



Mathematical Neuroscience: from neurons to networks*

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Abstract. The tools of dynamical systems theory are having an increasing impact on our understanding of patterns of neural activity. In this talk I will describe how to build tractable tissue level models that maintain a strong link with biophysical reality. These models typically take the form of nonlinear integro-differential equations. Their non-local nature has led to the development of a set of analytical and numerical tools for the study of waves, bumps and patterns, based around natural extensions of those used for local differential equation models. Here I will present an overview of these techniques. Time permitting I will also present recent results on next generation neural field models obtained via a mean field reduction from networks of nonlinear integrate-and-fire neurons. ©EDP-Normandie. All rights reserved.

Keywords. Neural field models; Turing instability; Interface dynamics; Ott-Antonsen ansatz.

1. Introduction

Ever since Hans Berger made the first recording of the human electroencephalogram (EEG) in 1924 there has been a tremendous interest in understanding the physiological basis of brain rhythms. This has included the development of mathematical models of cortical tissue – which are often referred to as neural field models. These have remained pretty much in their current form since the seminal work of Wilson and Cowan [17] and Amari [1] in the 1970s. Here I will develop the discussion of a particular neural field model that incorporates much of the spirit of these original formulations, though with refinements that make a stronger connection to models of both synaptic and dendritic processing.

For a recent review of neural field modelling see [3], and for a set of tutorial notes covering tissue level firing rate models, amplitude equations, brain wave equations, travelling waves and localised states, their construction and stability (Evans functions), waves in random neural media and tissue level spiking models see [2].

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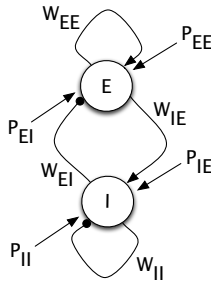


Fig. 2.1. A diagram of a local cortical module represented by the interaction of two neuronal populations, one excitatory (E) and the other inhibitory (I).

2. Neural mass models

It is common practice to define a neural mass as a collection of thousands of near identical interconnected neurons with a preference to operate in synchrony. The spatial extent of this population is taken to be on the order of a few hundred micrometers. The state variable describing the activity of the population is the average membrane potential. Such lumped parameter models are capable not only of producing EEG style alpha rhythms (8-13 Hz) but can generate more complex signals ranging from delta (1-4 Hz) to gamma (30-70 Hz) [7]. Moreover they are amenable to mathematical analysis using techniques from dynamical systems theory and notably bifurcation theory [8]. However, it is well to mention here that because of the “near to synchrony” assumption, neural mass models are unable to say anything about more complex behaviours within a single population, such as phase-locked states — see section 5.

One of the more successful population models for generating rhythms consistent with those found in the human EEG spectrum is that of Liley *et al.* [10]. In this mesoscopic model cortical activity is locally described by the mean soma membrane potentials of an interacting excitatory and an inhibitory population. The interaction is through a model of the synapse that treats both shunting currents and a realistic time course for post-synaptic conductance changes. Referring to the diagram in Fig. 2.1 the model can be written in a succinct form as

$$\tau_a \dot{a} = -a + \sum_b W_{ab}(h_b - a), \quad (2.1)$$

with $a, b \in \{E, I\}$, where E (I) is the mean membrane potential in the excitatory (inhibitory) population. The relaxation time constants for the populations are given by τ_a , whilst h_a describes a reversal potential such that h_E (h_I) is positive (negative) with respect to the resting state. The weights W_{ab} are the product of a static strength factor and a dynamic conductance $W_{ab} = \bar{W}_{ab}g_{ab}$, where

$$Q_{ab}g_{ab} = f_b(b(t - \Delta_{ba})) + P_{ab}. \quad (2.2)$$

Here Q_{ab} represents a linear differential operator:

$$Q_{ab} = \left(1 + \frac{1}{\alpha_{ab}} \frac{d}{dt} \right)^2,$$

and the conductances are considered to be driven by a combination of firing from populations to which they are connected and some external drive. The former is modelled using a sigmoidal function:

