{R^n} w(x-y)v(x,t)v(y,t)\ dxdy + \int_{R^n}\int_0^{u(x,t)} g(s)g'(s)\ ds\ dx. \tag{6}$$

We now consider the second term in (3);

$$\int_{R^n} F(u)\ dx = \int_{R^n}\left(\int_0^u g'(s)s\ ds - \int_0^u g'(s)g(s)\ ds\right)\ dx$$

The second term on the right side of the above equation will cancel with the second term on the right side of (6). Then, for the remaining term,

$$\int_0^u g'(s)sds = \int_{g(0)}^{g(u)} g^{-1}(r)\ dr$$

where we let $r = g(s)$ and thus $dr = g'(s)\ ds$. Hence

$$\int_0^u g'(s)s\ ds = \int_0^v g^{-1}(r)\ dr$$

which shows that once integrals over R^n in x are connected to sums over an index i the energy E is the same as in [15]. Note furthur that the rate of decay terms match also; from (3) we have

$$-\int_{R^n} g'(u)u_t^2 dx = -\int_{R^n}\frac{1}{g'(u)}\left(g'(u)u_t\right)^2\ dx = -\int_{R^n}(g^{-1})'(v)v_t^2\ dx$$

which is similar to equation (9) in [15].

4. Critical Points of E: Here, we compute the functional derivative of E with respect to u. This returns, as expected, the steady state equation.

A short calculation using the meanvalue theorem shows that

$$\lim_{\epsilon \to 0} \left(\frac{E(u + \epsilon\phi) - E(u)}{\epsilon} \right) = -\int_{R^n} (w * g(u))g'(u)\phi \, dx + \int_{R^n} g'(u)u\phi \, dx$$

where ϕ is a smooth test function with compact support. Thus critical points of the energy satisfy

$$(-w * g(u) + u)g'(u) = 0$$

and, if $g'(u) \neq 0$, we obtain the steady state equation

$$-w * P(u - \theta) + u = 0$$

where we replaced $g(u)$ by our original formula $P(u - \theta)$.

5. Concluding Remarks: Certain integro-differential equations models are emerging as mathematically interesting and important models of neuronal network activity. Energy functionals, if available, are often useful in the analysis of evolution problems. In this letter we have introduced such an energy for a prototype integro-differential equation neuronal network model and briefly discussed connections with earlier literature on these energies in the setting of evolution problems. We anticipate the energy (3) will be useful in studying the dynamics of this model of neuronal activity.

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