Lattices with spatially extended coupling and the statistical properties of neural populations

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Abstract. The statistical properties of a population of neurons is examined by a study of the invariant measures generated by a coupled map lattice. The coupling between lattice neighbors is extended beyond nearest to include all members of the lattice (mean field coupling), to a portion of the lattice, and as a decreasing function of distance between lattice members. Sufficient conditions for the asymptotic stability of these lattices are discussed.

1. Introduction

A characteristic of the central nervous system is that each neuron in interconnected to large numbers of neurons ($\sim 10^3 - 10^4$) [1,16]. These interconnections occur on two length scales: short range connectivity ($\sim$ 200-500 μ) and long range connectivity ($\sim 1 - 30$ cm.). The relationship between the activity of a single neuron, measured by recording neuronal spikes, to that of a population of neurons, measured by, for example, the electroencephalogram (EEG) requires considerations of the statistical properties of neuronal populations [1,2,14,17]. Under baseline conditions neurons of the same type and in the same cortical layer, or region, display very similar histograms of interspike intervals (ISH) [9]. In the terminology of dynamical systems, the ISH corresponds to a measure. Here we examine the relationship between the invariant measure generated by a single neuron to that generated by a population of neurons.

The study of the invariant measures generated by spatially extended dynamical systems, such as turbulent fluids, has recently attracted a great deal of attention [3,5,8,15]. Particular attention has focused on establishing the existence of these measures for diffusively coupled map lattices. Typically, for one space dimension, diffusively coupled map lattices are written in the form [4]

$$x_{t+1}^j = (1-\epsilon)S(x_t^j) + \frac{\epsilon}{2}\left[S(x_t^{j-1}) + S(x_t^{j+1})\right], \quad \epsilon \in (0,1] \quad j = 1,\cdots,L, \qquad (1)$$

where the map $S : [0,1] \to [0,1]$ determines the local dynamics and generates a unique invariant measure and ϵ is the coupling coefficient. The index $j = 1, \cdots, L$ specifies the lattice position; $j = L+1$ is to be identified with $j = 1$, so the boundary conditions are periodic.

It is tempting to initiate the study of the statistical properties of neuronal populations by using the formulation provided by (1). For example, if we restrict our attention to short range connections, then S could be imagined as describing the t-th interspike interval produced by the j-th neuron due to the influence of the long range afferents. However, in contrast to diffusively coupled dynamical system in which interactions are limited to nearest neighbors on the lattice, in neuronal networks interactions are not so restricted but may occur over many neighbors.

Here we discuss sufficient conditions to insure that a unique invariant measure exists in which the coupling terms in (1) extends beyond nearest neighbor. One example is mean field coupling, in which (1) becomes

$$x_{t+1}^j = (1 - \epsilon)S(x_t^j) + \frac{\epsilon}{L-1} \sum_{k=1, k \neq j}^{L} S(x_t^k)$$

$$= \mathcal{W}(x_t^1, \cdots, x_t^L) \qquad j = 1, \cdots, L. \tag{2}$$

However, our conditions also apply to cases in which the coupling includes any number $\leq L - 1$ of the elements of the lattice. These results can also be extended to situations in which the coupling decreases with inter-lattice element distance as is known to occur in the nervous system [13]

After some mathematical preliminaries in section 2, in section 3 we review some recent results on the existence of invariant measures for (1). In section 4 we demonstrate how these properties can be extended to maps with spatially extended coupling.

2. Mathematical Preliminaries

Here we briefly review the evolution of densities under the action of the map $\mathcal{W} : X \to X$ [6]. By a density we mean a positive normalized L^1 function $f : X \to R$, i.e. f is a **density** if $f \geq 0$ and $\int_X f \, dx = 1$. Given a density f, then the corresponding **measure** $\mu_f(A)$ of a set $A \subset X$ is defined by $\mu_f(A) = \int_A f(x) \, dx$, and f is called the density of the measure μ_f. Having a density f, the associated measure μ_f, and a non-singular map $\mathcal{W} : X \to X$ then $\mathcal{W}$ is said to be **measure preserving** with respect to μ_f if $\mu_f(\mathcal{W}^{-1}(A)) = \mu_f(A)$, where $\mathcal{W}^{-1}(A)$ is the counterimage of the set A. Alternately, this is expressed by saying that μ_f is an **invariant measure** with respect to $\mathcal{W}$.