$$f_a(u) = \frac{1}{1 + e^{-\beta_a(u-\theta_a)}}, \quad \beta_a > 0,$$

and the latter, P_{ab} , is considered constant. Note the inclusion of delays Δ_{ba} in (2.2) that represent the fixed axonal communication lag for action potentials propagating from population b to a . Exploiting the linearity of Q_{ab} the model for the conductance can be integrated to give $g_{ab} = \eta_{ab} * [f_b + P_{ab}]$, where $*$ denotes a temporal convolution: $(\eta * f)(t) = \int_0^t \eta(t-s)f(s)ds$ and

$$\eta_{ab}(t + \Delta_{ba}) = \alpha_{ab}^2 t e^{-\alpha_{ab} t} H(t),$$

where H is a Heaviside step function. We recognise $\eta_{ab}(t)$ as a delayed α -function, commonly used in computational neuroscience to mimic the rise and fall of a post-synaptic conductance change.

A numerical bifurcation analysis of the model shows the coexistence of a large and small amplitude periodic orbit (for physiologically realistic parameter sets). The large amplitude, (~ 5 Hz) orbit has been suggested to correspond to a form of epileptic dynamics, whilst the smaller amplitude (~ 10 Hz) oscillation is more consistent with the alpha band of the EEG spectrum. Moreover, a period doubling cascade is supported and beyond this the model is known to support chaos via a novel Shilnikov saddle-node bifurcation [16].

3. Neural field models

Here we will view a macroscopic part of the neocortex as being adequately modelled as a spatial assembly of population models – a neural field model. Such a viewpoint has already proven useful in understanding spatial aspects of the alpha rhythm and in particular cortical travelling waves [13].

To develop the extension of (2.1) to treat spatially continuous neural sheets (such as a two-dimensional cortex) we will adopt the *continuum* assumption and treat a density of neurons at a point with inputs that arise from the delayed and weighted contribution of activity at other points in the tissue. Because these interactions are mediated by long-range axonal fibres the resulting tissue-level model is inherently non-local and is often cast in the form of an integral equation. We represent this symbolically in the form

$$g = w \otimes \eta * f, \tag{3.1}$$

where the operator \otimes captures information about both anatomical connectivity patterns and the distribution of axonal delays. As a concrete example consider a set of two-dimensional interacting layered sheets (with both self and layer

to layer interactions), each containing only one cell type (either excitatory or inhibitory). The activity in layer a induced by that in layer b then takes the form

$$u_{ab} = \eta_{ab} * \psi_{ab},$$

where $\psi_{ab} = \psi_{ab}(\mathbf{r}, t)$ is given by

$$\psi_{ab}(\mathbf{r}, t) = \int_{\mathbb{R}^2} d\mathbf{r}' w_{ab}(\mathbf{r}, \mathbf{r}') f_b(\mathbf{r}', t - |\mathbf{r} - \mathbf{r}'|/v_{ab}), \quad (3.2)$$

and f_b is the firing rate in layer b . Here $\mathbf{r} \in \mathbb{R}^2$ and $w_{ab}(\mathbf{r}, \mathbf{r}')$ prescribes the coupling strength between position \mathbf{r} in layer a and position \mathbf{r}' in layer b . The velocity of an action potential travelling along a fibre connecting layer b to layer a is denoted v_{ab} and underlies the space-dependent delay $|\mathbf{r} - \mathbf{r}'|/v_{ab}$ for signals propagating over a distance $|\mathbf{r} - \mathbf{r}'|$. Note that (3.2) provides meaning for the operator on the right hand side of the expression $\psi = w \otimes f$. To close the system of equations one could choose the firing rate to depend on some dynamic mean-membrane potential as in the Liley model. Alternatively, to recover a purely activity based model in the spirit of Wilson-Cowan and Amari one could set $f_a = f_a(h_a)$, where $h_a = \sum_b u_{ab}$. For simplicity we shall restrict further discussion to this case. Suffice to say that, apart from their relevance to neuroimaging, neural field models have found many applications in neuroscience, including to understanding the generation of visual hallucinations, modelling orientation tuning in visual cortex area V1, describing travelling waves of activity in V1 during binocular rivalry, models of working memory and encoding of continuous stimuli, motion perception, somatosensory illusions, and developing a theory of cognitive robotics — see [3] for further discussion.

