Tuned solutions in dynamic neural fields as building blocks for extended EEG models

Thomas Wennekers

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Abstract The most prominent functional property of cortical neurons in sensory areas are their tuned receptive fields which provide specific responses of the neurons to external stimuli. Tuned neural firing indeed reflects the most basic and best worked out level of cognitive representations. Tuning properties can be dynamic on a short time-scale of fractions of a second. Such dynamic effects have been modeled by localised solutions (also called “bumps” or “peaks”) in dynamic neural fields. In the present work we develop an approximation method to reduce the dynamics of localised activation peaks in systems of n coupled nonlinear d -dimensional neural fields with transmission delays to a small set of delay differential equations for the peak amplitudes and widths only. The method considerably simplifies the analysis of peaked solutions as demonstrated for a two-dimensional example model of neural feature selectivity in the brain. The reduced equations describe the effective interaction between pools of local neurons of several (n) classes that participate in shaping the dynamic receptive field responses. To lowest order they resemble neural mass models as they often form the base of EEG-models. Thereby they provide a link between functional small-scale receptive field models and more coarse-grained EEG-models. More specifically, they connect the dynamics in feature-selective cortical microcircuits to the more abstract local elements used in coarse-grained models. However, beside amplitudes the reduced equations also reflect the sharpness of tuning of the activity in a d -dimensional feature space in response to localised stimuli.

Keywords Nonlinear field model · Spatio-temporal dynamics · Cortex · Feature-selectivity · Dynamic receptive fields

Introduction

Electrical activity in the brain reveals complex spatio-temporal activation patterns on different length- and time-scales. On a macroscopic level electro- and magnetoencephalographic methods (EEG and MEG) are widely employed to measure the global brain activity in normal as well as pathological states (Nunez 1995). Continuum models have been successfully developed to describe spatio-temporal pattern formation in EEG and MEG on roughly a centimetre-scale. These models take the form of partial differential equations comprising diffusively coupled local nonlinear oscillators. They are useful to explain properties of experimental EEG data like its frequency spectrum, wave propagation, and selforganising excitation patterns (Ingber 1994; Jirsa and Haken 1996, 1997; Rennie et al. 1999; Robinson et al. 1997, 1998; Hutt et al. 2003; Wright et al. 2003; Robinson and Rennie 2006; Coombes et al. 2007).

On a finer spatial scale of less than perhaps a millimetre the assumption of diffusive couplings becomes inappropriate. The connectivity pattern there is spatially modulated in various ways dominated in first approximation by local excitatory and lateral inhibitory couplings extending over certain ranges. The neural dynamics on this scale can well be described by another type of nonlinear field equation than the more global EEG-patterns, namely integro-differential equations with appropriate non-local interaction kernels (Amari 1977; Ben-Yishai et al. 1995; Bressloff and Cowan, 2002; Somers et al. 1995; Taylor 1999; Wennekers 2001; Wilson and Cowan 1972, 1973).

T. Wennekers (✉)
Centre for Theoretical and Computational Neuroscience,
University of Plymouth, Drake Circus PL4 8AA, UK
e-mail: thomas.wennekers@plymouth.ac.uk

The local-excitation/lateral-inhibition type connectivity structure supports localised solutions in neural fields in favour of travelling waves or far reaching self-organising patterns more commonly studied in EEG-models. Such localised neural activation patterns are tightly related to one of the most important functional properties of cortical neurons: Their selectivity for certain stimulus features. Neurons in many cortical areas are organised in feature maps such that nearby cells respond selectively to similar features of external stimuli. Such maps have been demonstrated to exist experimentally up to high levels of cognitive representations, e.g., Quiroga et al. (2005); Tsunoda et al. (2001). A specific stimulus thus excites a local group of cells, but cells in the lateral surround are suppressed. The responding local group thereby encodes the presence of the respective stimulus in the outer world, a functional aspect of neural dynamics seldom covered in more coarse-grained EEG-models. Furthermore, since they relate neural response properties to external stimuli, localised solutions in neural fields must naturally be studied in response to external input. Waves and selforganising patterns in EEG-models in contrast typically represent autonomous dynamic behaviour (Amari 1977; Ben-Yishai et al. 1995; Somers et al. 1995; Taylor 1999; Wennekers 2001; Wilson and Cowan 1972, 1973; Coombes et al. 2007) although they can reflect the fine structure of maps in the real cortex (Tsodyks et al. 1999; Kenet et al. 2003).

The tuning of cells in different brain areas is known for long and was long believed to provide basically static mappings between external stimuli and internal neural representations that are mediated by feedforward projections with appropriate spatial filter properties (Hubel and Wiesel 1962). More recent electrode recordings revealed that tuning properties are not fixed but shaped dynamically by cortical feedforward and feedback connections, probably related to efficient information transmission within and between cortical areas and layers (Schummers et al. 2007; Friston 2005; Shapley et al. 2003). They can further depend on the global mental state (Eckhorn et al. 1993; Suder et al. 2001; Wörgötter et al. 1998): Suder et al. (2001), for instance, studied a special one-dimensional field model to describe arousal-dependent dynamic tuning properties observed in real data (Wörgötter et al. 1998) where the selectivity of simple cells in cat primary visual cortex in response to flashed small bars differed between more and less aroused states, and also sharpened over time after brief initial transients with broad tuning in more alert states. These effects indicate an adaptation of the visual system to cognitive demands during different states, i.e., a higher resolution during wakefulness. They were explained by a field model of the class used in this work and revealed dynamic tuning as an excellent example of cognitive neurodynamics.