Since $x_{t+1} = \mathcal{W}(x_t)$, the evolution of a density f under the action of $\mathcal{W}$ is formally given by

$$\int_A P_{\mathcal{W}} f(u) \, du = \int_{\mathcal{W}^{-1}(A)} f(u) \, du \qquad A \subset X,$$

where the operator P_W is known as the **Frobenius-Perron operator** corresponding to W. If there is a density f_* such that $P_W f_* = f_*$, then we call f_* a **stationary density** of P_W. If f_* exists, then it can be shown that this is equivalent to the invariance of the measure μ_{f_*} with respect to the dynamics W.

Since the dynamics W generate a sequence of densities $\{P_W^t f\}_{i=0}^{\infty}$, it is interesting to know the types of convergence that this sequence may display. The first is ergodicity. We say that a Frobenius Perron operator P_W is **ergodic** if there exists a stationary density f_* of the operator P_W such that

$$\lim_{t \to \infty} \frac{1}{t} \sum_{k=0}^{t-1} < P_W^k f, g > = < f_*, g > \qquad \text{for all initial densities} \quad f.$$

Ergodicity is important because it also implies that the stationary density f_* is unique and thus it is the density of a measure invariant with respect to the dynamics [6]. Furthermore, by the Birkhoff individual ergodic theorem if a system is ergodic statistical averages may be calculated either along trajectories, or across the phase space with appropriate weighting by f_*.

Beyond ergodicity is mixing, a second type of convergence behaviour for densities. We say that P_W is **mixing** if there exists a unique stationary density f_* of the operator P_W and

$$\lim_{t \to \infty} < P_W^t f, g > = < f_*, g > \qquad \text{for all initial densities} \quad f.$$

Finally, the third type of convergence is known as asymptotic stability [6]. We say that P_W is **asymptotically stable** if there exists a unique stationary density f_* of the operator P_W and

$$\lim_{t \to \infty} \|P_W^t f - f_*\| = 0 \qquad \text{for all initial densities } f.$$

Asymptotic stability implies mixing which implies ergodicity, but not *vice versa*.

3. Nearest Neighbor Coupling

The correct form of S in (1) which describes the local dynamics of the j-th neuron under the influence of its long range afferent inputs is not known. Therefore, we illustrate our approach with a very simple choice of S, namely the Rényi map [12]

$$S(x) = \tau(x) \qquad \mod 1 \qquad 0 \le x \le 1, \tag{3}$$

where $\tau : [0,1) \to [0,\infty)$ is a piecewise C^2 function such that $\inf_x \tau' > \alpha > 1$ and $\tau(0) = 0$. Extensions to cases in which the slope of S changes sign are discussed elsewhere [Mackey and Milton, in preparation].

Consider lattices of nonsingular maps $S : [0,1] \to [0,1]$ such that $S(0) = 0$. and assume that the full lattice dynamics W defined by (1) operate in a phase space X_L consisting of the L-dimensional unit cube $X_L = [0,1] \times \cdots \times [0,1]$, and we specifically

do not associate the point 1 with 0. $\mathcal{W}$ maps the triple (x^{j-1}, x^j, x^{j+1}) to a point $\tilde{x}^j$ so $\tilde{x}^j = \mathcal{W}(x^{j-1}, x^j, x^{j+1})$, or $x_{t+1} = \mathcal{W}(x_t)$ where $x = (x^1, \cdots, x^L)$.

To study systems like (1) we make the following observations. We will say that a mapping $\mathcal{W} : X_L \to X_L$ is **expanding** if there exists a constant $\lambda > 1$ such that the differential $d\mathcal{W}$ satisfies $\|d\mathcal{W}(x)x\| \geq \lambda\|x\|$ at each $x \in X_L$, where $\|x\|$ denotes the norm of the vector x so $\|x\| \equiv <x, x>^{\frac{1}{2}}$ and $< \cdot, \cdot >$ denotes the scalar product. Then we have

Theorem 1. *Let S satisfy the properties above, $\mathcal{W} : X_L \to X_L$ be given by (1) and $P_{\mathcal{W}}$ be the corresponding Frobenius Perron operator. If $\mathcal{W}$ is expanding then $P_{\mathcal{W}}$ is asymptotically stable.*

Proof. The proof of the theorem follows from the derivation of the Frobenius Perron operator $P_{\mathcal{W}}$ corresponding to $\mathcal{W}$, demonstrating that $P_{\mathcal{W}}$ has a nontrivial lower bound, and showing that the existence of a lower bound function is necessary and sufficient for asymptotic stability.

From Theorem 1 it is possible to determine sufficient conditions for the aymptotic stability of broad classes of CMLs. In particular when S is given by (3) we have the following corollary.