Neural field models of the type (3.1) are nonlinear spatially extended systems and thus have all the necessary ingredients to support pattern formation. The analysis of such behaviour is typically performed with a mixture of linear Turing instability theory, weakly nonlinear perturbative analysis and numerical simulations. In the absence of detailed anatomical data it is common practice to consider cortico-cortical connectivity functions to be homogeneous and isotropic so that $w_{ab}(\mathbf{r}, \mathbf{r}') = w_{ab}(|\mathbf{r} - \mathbf{r}'|)$. In this case a homogeneous steady state is expected and can be defined by $h_a^{\text{ss}} = \sum_b W_{ab} f_b(h_b^{\text{ss}})$, where $W_{ab} = \int_{\mathbb{R}^2} d\mathbf{r} w_{ab}(\mathbf{r})$. For concreteness we shall take

$$w_{ab}(r) = w_{ab}^0 e^{-r/\sigma_{ab}} / (2\pi),$$

where $r = |\mathbf{r}|$. Linearising around the steady state and considering perturbations of the form $h_a(\mathbf{r}, t) \sim e^{\lambda t} e^{i\mathbf{k} \cdot \mathbf{r}}$, gives an equation for the continuous spectrum $\lambda = \lambda(k)$, for $k = |\mathbf{k}|$, in the form $\mathcal{E}(k, \lambda) = 0$ [6], where $\mathcal{E}(k, \lambda) = \det(\mathcal{D}(k, \lambda) - I)$, and

$$[\mathcal{D}(k, \lambda)]_{ab} = \tilde{\eta}_{ab}(\lambda) G_{ab}(k, -i\lambda) \gamma_b.$$

Here $\gamma_a = f'_a(h_a^{\text{ss}})$, $\tilde{\eta}_{ab}(\lambda)$ is a Laplace transform given by

$$\int_0^\infty ds \eta_{ab}(s) e^{-\lambda s} = \frac{e^{-\lambda \Delta_{ba}}}{(1 + \lambda/\alpha_{ab})^2},$$

and $G_{ab}(k, \omega)$ is the Fourier transform of $G_{ab}(r, t) = w_{ab}(r) \delta(t - r/v_{ab})$ given by

$$G_{ab}(k, \omega) = \int_{\mathbb{R}^2} d\mathbf{r} \int_{\mathbb{R}} dt G_{ab}(r, t) e^{-i(\mathbf{k}\cdot\mathbf{r} + \omega t)} = w_{ab}^0 \frac{A_{ab}(\omega)}{(A_{ab}^2(\omega) + k^2)^{3/2}},$$

where $A_{ab}(\omega) = 1/\sigma_{ab} + i\omega/v_{ab}$. Here we use a notation that distinguishes functions and their transforms simply by their arguments, namely (r, t) for the original space and (k, ω) for the Fourier space. An instability occurs when for the first time there are values of k at which the real part of λ is non-negative. A Turing bifurcation point is defined as the smallest value of some order parameter for which there exists some non-zero \mathbf{k}_c satisfying $\text{Re}(\lambda(|\mathbf{k}_c|)) = 0$. It is said to be *static* if $\text{Im}(\lambda(|\mathbf{k}_c|)) = 0$ and *dynamic* if $\text{Im}(\lambda(|\mathbf{k}_c|)) \equiv \omega_c \neq 0$. The dynamic instability is often referred to as a Turing-Hopf bifurcation and generates a global pattern with wavenumber $|\mathbf{k}_c|$, which moves coherently with a speed $c = \omega_c/|\mathbf{k}_c|$, i.e. as a periodic travelling wave train. If the maximum of the dispersion curve is at $|\mathbf{k}_c| = 0$ then the mode that is first excited is another spatially uniform state. If $\omega_c \neq 0$, we would then expect the emergence of a coherent network oscillation with frequency ω_c .

