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Systematic approximations of neural fields through networks of neural masses in the virtual brain

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ABSTRACT

Full brain network models comprise a large-scale connectivity (the connectome) and neural mass models as the network's nodes. Neural mass models absorb implicitly a variety of properties in their constant parameters to achieve a reduction in complexity. In situations, where the local network connectivity undergoes major changes, such as in development or epilepsy, it becomes crucial to model local connectivity explicitly. This leads naturally to a description of neural fields on folded cortical sheets with local and global connectivities. The numerical approximation of neural fields in biologically realistic situations as addressed in Virtual Brain simulations (see http://thevirtualbrain.org/app/ (version 1.0)) is challenging and requires a thorough evaluation if the Virtual Brain approach is to be adapted for systematic studies of disease and disorders. Here we analyze the sampling problem of neural fields for arbitrary dimensions and provide explicit results for one, two and three dimensions relevant to realistically folded cortical surfaces. We characterize (i) the error due to sampling of spatial distribution functions; (ii) useful sampling parameter ranges in the context of encephalographic (EEG, MEG, ECoG and functional MRI) signals; (iii) guidelines for choosing the right spatial distribution function for given anatomical and geometrical constraints.

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Introduction

With the availability of full brain structural connectivity information, the so-called *connectome* (Sporns, 2011), a new type of network models emerged that needed to address novel challenges characteristic for this macroscopic level of description. These challenges included the handling of a complex connectivity matrix in three-dimensional physical space, the inclusion of many time delays as a function of fiber lengths, as well as the correct choice of the mathematical model for a network node. Depending on the structural parcellation (Kötter and Wanke, 2005), a network node typically comprised a brain region of the size of multiple square centimeters (Hagmann et al., 2008). The full brain modeling approach proved successful in explaining the mechanisms underlying the emergence of network patterns and their coherent intermittent dynamics for resting state conditions (Deco and Jirsa, 2012; Deco et al., 2009, 2011; Ghosh et al., 2008). Crucial elements of the resting state dynamics include stochastics and multistability (Freyer et al., 2009, 2011, 2012). The resting state patterns and its dynamics are robust and reproducible within healthy populations (Damoiseaux et al., 2006; He et al., 2007; Mantini et al., 2007; Raichle et al., 2001), but differ quite significantly across diseases, such as schizophrenia, autism, epilepsy and others (Buckner et al., 2008; Cherkassky et al., 2006; Corbetta et al., 2005; Kennedy et al., 2006; Symond et al., 2005; Uhlhaas and

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Singer, 2006, 2010), as well as the aging brain (Beason-Held et al., 2009; Damoiseaux et al., 2008; Fransson et al., 2007; Koch et al., 2010; Supekar et al., 2010). For this reason the resting state dynamics finds enormous interest as a potential biomarker for disease or disorder. Of particular interest in these network manipulations is the ratio of local versus global connectivity. Local connectivity represents intracortical connections, whereas the global connectivity is the connectome comprising the white matter fibers between cortical and subcortical areas. Often local connectivity is absorbed in the parameters of the network node model. Manipulations of local connectivity (such as pruning of fibers during development or sprouting in epileptic tissue), however, are a key to modeling studies in a number of situations and require a representation of the full brain network, in which the brain region as a network node acquires more complexity and encompasses the notion of local connectivity. A natural extension of a network of coupled brain regions towards a spatially continuous sheet is provided by the neural field theory (Coombes, 2010; Deco et al., 2008; Jirsa, 2004). The aim of this work is to develop accurate numerical approximations of neural field models on folded cortical sheets with local and global connectivities, the latter typically obtained from tractographic data.

The numerical approximation of a neural field is realized via a network of *neural masses*. Neural field models cover the continuous description of interacting *neural ensembles*. A neural ensemble refers to a local set of commonly interacting neurons (Freeman, 1992). An ensemble of neurons of a certain class (e.g., due to receptor, location and/or morphological classifications) can be described in terms of









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mean firing rate and mean postsynaptic potential as a so-called neural mass. Hence, a neural mass model is a lumped representation, especially neglecting the spatial extend of a neural ensemble (Spiegler et al., 2010). Note that a single neural ensemble (or even a cortical area under certain functional circumstances Spiegler et al., 2011) can be described as a set of interacting neural masses, for instance, a neural mass of pyramidal cells, a neural mass of glutamatergic spiny stellate cells and a neural mass of GABAergic neurons (Spiegler et al., 2010). Usually nonlinear differential equations are used to mimic the complex behavior of neural ensembles. These equations are difficult to solve analytically and therefore such models are, nowadays, translated into a digital scheme for integration. This approach brings a discretization problem in its wake. That means that a neural field model is translated into a network of spatially separated sets of neural masses. For this purpose, a crucial step is the sampling of the spatial distribution function of the connections.