Corollary 2. *Let the map $S : [0,1] \to [0,1]$ satisfy $S(0) = 0$, and $\inf_x S' > \alpha > 1$. Then $\mathcal{W}$ is expanding and, consequently, $P_{\mathcal{W}}$ is asymptotically stable when $\alpha > 1/(1 - \epsilon)$.*

Results like the above for asymptotic stability in a CML with constant coupling can be extended to the case of variable coupling [Mackey and Milton, in preparation], specifically

$$x_{t+1}^j = [1 - \epsilon(S(x_t^j))] + \frac{\epsilon(S(x_t^j))}{2}[S(x_t^{j-1}) + S(x_t^{j+1})], \qquad j = 1, \cdots, L.$$

In this case it is assumed that the full lattice dynamics operate on a finite dimensional smooth connected compact C^∞ manifold with a Riemannian metric, and some technical requirements are placed on ϵ.

4. Spatially Extended Coupling

The obvious extension of nearest neighbor coupling embodied in (1) is the type of mean field coupling illustrated in (2), and for many situation of physical interest this is appropriate. However, in a neurophysiological context, it is perhaps more realistic to consider the situation in which

$$x_{t+1}^j = (1 - \epsilon)S(x_t^j) + \frac{\epsilon}{N} \sum_{k=1, k \neq j}^{N} S(x_t^k),$$

so each lattice site is coupled with the same strength to $N \leq L - 1$ neighbors with the same strength. Alternately, since measurements of the connectivity of cortical neurons indicate that the probability of connectivity between two neurons decreases exponentially

with distance [13], one might examine

$$x_{t+1}^j = (1 - \epsilon)S(x_t^j) + \frac{\epsilon}{N} \sum_{k=1, k \neq j}^{N} S(x_t^k)e^{-\kappa|k-j|}.$$

Situations like both of these have been considered by Keller and Künzle [5] and Mackey and Milton [in preparation], and once again sufficient conditions for asymptotic stability are relatively straightforward to obtain.

5. Discussion

Our results illustrate that previous results on the existence of invariant measures for (1) can be extended to lattices in which the coupling extends beyond nearest neighbors. The invariant measure generated by the lattice through $\mathcal{W}$ is not, in general, the same as that generated by S. These results do not exclude the possibility that the lattice can generate an invariant measure whereas S does not.

The neural analogue of (1) would be a population of interconnected identical neurons each with the same "long range" input. It has long been felt that neurons in the central nervous system are organized into modular units composed of $\sim 200 - 300$ neurons ("mini-columns") or $\sim 10^5$ neurons ("macro-columns") [16]. The identification of these functional columns, or units, rests on anatomical and physiological evidence indicating that the neurons have similar afferent inputs. The formulation of a network in terms of (1) becomes more realistic as better choices of S are made and as both inhibitory and excitatory inter-connections are included. One possibility is to consider that the map S describes the dynamics produced by a recurrent inhibitory loop (i.e. a pyramidal neuron plus its inhibitory interneurons) and its long range input. Using a delay-differential equation model for recurrent inhibition proposed by Mackey and an der Heiden [7], we have derived

$$S(x) = A - \frac{Bx\phi^n}{\phi^n + x^n}$$

where A, B, ϕ, n are positive constants. When this map is onto a closed finite interval, then many of the results quoted above and presented elsewhere [Mackey and Milton, in preparation] can be shown to also hold, but significant mathematical difficulties present themselves when this condition is not attained in spite of the fact that the map is still physiologically realistic and numerical simulations reveal a variety of interesting phenomena.

Neurons are excitable elements and hence a network of neurons might be anticipated to be dynamically similar to an excitable medium [18]. A variety of beautiful and self-maintaining complex spatio-temporal patterns including traveling spiral waves can arise in chemical media and cardiac tissue. Although it is still uncertain whether traveling waves of cortical excitation occur [11], it is likely that they can arise, particularly in certain pathological situations such as spreading depression [10] and the spread of activity from an epileptic focus. We have not yet been able to produce self-maintaining traveling waves

in the network described by (1). At present we do not know whether the apparent inability of (1) to produce self-maintaining traveling waves reflects our choice of S or whether the limitation lies in the manner by which neighbouring elements on the lattice interact.

Understanding phenomena such as cognition and the generation of an epileptic seizure ultimately requires the study of dynamics of large ($\sim 10^6 - 10^{10}$) populations of neurons. Although numerous techniques exist to study properties of single neurons, techniques capable of measuring functional properties of large populations of neurons are limited to EEG and radiological techniques such as magnetic resonance and positron emission tomography. An important step will be the demonstration of how the properties of single neurons contribute to these population measures.

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