Fitting of spatio-temporal receptive fields by sums of Gaussian components

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Abstract

In previous work we have shown that spatio-temporal tuning functions can often be envisaged as a superposition of several amplitude-modulated spatial components, each resulting from a particular synaptic pathway between cell classes contributing to the response. The present work investigates this possibility by fitting sums of Gaussians to tuning curves simulated by neural field models. The time-course of fitted amplitudes and component tunings is shown to provide information about the contribution of input and recurrent synaptic connections to cortical tuning.

Key words: Receptive fields; Spatio-temporal tuning; Field Model; Fitting method

1 Introduction

Cortical simple cells have been shown to reveal dynamic receptive fields (RFs) comprising phases of specifically tuned enhanced and suppressed activity [2,3,8]. A recently developed method to analyze such responses suggests that the space-time orientation tuning curve of a simple cell should be approximately separable into a sum of temporally amplitude-modulated spatially Gaussian components [7], where each single component relates to an anatomical connectivity kernel between two of the contributing cell classes (e.g., LGN cells, excitatory and inhibitory cortical neurons). This provides a structure-function relationship between synaptic connectivity densities and physiological observations and suggests to fit dynamic tuning functions by sums of spatial Gaussians in order to quantify the relative contribution of the LGN-input and

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cortex-intrinsic mechanisms to single cell tuning in experimental data. This approach is demonstrated here for computer simulated data.

2 Neural field model

We consider a set of n neural fields, for instance describing different classes of cells topographically arranged in some feature space $R^d,\ d \geq 1$,

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

Depending on the application the variable $x \in R^d$ may represent cortical location, visual space, stimulus orientation, or some other feature domain. In (1) the $\phi_i(x,t)$ and f_i denote the membrane potentials and rate-functions of cells in layer i, respectively. The symbol '*' denotes spatial convolution and the D_i are linear differential operators in time t, e.g., first order low-pass filters with time constants τ_i, $D_i = \tau_i\partial_t$. The kernels k_{ij} in (1) represent distance-dependent synaptic densities from cells in layer j to layer i. We use Gaussians with variance matrix σ_{ij}^2 because neurons encoding similar features are often coupled stronger than those with differing preferences

$$k_{ij}(x) = \frac{K_{ij}}{(2\pi)^{d/2}} \exp\left[-\frac{1}{2}x^T\sigma_{ij}^{-2}x\right] \ . \tag{2}$$

$I_i(x,t)$ in (1) is external input which we also choose Gaussian with amplitude $I_{i0}T_i(t)$ and variance matrix σ_{i0}^2. I_{i0} and $T_i(t)$ define the input strength and time-course, and σ_{i0}^2 the input tuning into layer i. Rate functions f_i in (1) are kept general in (1), but may be semilinear with gain β_i and threshold ϑ_i, $f_i(\phi_i) := \beta_i \max(0, \phi_i - \vartheta_i)$, or the logistic function, $(1+\exp(-\beta_i(\phi_i - \vartheta_i)))^{-1}$.

3 Nonlinear superposition principle

Networks of the type (1) can reveal localized responses (cf., e.g., Fig. 1A) which reflect selectivity of cells in the studied feature space. The activity is usually dynamic, if the input is already temporally modulated or due to network intrinsic processes. One would expect that features of such spatio-temporal response functions provide information about the mechanisms underlying cortical tuning phenomena. Therefore, in previous work [7] we developed methods to characterize spatial and temporal properties of dynamic localized solutions of (1) in terms of the underlying anatomical network structure and membrane

dynamics. A special outcome of the method (cf., [7] for details) is that it should often be possible to approximate the potential profiles $\phi_i(x,t)$ by sums of amplitude-modulated spatial Gaussian components

$$\phi_i(x,t) \approx \sum_{j=0}^{n} a_{ij}(t) \exp\left[-\frac{1}{2} x^T \Sigma_{ij}^{-2}(t) x\right] \ , \tag{3}$$

where the component tunings Σ_{ij} and amplitudes a_{ij} are in general functions of time (Note, that the input has been given an index 0 in (3)). Most importantly, each particular component in (3) results from an individual coupling kernel k_{ij} in (1). Because those reflect the distance-dependent synaptic densities from cells in layer j to layer i, Eqn. (3) links physiological potential profiles to anatomical connectivities and thereby provides some kind of "structure function relationship". Moreover, it also provides an intuitive picture of spatio-temporal responses as dynamic mixtures of different tuned components. This way, large weight coefficents a_{ij} during certain phases of a response may, for instance, reveal the predominating impact of particular cell classes via k_{ij} on the potential profile in a target layer.