Spatio-temporal tuning effects are well described by neural field models in the form of integro-differential equations of the Amari- or Wilson–Cowan type (Amari 1977; Wilson and Cowan 1972, 1973). They cover the activation dynamics of local masses of neurons in topographically organised domains, i.e., they possess a neighbourhood structure. The topography may in general represent any abstract continuous feature space like location, orientation or tonotopy, but to the extent that in many cortical areas features are roughly mapped across the surface of the cortex it can also be related to physical space as parametrised by coordinates on the cortical sheet. A specific stimulus representing a feature (a small visual spot, oriented bar, or pure tone) would thereby evoke localised activity in the feature domain under consideration, which in turn is reflected in physically localised activity. This way the abstract cognitive domain of brain function meets the physical domain of electrical signals and their dynamics. To the degree that the neural field models under study in this paper aim at explaining selectivity in some feature domain, they permit an immediate access to cognitive function insofar as feature-based processing is fundamental for neural representations in many cortical areas (Friston 2005; Wennekers and Palm 2007).

Different functional aspects become evident in observations on different spatial scales as a consequence of restrictions in the resolution of modern recording technologies. The mesoscopic fine structure of cortical maps for instance is practically invisible in EEG or fMRI recordings although there can be some signatures of cortical tuning in such signals (Haynes and Rees 2006). In contrast, maps are well observable in optical recordings, e.g., Tsodyks et al. (1999); Kenet et al. (2003); Tucker and Katz (2003). Thereby, complementary information about functional cortical processes is reflected on different scales, such that it is of interest to study how these resolution scales relate to each other, and how cortical microcircuits for feature specificity give rise to more globally observable activation patterns like the EEG, MEG, or fMRI (Friston 2005; Rennie et al. 1999; Robinson et al. 1998; Wright et al. 2003; Robinson and Rennie 2006).

In the present paper we consider the dynamics of feature selectivity in the framework of neural field models. Extending previous work (Wennekers 2001) we derive a general dynamic approximation scheme for cortical tuning properties valid for any number of mutually coupled recurrent network layers of arbitrary dimension. The method simplifies an analysis of dynamic tuning properties by reducing the full field model to a low-dimensional set of differential equations for the most interesting descriptors of activation peaks: Their amplitudes and widths in the respective layers. An analysis of these reduced equations is much simpler than for the full system and can be done

using well known methods from dynamical systems and bifurcation theory.

More importantly for the present work, a special outcome of the method is that the dynamic of localised peaks can to lowest order be well described by reduced non-linear circuits comprising just a small number of representative neurons. Each of these reflects the response strength of one of the cell classes that contribute to the full spatio-temporal response on the fine scale. In the simple case of just two classes of excitatory and inhibitory model cells, the tuned responses in the neural fields can for instance be represented by the standard excitatory–inhibitory Wilson–Cowan oscillator (Wilson and Cowan 1972, 1973). Note, however, that our method derives it from a neural field model for tuning on the sub-millimetre scale in a way that in addition links spatial properties of the connections in the fine-scale model to the coupling parameters in the Wilson–Cowan model. More realistic connectivity schemes including, for instance, cell classes in different cortical laminae are possible, too, and would result in an accordingly increased number of representative units. The dynamics of local cortical circuits of roughly the size of a column or less is this way reduced to a low-dimensional dynamical system that describes the typical amplitudes of tuned responses across the modeled cell classes.

Many EEG models start from local oscillators as the Wilson–Cowan oscillator, which are usually interpreted as reflecting the mutual interaction between excitatory and inhibitory cell masses (Freeman, 1975)—in a second step such oscillators become laterally coupled in order to derive spatially extended models for brain waves. As a simple special case, which is studied in Section “Example: excitatory–inhibitory neural field model” as an instructive example, the same type of excitatory–inhibitory oscillator results from the approximation method outlined in Section “Approximation of localised solutions”, however, in a way that links the parameters of the oscillator to underlying connectivity patterns and tuning properties in the model. This provides a microscopic motivation for the use of local oscillators in distributed EEG models. More sophisticated (and not yet available) models of the laminar cortical microcircuitry are likely required to explain cortical tuning more realistically than by means of just two excitatory and inhibitory pools. Such models might render higher-dimensional adaptations to the standard equations in EEG models necessary. This can include generators in different laminae and with different spectral properties as they have been reported in experiments (see, e.g., Einevoll et al. 2006; Buzsaki 2004 and references therein). Following the way outlined here, the gap between coarse-grained EEG models and more local models for cortical tuning may be bridged one step further.