For example, consider two populations, one excitatory and one inhibitory with a common firing rate function $f_a = f$ and single axonal conduction velocity $v_{ab} = v$, and use the labels $a \in \{E, I\}$, with $w_{EE,IE}^0 = 1$, $w_{II,EI}^0 = -4$, $\alpha_{ab} = 1$ and $\Delta_{ba} = 0$. In neocortex the extent of excitatory connections W_{aE} is broader than that of inhibitory connections W_{aI} , and so we take $\sigma_{aI} = 1$ and $\sigma_{aE} = 2$. In Fig. 3.1 we show a plot of the critical curves in the (v, γ) plane above which the homogeneous steady state, $h_{E,I}^{\text{ss}} = h^{\text{ss}}$, is unstable to dynamic instabilities with $|\mathbf{k}_c| = 0$ (bulk oscillations) and $|\mathbf{k}_c| \neq 0$ (travelling waves), as well as a pattern of parallel moving stripes seen beyond the Turing-Hopf bifurcation.

It is also possible to formulate and analyse the neural field model described above on the surface of a sphere, so that the topology more closely resembles the cortical white matter system. This gives rise to the Nunez large-scale brain model [13] that has recently been mathematically analysed using a mixture of Turing instability analysis, symmetric bifurcation theory, center manifold reduction and direct simulations with a bespoke numerical scheme [4]. This work has examined standing and travelling wave solutions using normal form computation of primary and secondary bifurcations from a steady state, and uncovered large-scale spatio-temporal patterns that have counterparts seen in the EEG patterns of both epileptic and schizophrenic brain conditions.

4. Interface dynamics

The sorts of dynamic behaviour that are typically observed in neural field models includes, spatially and temporally periodic patterns (beyond a Turing

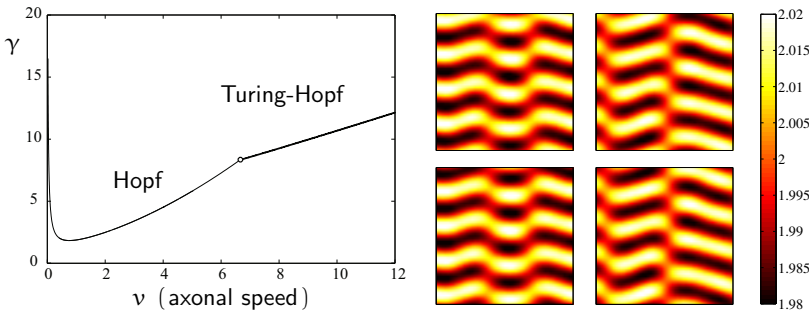


Fig. 3.1. *Left: Critical curves showing the instability borders for dynamic instabilities in the (v, γ) plane, where $\gamma = f'(h^{ss})$. Right: Snapshots of a periodic travelling wave in u_{EE} , each $1/4$ of a period later than the previous one (ordered top left, top right, bottom left, bottom right), see in direct numerical simulations at $v = 12$ and $\gamma = 15$ (on a 30×30 domain).*

instability) (see Sect. 3), localised regions of activity (bumps and multi-bumps) and travelling waves (fronts, pulses, target waves and spirals). Interestingly, spatially localised bumps of activity have been linked to working memory (the temporary storage of information within the brain) in prefrontal cortex, representations in the head-direction system, and feature selectivity in the visual cortex, where bump formation is related to the *tuning* of a particular neuron's response — see [3] for further discussion.