Spatio-temporal orientation tuning profiles can be measured experimentally using correlation methods [3,2]. To the degree that the assumptions made in the approximation method in [7] are satisfied, Eqn. (3) suggests that it should be possible to fit these dynamic profiles by sums of amplitude modulated Gaussians. The resulting time-course of amplitudes and tunings then should provide information about the anatomical substrate generating the response. The next section gives an example for this procedure using artifically generated data, where all parameters are well controlable. Reference [5] presents an application of the approach to real data. There, certain dynamic receptive field effects in cortical simple cells –reported in detail in [8]– were tracked down by Gaussian fits as resulting from the feedforward projection from visual thalamus to cortex, and distinct firing patterns of thalamic relay cells.

4 Numerical example

We consider a network of two one-dimensional layers of cells comprising excitatory and inhibitory neurons, respectively (i.e., $n = 2,\ d = 1$ in (1)). Membranes are first order low-pass filters, rate functions logistic functions in the excitatory layer and semilinear in the inhibitory layer. Parameters used are $\tau_1 = 2,\ \tau_2 = 5,\ I_{10} = 0.3,\ I_{20} = 0,\ \beta_1 = 4,\ \theta_1 = 0.5,\ \beta_2 = 1,\ \theta_2 = 0,\ K_{11} = 1,\ K_{12} = -0.25,\ K_{21} = .047,\ K_{22} = 0,\ \sigma_{11} = 2.5,\ \sigma_{10} = 15,\ \sigma_{12} = \sigma_{21} = 30$. The above parameters are quite arbitrary choices. For a general discussion of the model behavior and its relation to previous models for cortical ori-

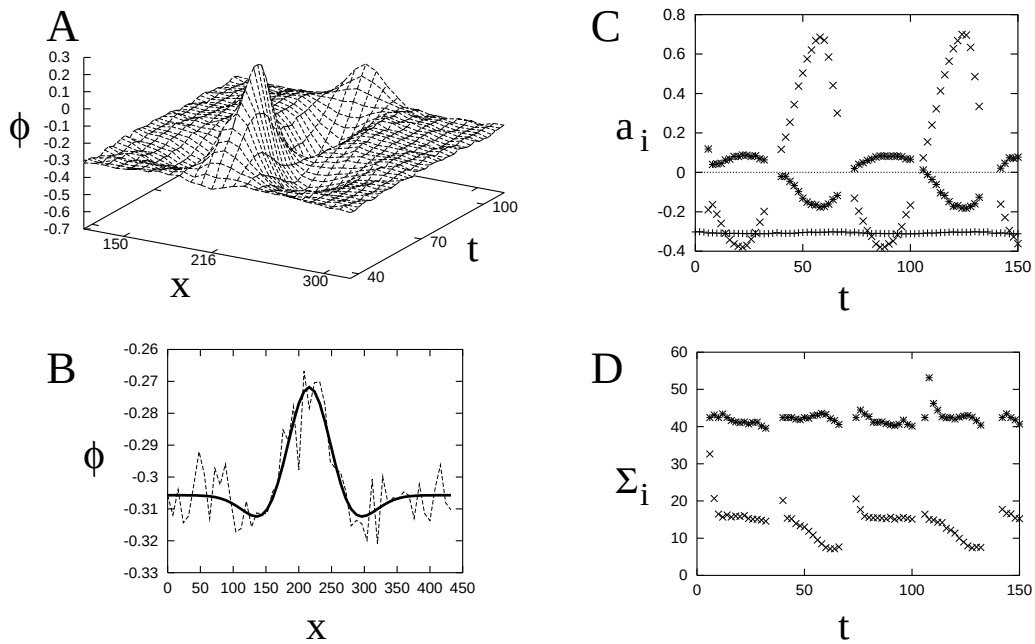

Fig. 1. A) A simulated spatio-temporal response in a lateral inhibition type neural field (counterphase input, 1 period shown, arbitrary units). B) Example fit of data in A at $t = 40$ to a sum of 2 Gaussians plus baseline. C,D) Time-course of fitted component amplitudes (C) and tunings (D).

entation tuning cf. [7]. The simulations employed a simple Euler integration scheme with temporal stepsize of 0.1 and a spatial discretization interval of 1 (433 grid points or "units" in total). Equidistributed noise in the interval $[-.075, .075]$ was added to the potentials of each unit in every time-step. Data were fitted using the Levenberg-Marquardt method.