Neural field model

We consider n mutually coupled neural fields, $\phi_i(x, t)$,

$$D_i \phi_i(x, t) = -\phi_i(x, t) + I_i(x, t) + \sum_{j=1}^n k_{ij}(x) * f_j(\phi_j(x, t - \Delta_{ij})) \quad (1)$$

with vanishing initial conditions for $t \leq 0$. In (1) the field $\phi_i(x, t)$, $i = 1, \dots, n$, describes the membrane potentials of cells at location $x \in R^d$ and time t in the i th layer. The symbol $*$ denotes d -dimensional spatial convolution and the D_i are linear differential operators in t that contain only first or higher order derivatives in t . A most common choice are first order low-pass filters with time-constants τ_i , i.e., $D_i = \tau_i \partial_t$. The $\Delta_{ij} \geq 0$ further represent total axonal and synaptic transmission delays. The $I_i(x, t)$ are space and time dependent inputs, and the k_{ij} synaptic coupling kernels. Connections between cells in a single layer ($i = j$) are possible. Coupling kernels and external inputs are assumed to be of Gaussian shape with amplitudes K_{ij} and I_{i0} $T_i(t)$, and variance matrices Σ_{ij} and Σ_{i0} , respectively:

$$k_{ij}(x) = K_{ij} \exp \left[-\frac{1}{2} x^T \Sigma_{ij}^{-1} x \right] \quad (2)$$

and

$$I_i(x, t) := I_{i0} T_i(t) \exp \left[-\frac{1}{2} x^T \Sigma_{i0}^{-1} x \right]. \quad (3)$$

In (3) I_{i0} is the intensity of the input and $T_i(t)$ its time-course. Because x represents a feature space (e.g., spanned by all possible locations and orientations of small bars), the Gaussian input reflects a stimulus with properties given by its centre value x_0 and an encoding precision determined by its variance matrix Σ_{i0} . Without loss of generality we choose $x_0 = 0$. The rate-functions f_i in (1) further describe the transformation of membrane potentials into output signals of real neurons. A suitable choice are “semi-power” functions, $f_i(\phi_i) = \beta_i [\phi_i - \vartheta_i]_+^{p_i} := \beta_i \max(0, \phi_i - \vartheta_i)^{p_i}$, with exponent $p_i > 0$, gain β_i , and threshold ϑ_i ; they fit the static nonlinearity of real neurons for p_i in roughly the range 0.5 ... 3.0 (Anderson et al. 2001; Heeger 1992) but may also be seen as a polynomial approximation of sigmoid rate-functions employed by others in the most relevant regime of low and intermediate activity (Amari 1977; Jirsa and Haken 1996, 1997; Rennie et al. 1999; Robinson et al. 1997, 1998; Taylor 1999; Wilson and Cowan 1972, 1973).

Note that all potentials are measured against a resting potential of zero without loss of generality: Any non-zero resting potential would appear in (1) as a constant offset on the right hand side, say, $+\phi_i^{bg}$. A linear transformation

$\tilde{\phi}_i(x, t) = \phi_i(x, t) - \phi_i^{bg}$ would move these offsets into the arguments of the rate-functions where they could be integrated into the firing thresholds leaving us with the form (1) again, this time for the transformed potentials (the “firing thresholds”, so-to-speak, measure the relative distance between the “true” resting potential and the “true” threshold). The units of measure are arbitrary, too, (again without loss of generality) because we can rescale the potentials by arbitrary constants which can afterwards be integrated into the amplitudes of the inputs, I_{i0} , the coupling constants, K_{ij} , and/or the slopes, β_i , of the rate functions (there is some ambiguity here).

Approximation of localised solutions

We are concerned with “localised” solutions of (1). An example for demonstration purposes is displayed in Fig. 1 where the step response of an excitatory–inhibitory two-layer model—discussed in more detail in Section “Example: excitatory–inhibitory neural field model”—is shown. The example plots the membrane potential profile of the excitatory cells over time in response to a localised input switched on at time zero. The input represents a simple stimulus in the feature domain under consideration, e.g., a tone or a bar, which excites only well-tuned cells strongly. Note how $\phi_1(x, t)$ is spatially confined or *tuned*, such that the output firing rate profile $f_1(\phi_1(x, t))$ would be bell-shaped (not shown). Neural activity can thus reveal a time-dependent amplitude and tuning, and only eventually may reach a stationary state.

Fig. 1 Space-time example profile of the potentials of the excitatory cells in a two-layer excitatory–inhibitory neural field model with local excitation and more far reaching lateral inhibition. Input is a Gaussian profile representing a stimulus at $x = 0$ switched on at $t = 0$, for instance, a tone or an oriented bar. The spatial dimension, x , reflects an arbitrary feature domain depending on the precise application. The response shown results from a simulation of (13) and (14) for $d = 1$, see Section “Example: excitatory–inhibitory neural field model”. It exemplarily shows the type of amplitude and width modulation of neural responses we are dealing with