For the case that f is a Heaviside function with threshold h the full neural field dynamics for localised states, such as spots and fronts, can be reconstructed solely in terms of data on the boundary of an *active* region [5]. For clarity of exposition consider a single population neural field model in the absence of axonal delays and defined on the infinite plane with a first order synaptic response function $\eta(t) = e^{-t}H(t)$. This minimal model can be written as an integro-differential equation for a scalar field u in the form

$$u_t(\mathbf{r}, t) = -u(\mathbf{r}, t) + \int_{\mathbb{R}^2} w(\mathbf{r} - \mathbf{r}')H(u(\mathbf{r}', t) - h)d\mathbf{r}', \quad (4.1)$$

where $\mathbf{r} \in \mathbb{R}^2$ and $t \in \mathbb{R}^+$. It is convenient to introduce $\Omega(t) = \{\mathbf{r} \in \mathbb{R}^2 | u(\mathbf{r}, t) \geq h\}$. Differentiation of the level set condition $u(\mathbf{x}, t) = h$ along the boundary of the active region can be used to generate a rule advancing the boundary in terms of a normal velocity with magnitude $c_n = a/|\mathbf{b}|$, where $(a, \mathbf{b}) = (\mathcal{F}(c_n), \mathcal{F}(\mathbf{n}))$ with

$$\mathcal{F}(x(s, t)) = \int_0^\infty dt' \eta(t') \oint_{\partial\Omega(t-t')} ds' w(\mathbf{y}(s, t), \mathbf{y}(s', t'))x(s', t-t').$$

Here \mathbf{n} is a unit normal to the boundary and \mathbf{y} is a point on the boundary. The shape $\Omega(t + \Delta t)$ is computed under the replacement $\mathbf{y} \rightarrow \mathbf{y} + c_n \mathbf{n} \Delta t$ with $\mathbf{y} \in \partial\Omega(t)$. This yields a significant reduction of the original space-time

model (4.1), and the interface dynamics can be readily implemented numerically using spectral schemes, based on those already used in fluid mechanics for the evolution of vortices, as well as level set methods and associated data structures now ubiquitous throughout the computer graphics industry. Moreover, the linear stability of localised states can be assessed to understand the mechanisms of pattern formation that arise from instabilities of spots, rings, stripes and fronts. An example of a spot instability giving rise to a labyrinthine structure with a 4-fold symmetry is shown in Fig. 4.1.

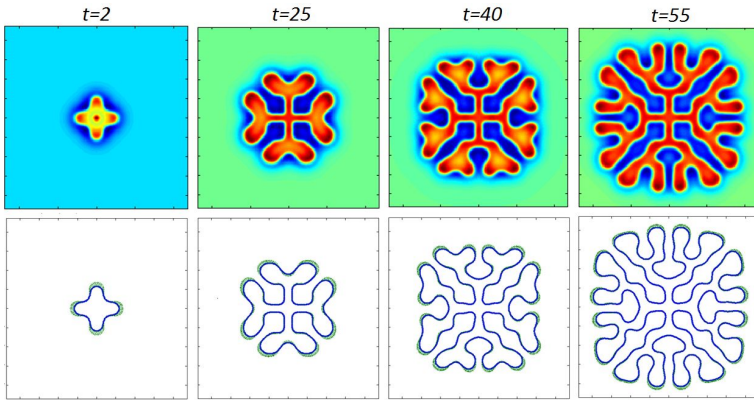


Fig. 4.1. An example of the destabilisation of a localised state to a labyrinthine structure. Top: direct simulations of the neural field model given by (4.1) with a radially symmetric Mexican hat interaction kernel. Hot colours (red) show the active region. Bottom: Simulation of the corresponding interface equations. The green arrows show the normal velocity of the interface.