Figure 1A displays an excitatory potential profile where the network was stimulated by a spatial Gaussian centered at $x = 216$ with amplitude $I_{10} = 0.3$ and width $\sigma_{10} = 15$. The input was modulated sinusodially at a frequency of $\omega/(2\pi) = 0.015$, i.e., a period of 67 units of time. Figure 1B shows an example profile for $t = 40$ superimposed with a best fit comprising two Gaussian components and a baseline. Figures C and D reveal fitted component amplitudes and tunings over time. During most of the response, fits as in B consisted of a sharp central component (crosses in C and D) and a weaker and broad peripheral one (stars). Fits often failed where amplitudes were small compared to the noise, cf. the gaps in the fitted amplitudes near zero crossings in Fig. 1C. Observe also that the baseline in C is virtually constant at resting potential.

In principle we know from the model equations, that the excitatory response profile should consist of *three* tuned components, one for the input, and two for k_{11} and k_{12}, respectively. We have nonetheless chosen only two tuned com-

ponents because visual inspection of the data reveals only two, cf. Fig. 1B. In fact, the sharp central component actually consists of two sub-components, which can hardly be resolved: the input and the recurrent excitation. The latter is strong only during the positive phase of the stimulus where firing activity becomes high and is further amplified by the relatively strong recurrent excitation via k_{11}. For that reason, the amplitude time-course of the sharply tuned central component is not sinusoidal as one would expect for the pure input component alone (Fig. 1C, crosses). Also, as Fig. 1D shows, the width of the central component is roughly $\Sigma_1 = 16$ and almost constant near to the input tuning during the negative stimulus phase, whereas it changes to small values around $\Sigma_1 \approx 8$ (nearer to the width of the excitatory coupling kernel) during the positive half-wave. This change in tuning again indicates that the nature of the central response carries over from input driven to recurrently driven during the positive stimulus half-wave, but is mainly stimulus driven during the negative half-wave. The second fitted, broadly tuned component on the other hand reflects lateral inhibition (positive stimulus half-wave) or disinhibition (negative half-wave) due to the excitatory-inhibitory loop.

5 Discussion

The example in the previous section shows that it is in principle possible to fit spatio-temporal response profiles to sums of amplitude modulated spatial Gaussians as predicted theoretically. The example also points at possible difficulties if the method is applied to real data. First, the number of components is usually not known in experiments. Visual inspection of the data or theoretical reasoning about mechanisms underlying the observed responses may, however, give hints for a proper choice of the component number. This has been successfully demonstrated in [5] and inspection of spatio-temporal orientation tuning functions recorded by Ringach et al. [3,2] also suggest only one or two components. Second, noise in experimental data may complicate the detection of small components. This again asks for a low number of components. Third, some components may have a similar tuning such that their superposition is hardly distinguishable from a single component, cf., e.g., Troyer et al.'s model for orientation tuning [6], where excitatory and inhibitory kernels are assumed equally tuned. In all these cases the number of fitted components would supposedly be lower than the number of actually present ones. Nonetheless, as in the presented example the precise time course of amplitudes and tunings of incompletely separated components may still give hints about the underlying dynamic mechanisms. It should also be possible to design special stimulus time-courses, $T_i(t)$, which enable a separation of otherwise unresolvable components during different stimulus phases, as, e.g., visible in the response differences during positive and negative half-waves in the example.

Finally, we should mention that the observed sharpening of tuning during the positive stimulus half-wave should be present also in real data *if* sharply tuned strong excitatory recurrent connections contribute to simple cell tuning as it has been proposed by several authors [1,4]. Such data could be obtained experimentally by presenting counterphase graitings at different orientations and phase-locked averaging of the respective simple cell responses.

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