We seek for approximate equations that describe the most interesting properties of spatio-temporal profiles as that in Fig. 1, i.e., their amplitudes and tuning widths. For that purpose we approximate the bell-shaped profiles, $f_i(\phi_i(x, t))$, in any of the network layers by equivalent Gaussian ones. Taylor expansion yields:

$$f_i(\phi_i(x, t)) \approx f_i(\phi_{0i}) + \frac{1}{2} f'_i(\phi_{0i}) x^T \phi_{2i} x + O(|x|^4) \quad (4)$$

$$\approx f_i(\phi_{0i}) \exp \left[\frac{1 f'_i(\phi_{0i})}{2 f_i(\phi_{0i})} x^T \phi_{2i} x \right], \quad (5)$$

where $\phi_{0i}(t) := \phi_i(0, t)$ and $\phi_{2i}(t) := (\partial_{x_j} \partial_{x_k} \phi_i(0, t))_{jk}$. Thus, the equivalent Gaussian profile in layer i has amplitude $f_i(\phi_{0i})$ and variance matrix $\Sigma_{pi}^{-1} := -f'_i(\phi_{0i})/f_i(\phi_{0i}) \cdot \phi_{2i}$. Semipower rate-functions, for example, result in $\Sigma_{pi}^{-1} = -p_i/[\phi_{0i} - \vartheta_i]_+ \cdot \phi_{2i}$.

Using this Gaussian approximation the convolution integrals in (1) can be solved in closed form

$$k_{ij} * f_j(\phi_j) \approx c_{ij} f_j(\phi_{0j}) \exp \left[-\frac{1}{2} x^T \Sigma'_{ij}{}^{-1} x \right], \quad (6)$$

where $\Sigma'_{ij} = \Sigma'_{ij}(t) := \Sigma_{ij} + \Sigma_{pj}(t)$ and

$$c_{ij} = c_{ij}(t) := K_{ij} (2\pi)^{d/2} \frac{|\Sigma_{ij}|^{1/2} |\Sigma_{pj}(t)|^{1/2}}{|\Sigma'_{ij}(t)|^{1/2}} \quad (7)$$

with $|A| := \det(A)$ the determinant of A . Inserting (6) into (1) one finds

$$D_i \phi_i(x, t) \approx -\phi_i(x, t) + I_i(x, t) + \sum_{j=1}^n c_{ij}(t - \Delta_{ij}) f_j(\phi_{0j}(t - \Delta_{ij})) \exp \left[-\frac{1}{2} x^T \Sigma'_{ij}{}^{-1}(t - \Delta_{ij}) x \right]. \quad (8)$$

To obtain expressions for ϕ_{0j} and ϕ_{2j} we approximate (8) further by a low-dimensional system of delay differential equations. To this end we expand the $\phi_i(x, t)$ into a power series near $x = 0$ and consider only the temporal evolution of the lowest order coefficients of the series. Using (3), the zeroth and second order read

$$D_i \phi_{0i}(t) = -\phi_{0i}(t) + I_{i0} T_i(t) + \sum_{j=1}^n c_{ij}(t - \Delta_{ij}) f_j(\phi_{0j}(t - \Delta_{ij})) \quad (9)$$

$$D_i \phi_{2i}(t) = -\phi_{2i}(t) - I_{i0} T_i(t) \Sigma_{i0}^{-1} \quad (10)$$

$$- \sum_{j=1}^n c_{ij}(t - \Delta_{ij}) f_j(\phi_{0j}(t - \Delta_{ij})) \Sigma'_{ij}{}^{-1}(t - \Delta_{ij}). \quad (11)$$

Initial conditions to be used with (9) to (11) are zero, because vanishing initial conditions have been assumed for the full system (1). Equations (9) to (11) provide a low-dimensional closed system of delay differential equations for the response amplitudes $f_i(\phi_{0i})$ and the effective tuning

widths of the rate profiles (by means of the relation $\Sigma_{pi}^{-1} : = -f'_i(\phi_{0i})/f_i(\phi_{0i}) \cdot \phi_{2i}$). Thereby they do not only simplify the original equations (1) significantly, but provide information about exactly the most interesting response properties: the peak amplitudes and tunings.

If certain symmetry conditions are satisfied, the reduced equations can be simplified further. For example, if the variance matrices of all inputs and coupling kernels, Σ_{ij} , $i = 1, \dots, n$; $j = 0, \dots, n$, can be simultaneously diagonalised we can choose new coordinates along the common principal axes, such that $\Sigma_{ij} = \text{diag}(\sigma_{ij1}^2, \dots, \sigma_{ijd}^2)$. In that base (11) reduces to

$$D_i \phi_{2ik} = -\phi_{2ik} - \frac{I_{i0} T_i}{\sigma_{i0k}^2} - \sum_{j=1}^n c_{ij} \frac{f_j(\phi_{0j})}{\sigma_{ijk}^2} \quad (12)$$

for $k = 1, \dots, d$ and with

$$c_{ij} = K_{ij} (2\pi)^{d/2} \Pi_{k=1}^d (\sigma_{ijk} \sigma_{pjk} / \sigma'_{ijk}).$$

In (12) we suppressed time-arguments for notational simplicity; these are the same as in (11). Equation (12) describes the temporal behaviour of the scalar peak tunings along the d principal axes of the model, whereas the ϕ_{2i} , $i = 1, \dots, n$ in (10) and (11) are full $d \times d$ matrices.