5. Low dimensional macroscopic dynamics for spiking networks

The self-organisation of large networks of coupled neurons into macroscopic coherent states, such as observed in phase-locking, has inspired a search for equivalent low-dimensional dynamical descriptions. However, the mathematical step from microscopic to macroscopic dynamics has proved elusive in all but a few special cases. For example, neural mass and field models of the type described in Sect. 2 and Sect. 3 only track mean activity levels and not the higher order correlations of an underlying spiking model. Only in the thermodynamic limit of a large number of neurons firing asynchronously (producing null correlations) are such rate models expected to provide a reduction of the microscopic dynamics. Moreover, even here the link from spike to rate is often phenomenological rather than rigorous. Unfortunately only in some rare instances has it been possible to analyse spiking networks directly (usually under some restrictive assumptions). However, recent progress in obtaining a

mean field reduction for a very specific choice of large scale spiking model has been made. The single neuron model of choice being either a θ -neuron [15, 11] or a (formally equivalent) quadratic integrate-and-fire (QIF) neuron [14], and the coupling being global and mediated by pulses (namely instantaneous synapses). Moreover, the extension to neural fields is straight forward [9]. These approaches makes use of the Ott-Antonsen (OA) ansatz, which was originally used to find solutions on a reduced invariant manifold of the Kuramoto model. Here I will discuss a generalisation of this approach to treat more realistic forms of synaptic coupling for globally coupled networks of θ -neurons in the thermodynamic limit. This allows us to track the evolution of a complex valued Kuramoto order parameter z as:

$$\frac{dz}{dt} = -i \frac{(z-1)^2}{2} + \frac{(z+1)^2}{2} [-\Delta + i\eta_0 + iV_{syn}G] - \frac{z^2-1}{2}G,$$

$$\left(1 + \frac{1}{\alpha} \frac{d}{dt}\right)^2 G = \frac{k}{\pi} H(z, \bar{z}),$$

where

$$H(z, \bar{z}) = 1 + \frac{z}{1-z} + \frac{\bar{z}}{1-\bar{z}}.$$

Here η_0 and Δ are the centre and width of a Lorentzian distribution respectively (which provides some heterogeneity in the firing rate of individual spiking neurons), k is the global synaptic coupling strength, and V_{syn} a synaptic reversal potential. Without invoking the OA ansatz, Montbrió *et al.* [12] have recently shown that QIF networks also admit to a mean field description for the population firing rate and the mean membrane voltage. Interestingly they show how to relate these macroscopic variables back to the complex Kuramoto order parameter via a conformal mapping. I will present some initial bifurcation analysis of the next generation neural mass model incorporating synaptic currents described above, as well as simulations of the power spectrum in response to stimulation to show that this level of description is ideally suited to explaining the phenomenon known as post-movement beta rebound. Here a sharp increase in magnetoencephalography power is seen in the beta frequency band (13–30 Hz) following movement, typifying event-related synchronisation of brain activity. Existing neural mass or field models are unable to capture this phenomenon since they do not track any notion of network coherence (only firing rate).

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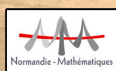
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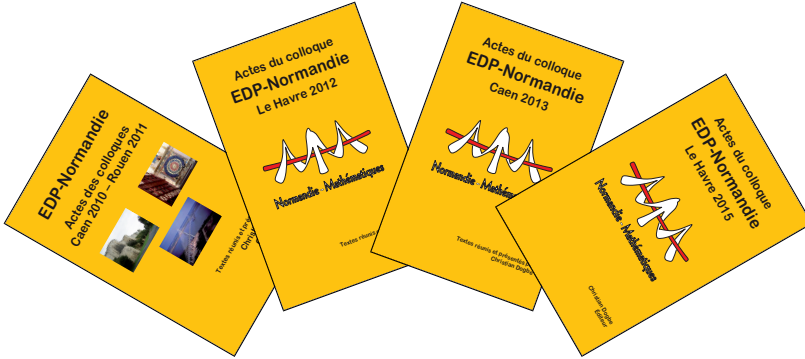
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