The assumption of simultaneously diagonalisable connection kernels is less restrictive as it may appear because processing in different feature domains often decouples, reflected by a product structure of the connectivity kernels and principle axes aligned with the sub-feature domains. Information theoretic arguments have indeed been given for a processing of information in orthogonal channels (Rao et al. 2002). In the visual cortex, for example, the tuning properties of simple cells for location, orientation, and spatial frequency are largely independent of each other. Stimuli likewise are often of (local) product structure, at least in experiments: Gabor patches (localised moving gratings) for example have independent centre location, orientation, spatial frequency and phase.

In case of rotation symmetry, $\sigma_{ijk} = \sigma_{ij}$, $k = 1, \dots, d$, we further have $c_{ij} = K_{ij} (2\pi)^{d/2} (\sigma_{ij} \sigma_{pj} / \sigma'_{ij})^d$ such that the d equations for ϕ_{2ik} , $k = 1, \dots, d$ in (12) become identical. Rotation symmetric localised solutions of (1) can therefore be approximated by just 2 differential equations per layer for any network dimension d . This situation applies approximately to cortical point-spread functions in response to small stimuli assuming isotropic connectivity.

In general the coefficients c_{ij} are not constant but couple (9) and (11) dynamically via the time-dependent tuning matrices Σ_{pi} in (7). As a consequence, dynamic network properties as the stability of fixed points depend on the network dimension. However, as long as the amplitude dynamics dominates over relatively small variations in tuning widths, we can neglect the latter and expect that

already (9) with steady state couplings c_{ij}^* gives a rough picture of the peak dynamics. Thereby, the dynamics of localised solutions in the full system (1) is represented by just n differential equations for the peak amplitudes alone.

Equations of the form (9) with constant couplings c_{ij}^* are known to describe also the average or ‘mean-field’ behaviour of n mutually interacting pools containing a large number of homogeneously or randomly connected cells (Wilson and Cowan 1972; Wennekers and Pasemann 1996). Thus, the well-studied behaviour of such pool-models can be expected to carry over to the amplitude dynamics of localised peaks in neural field models. Moreover, note that (9) with $c_{ij}(t) \equiv c_{ij}^*$ can be considered as a small neural network itself, comprising just n representative units with potentials ϕ_{0i} , rates $f_i(\phi_{0i})$, inputs $I_{i0} T_i$, and couplings c_{ij}^* . Therefore, to lowest order the amplitude dynamics of localised solutions in the field model (1) relates closely to the dynamics of a corresponding small neural system comprising just n units. This is quite different from other, more often studied, global activation patterns like waves or Turing patterns.

As outlined in the introduction, models for waves and Turing patterns often start from local oscillators or more complicated local neural circuits similar to (9) with constant couplings c_{ij}^* . Such local elements are then organised topographically into neural fields of some dimension and either coupled diffusively (partial differential equations) or by means of localised integral kernels (integro-differential equations), see, e.g., Freeman (1975); Ingber (1994); Nunez (1995); Jirsa and Haken (1996, 1997); Robinson et al. (1997, 1998). The local circuits indeed are interpreted as comprising masses of neurons that interact effectively with each other on the pool level. Our reduction method shows that the dynamics of field models for dynamic receptive fields can be simplified to such local pool equations. Each participating cell class that contributes to the tuning dynamics results on the coarse scale in one effective amplitude variable and corresponding reduced differential equation.

Example: excitatory–inhibitory neural field model

As an illustrative example, we consider a biologically inspired two-layer model in some detail. Similar models have been used to explain contrast-independent orientation tuning in the primary visual cortex (Ben-Yishai et al. 1995; Somers et al. 1995; Wennekers 2001). The analysis given here primarily aims at demonstrating that the approximation method works well in different dimensions ($d = 1, 2, 3$) and that the reduced equations cover all aspects of the full d -dimensional systems regarding static tuning properties, oscillatory solutions, and instabilities even quantitatively with good accuracy.

The model is furthermore especially important because it results in a two-dimensional reduced amplitude system very similar to the Wilson–Cowan oscillator (Wilson and Cowan 1973). As explained in the introduction, oscillators of this type form the local building blocks of many spatially extended models of wave-phenomena in EEG and MEG.

$$\tau_1 \frac{\partial \phi_1(x, t)}{\partial t} = -\phi_1(x, t) + I_1(x, t) + k_{11}(x) * f_1(\phi_1(x, t - \Delta_{11})) - k_{12}(x) * f_2(\phi_2(x, t - \Delta_{12})) \quad (13)$$

$$\tau_2 \frac{\partial \phi_2(x, t)}{\partial t} = -\phi_2(x, t) + k_{21}(x) * f_1(\phi_1(x, t - \Delta_{21})), \quad (14)$$

where $x \in \mathbb{R}^d$ and $f_i(\phi) = [\phi]_+$. Kernels are rotation symmetric and parameters used are $\tau_1 = \tau_2 = 10$, $\sigma_{10} = 8$, $\sigma_{11} = 3$, $\sigma_{12} = \sigma_{21} = 8$. The input level is arbitrarily taken as $I_{10} = 1$, because solutions of (13) and (14) are proportional to I_{10} but otherwise form-invariant (Wennekers 2002). We also fix $K_{21} = 1$, because K_{21} only scales $\phi_2(x, t)$ proportionally, but has no influence on $\phi_1(x, t)$ as long as $K_{12}K_{21}$ is held constant.

The reduced system equations are given by (9), (12), and (7), with $n = 2$, $I_{20} = c_{22} = 0$, $D_i = \tau_i \partial_t$. Moreover, the lowest order approximation for the amplitude dynamics only (denoted by $d = 0$, i.e., a zero-dimensional model) is just (9) with fixed point values c_{ij}^* .

Figure 1 displays the spatio-temporal profile $\phi_1(x, t)$ of the model for $d = 1$ in response to an input step $T_1(t) = \Theta(t)$ for vanishing delays $\Delta_{ij} = 0$ and $c_{11}^* = 1.7$, $c_{12}^*c_{21}^* = 1$. Given these parameters the system approaches a tuned fixed point in a damped oscillatory manner. Figure 2 compares numerical solutions of the full system (solid lines) with those of the reduced system (dashed). Plotted are the amplitude $\phi_{01} = \phi_1(0, t)$ and tuning width σ_{p1} obtained from the identity $\sigma_{p1}^2 = -\phi_{01}/\phi_{21}$. The reduced system reasonably approximates the qualitative behaviour of the full network, although it consists of just 4 ordinary differential equations.

With $c_+ := c_{11}$, $c_- := c_{12}c_{21}$, and $m_1 := (1 - c_+ + c_-)^{-1}$ one gets from the reduced equations for the fixed point amplitudes and tuning widths: $\phi_{02} = c_{21}\phi_{01}$, $\sigma_{p2}^2 = \Sigma_{21}^2 = \sigma_{21}^2 + \sigma_{p1}^2$, and

$$\phi_{01} = m_1 I_{10}, \quad \frac{1}{\sigma_{p1}^2} = \frac{1/m_1}{\sigma_{10}^2} + \frac{c_+}{\Sigma_{11}^2} - \frac{c_-}{\Sigma_{12}^2}, \quad (15)$$

where $\Sigma_{11}^2 = \sigma_{11}^2 + \sigma_{p1}^2$, $\Sigma_{12}^2 = \sigma_{12}^2 + \sigma_{p2}^2 = \sigma_{12}^2 + \sigma_{21}^2 + \sigma_{p1}^2$. Observe that the fixed points are independent of the transmission delays Δ_{ij} . The right equation in (15) is further independent of the input strength. Therefore, the tuning width σ_{p1} as well as $\sigma_{p2}^2 = \sigma_{21}^2 + \sigma_{p1}^2$ do not change with the input amplitude. It can be shown that this is in fact a universal property of neural field models with semilinear

Fig. 2 Comparison of numerical solutions for (a) the response amplitude and (b) the tuning width σ_{p1} (right) for the full model (solid lines) and the reduced model (dashed), respectively. Compare also Fig. 1 for the full profile $\phi_1(x, t)$

Fig. 3 Steady state amplitudes $m := m_1$ and tunings $\sigma := \sigma_{p1}$ resulting from (15) (solid) compared with values derived from simulations of the full network equations (dots). (a, b) $d = 1$; (c, d) $d = 2$

rate-functions f_i and zero thresholds (Wennekers 2002). Note also that in order to obtain fixed point tuning properties the only nonlinear equation to solve is that for σ_{p1} in (15). Solutions for ϕ_{0i} and σ_{pi} obtained from (15) further hold for rotation symmetric peaks in any dimension d . Figure 3 compares steady state amplification factors m_1 and tunings σ_{p1} for $d = 1$ and $d = 2$. Solid lines in each plot are solutions of the reduced set of equations (15) computed numerically. Dots represent results derived from simulations of the full field model. The full and reduced model results agree well and yield the same behaviour for $d = 1$ (upper plots) and $d = 2$ (lower plots) as predicted.

Figure 4a displays the tuning σ_{p1} and Fig. 4b the amplification m_1 as contour lines for varied c_+ and c_- . The figure also plots stability boundaries denoted by “S” and “H” and derived for vanishing delays. For $d = 0$ these

Fig. 4 (a) Steady state tuning width σ_{p1} and (b) amplification factor m_1 predicted by (15) as labelled contour lines in dependence of $c_+ = c_{11}$ and $c_- = c_{12}c_{21}$. “S” and “H” denote saddle-node and Hopf bifurcation lines predicted by the reduced system equations. Line “S” is the same in arbitrary dimension, but “H” depends on the model dimension, $d = 0, 1, 2, 3$. Symbols in (b) depict numerical simulations of the full systems for $d = 1$ and 2

boundaries can be readily calculated. One obtains from (9) for the two-layer model (13) and (14) the characteristic polynomial

$$D(\lambda) = \tau_1 \tau_2 \lambda^2 + (\tau_1 + \tau_2(1 - c_+))\lambda + 1 - c_+ + c_- \quad (16)$$

The condition $D(\lambda = 0) = 0$ predicts a saddle-node bifurcation for $c_- = c_+ - 1$, and condition $D(i\omega) = 0$ a Hopf-bifurcation line at $c_+ = 1 + \tau_1/\tau_2$, $c_- \geq \tau_1/\tau_2$ with $\omega^2 = c_-/(\tau_1 \tau_2) - 1/\tau_2^2$. The saddle-node line appears identical also for the reduced equations in higher dimensions, whereas the Hopf-branches for $d = 0, 1, 2, 3$ in Fig. 4 depend slightly on the dimension. Simulations of the full model (13) and (14) for $d = 1$ and 2 are depicted by symbols in Fig. 4b. As can be seen the reduced system predicts stability in the full model very well. We did not check the case $d = 3$ for computer time restrictions.

In the case of non-negative delays Δ_{ij} the fixed points resulting from (13) and (14) are obviously the same as before. Linear stability analysis for $d = 0$ leads to the quasi-polynomial

$$D(\lambda) = \tau_1 \tau_2 \lambda^2 + (\tau_1 + \tau_2)\lambda + 1 - (1 + \tau_2 \lambda)c_+ e^{-\lambda \Delta_+} + c_- e^{-\lambda \Delta_-} \quad (17)$$

where $\Delta_+ = \Delta_{11}$ and $\Delta_- = \Delta_{12} + \Delta_{21}$ are the total delays in the excitatory and inhibitory loops. The characteristic equation $D(i\omega) = 0$ still determines the location of fixed point instabilities, but the equation can now have infinitely many roots and is no longer explicitly solvable (Driver 1977). For $D(0) = 0$ we nonetheless recover the old stability condition: $c_- = c_+ - 1$. $D(i\omega) = 0$ yields after separation of the real and imaginary part of (17)

$$1 - \tau_1 \tau_2 \omega^2 = c_+ [\cos(\omega \Delta_+) + \tau_2 \omega \sin(\omega \Delta_+)] - c_- \cos(\omega \Delta_-) \quad (18)$$

$$(\tau_1 + \tau_2)\omega = c_+ [\tau_2 \omega \cos(\omega \Delta_+) - \sin(\omega \Delta_+)] + c_- \sin(\omega \Delta_-) \quad (19)$$

which can be written as $A \begin{pmatrix} c_+ \\ c_- \end{pmatrix} = b$, where the matrix A and vector b follow immediately from (17). Thus, $\begin{pmatrix} c_+ \\ c_- \end{pmatrix} = A^{-1}b$ as long as A is invertible. Because $A = A(\omega, \text{params})$ and $b = b(\omega, \text{params})$ the values of c_+ and c_- obtained this way provide stability boundaries parametrised by ω in the parameter subspace spanned by the loop gains c_+ and c_- .

Figure 5a displays the stability diagram for $d = 0$ and $\Delta_{11} = \Delta_{12} = \Delta_{21} = \Delta = 3$. The S- and H-lines are the same as in Fig. 4 for $\Delta = 0$. Increasing transmission delays bend the Hopf-bifurcation line leftwards, thereby decreasing the region in parameter space with stable fixed points. Circles in Fig. 5a denote the Hopf-branch for $d = 1$, i.e., a one dimensional field model. As in Fig. 4 the branch is shifted relative to that for $d = 0$, but apparently the full model (open circles) and the reduced system (filled circles) loose stability at virtually the same values.

The model with vanishing delays is always stable for small or zero c_+ however large c_- gets. In contrast, delays can destabilise fixed points even without recurrent excitation, $c_+ = 0$, because phase-shifts in the inhibitory feedback loop due to the delay can cause a positive self-exciting feedback for certain frequencies if the inhibitory loop gain c_- becomes strong enough. Figure 5b displays critical gains c_- for increasing delay $\Delta_+ = \Delta$, $\Delta_- = 2\Delta$, and $c_+ = .5$ and 1 , respectively. Again, results for the full (dashed lines) and reduced model (solid lines) coincide very well.

Taken together, the simulations and analyses in this section demonstrate a good qualitative and even quantitative agreement between the full neural fields and the reduced equations in different dimensions. Tuned peaks in excitatory–inhibitory field models can therefore be well described by the low-dimensional differential equation derived here. In the special example the reduced system has just two components, but for other than just first order low-pass membranes represented by higher order operators D_j in (1) the temporal dynamics can be more complex. Additional cell classes add further complexity to the reduced system.

We should also mention that the assumption of rotation symmetry used for $d = 2$ in this section can be relaxed. However, for non-isotropic kernels (or stimuli), the principal dynamics of tuned peaks will still be the same as before, only the effective couplings c_{ij}^* take the more general form (7) with different tunings in different directions. Given these c_{ij}^* , however, the amplitude equations take the exact same form as before, and are similar to the Wilson–Cowan equations.

Fig. 5 (a) Transmission delays ($\Delta_+ = \Delta$, $\Delta_- = 2\Delta$) for $\Delta = 3$ and $d = 0$ bend the Hopf-bifurcation line leftwards, whereas the saddle-node line remains unchanged as compared with $\Delta = 0$ (cf. also Fig. 4a). Simulations of the full (open circles) and reduced systems

(filled circles) for $d = 1$ coincide almost perfectly. (b) Critical coupling c_- for increasing delay in a one-dimensional model ($d = 1$) and c_+ fixed at .5 and 1, respectively. Solid lines: reduced system; dashed lines: full system

Discussion

In summary, we presented an approximation scheme to simplify the analysis of dynamic localised solutions in d -dimensional neural field models with transmission delays. The method replaces the full activity peaks by equivalent Gaussian ones and results in a system of delay differential equations for the amplitudes and tuning widths only. The reduced equations have been shown to reproduce the behaviour of a two-layer example model in one and two dimensions even quantitatively with good accuracy. The example system bears physiological relevance with respect to steady and dynamic tuning properties of cortical cells (Amari 1977; Ben-Yishai et al. 1995; Somers et al. 1995; Suder et al. 2001; Wennekers 2001; Wilson and Cowan 1973; Wörgötter et al. 1998). It may also serve as a starting point for an analysis of biologically more detailed applications.

Most importantly, the method provides a potential link between field models for cortical tuning and classical EEG-models: To lowest order we derived nonlinear oscillator equations for the peak amplitudes (9). Similar equations serve as basic local elements in EEG-models where they are arranged into one- or two-dimensional grids coupled diffusively or by means of local connectivity kernels representing interactions on a scale of perhaps millimetres or longer (Jirsa and Haken 1996; Nunez 1995; Rennie et al. 1999; Robinson et al. 1998).

A common example for such local elements is the well-known Wilson–Cowan oscillator which describes the interaction of local excitatory and inhibitory pools (masses) of neurons. The original derivation of the Wilson–Cowan equations relies on the assumption of not further structured random connections between neurons (Wilson and Cowan 1972, 1973), but here we have shown that it can also be obtained from an excitatory–inhibitory field model for

microcircuits underlying neural tuning. It might therefore be possible to derive the parameters of local oscillators in the coarse-grained model from the reduced equations of cortical microcircuit models of feature selectivity. Apparently this possibility is not restricted to just two pools of cells because the approximation scheme can cover higher numbers of contributing cell-classes which would accordingly result in local dynamic elements of greater complexity on the coarse-grained level. This is especially interesting as models of the form (1) focus on tuning properties of cell ensembles, that is, their capacity to represent information, which may thus have correlates in EEG-recordings like specific spectral or wave properties under different cognitive conditions.

An interesting Gedanken-experiment, beside leading to a clear testable prediction, illustrates this suggestion: Assume the visual system is stimulated by a moving whole-field grating. This evokes a patchy activation pattern in the primary visual cortex which can be made visible in optical recordings; already Hubel and Wiesel (1962) demonstrated this patchy pattern using radio-active tracers. Given a characteristic space constant of the orientation tuning map of about 0.7 mm (cat or monkey) not even high-resolution sub-dural surface-EEG would be able to reveal it. Instead each electrode would average over multiple patches in its neighbourhood thereby providing a smoothed activity pattern. Each patch can be treated using our approximation scheme. In a second step we can then connect the resulting amplitude equations into a two-dimensionally extended grid of patches given physiological constraints regarding cortical lateral connections. As (Buzas et al. 2006) have shown, these connections are predominantly between regions of similar orientation tuning if those are aligned along a possible contour, but weak (or even inhibitory) in a parallel configuration. This means that the effective connections in our grid would be stronger

in the direction parallel to the grating and weaker (or inhibitory) orthogonal to it. The effective connectivity therefore is unisotropic, such that wave dispersal would be different in different cortical directions. The important thing to note is, that the unisotropy is induced by the orientation of the stimulus. Changing orientation moves the patches slightly (but invisibly for the EEG electrodes) but changes the corresponding effective connections, too. Accordingly, the direction of unisotropy in EEG waves would depend on the stimulus orientation over V1. This predicts a situation where functional connectivity properties may show up in large-scale EEG activity. An obvious further extension of this Gedanken-experiment would be to combine it with binocular rivalry which would nicely strengthen the relation to perception.

A future application of the approximation method will be to reformulate Friston's predictive "empirical Bayesian" model of the layered cortical microcircuitry (Friston 2005) in terms of localised activity distributed across different layers in the cortex. This might match his empirical equations more closely with concrete inter- and intralaminar cortical circuits. The approach would likely result in higher-dimensional local oscillators than the Wilson–Cowan equations, which could reflect laminar cortical processes in potentially different frequency bands. A second important extension concerns lateral long-range interactions. It is known that intra-cortical long-range connections are often patchy connecting cells of similar feature selectivity (Amir et al. 1993). It is not difficult to extend the presented approximation scheme to this situation which would enable the study of interacting activity peaks in the cortex including their tuning dynamic. Predictions of such models could well be tested in optical recordings, for instance, in the visual domain. However, we have to leave these and further applications of the developed approximation scheme to future work.

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