The sampling task can be addressed from three points of view with the aim: (i) to construct a model based on biophysical or theoretical considerations, (ii) to describe spatial patterns in specific empirical data, or (iii) to assess dynamics of an implemented neural field model. All three approaches are subject to restrictions of the considered underlying techniques. The resolution of human brain measurements, for instance, electrocorticography (ECoG) and functional magnetic resonance imaging (functional MRI) is in the order of mm (e.g., Blakely et al., 2008; Freeman, 2000; Yoo et al., 2004; Zhang et al., 2008). In the case of electro- and magneto-encephalography (EEG and MEG) the spatial resolution is in the order of cm (e.g., Freeman et al., 2003; Hämäläinen et al., 1993; Malmivuo and Suihko, 2004; Srinivasan et al., 1999). Moreover, implementations of a model in a digital regime underlie, for instance, a finite representation of numbers and its precision, and a finite number of network nodes.

This work deals with the spatial sampling of two specific but widely used choices of the homogeneous connectivity distribution function, namely, the sum of Gaussian (e.g., Amari, 1977; Atay and Hutt, 2005; Markounikau et al., 2010) and the sum of Laplace distributions (e.g., Jirsa and Haken, 1996). Because the main focus is on cortical dynamics, the spatial distribution function is to a first approximation assumed to be independent of the location on the cortical surface.

The main three emphases of this paper are: (i) what is the error that appears due to sampling a spatial distribution function; (ii) what are the usable parameters for a spatial distribution function considering the resolution of such measurements as EEG, MEG, ECoG and functional MRI; and (iii) how can the parameters of a spatial distribution function be specified giving a specific discrete approximation of a cortical geometry.

This work extends previous studies of neural fields, such as Bojak et al. (2010) and Freestone et al. (2011) in three points: (i) the sampling procedure can be assessed using two measures (ii) that are applicable in any dimensional physical space (iii) for two widely used spatial distribution functions.

Material and methods

Let φ be a variable of activity captured by the model (e.g., currents or potentials), the evolution in time *t* can then be described by the following ordinary differential equation

$$D(\mathbf{d}/\mathbf{d}t)\varphi(t) = \epsilon(t),\tag{1}$$

where D(d/dt) is the temporal differential operator with the polynomial of constant coefficients $D(\lambda) = \sum_{u=0}^{U} b_u \lambda^u$ of order U and ϵ describes the (differentiable) input from interventions (e.g., transcranial magnetic stimulation) or other structures that are not explicitly described by the model (e.g., thalamic nuclei). A *neural mass* model

describes a neural ensemble by a set Φ of $n : n \in \mathbb{N}$ interconnected variables φ_n (Freeman, 1992), so that Eq. (1) becomes

$$\mathbf{D}(\mathbf{d}/\mathbf{d}t)\mathbf{\Phi}(t) = \mathbf{E}(t) - \mathbf{A}(\mathbf{\Phi}(t)), \tag{2}$$

where **D** = $(D_1, D_2, ..., D_n)^{\top}$, $\Phi = (\varphi_1, \varphi_2, ..., \varphi_n)^{\top}$, **E** = $(\epsilon_1, \epsilon_2, ..., \epsilon_n)^{\top}$ and the operator **A**(Φ) links the state variables within a neural mass Φ . For instance, in the case of the FitzHugh–Nagumo description of temporal dynamics (FitzHugh, 1955; Nagumo et al., 1962) the operator is given by **A**(Φ) = $(a_{11}\varphi_1 + a_{13}\varphi_1^3 + a_{21}\varphi_2, b_0 + b_{11}\varphi_1 + b_{21}\varphi_2)^{\top}$, where $a_{11} = a_{21} = -3a_{13} = 3$, $b_{11} = -10b_0 / 7 =$ $5b_{21} / 4 = -1 / a_{11}$, n = 2 with $D_1(\lambda) = D_2(\lambda) = \lambda$ and **E** = $\binom{\epsilon_1}{\epsilon_1}$; see Appendix A for further details. This type of dynamics has been shown to be a first good approximation of a population of FitzHugh– Nagumo neurons with global coupling and dispersion (Assisi et al., 2005; Stefanescu and Jirsa, 2008, 2011) and has appeal as a neural mass model due to its mathematical simplicity. A local area (where the spatial extension can be neglected) may consist of $m : m \in \mathbb{N}$ different neural masses (e.g., pyramidal cells, glutamatergic spiny stellate cells and GABAergic basket cells) composing a *network of neural masses*

$$\mathbf{P}(\mathbf{d}/\mathbf{d}t)\mathbf{\Psi}(t) = \mathbf{\Xi}(t) - \mathbf{\Lambda}(\mathbf{\Psi}(t)) + S(\mathbf{V}_{\text{loc}}\mathbf{\Psi}(t)), \tag{3}$$

with $\Psi = [\Phi_1; \Phi_2; ...; \Phi_m], \Xi = [E_1; E_2; ...; E_m], \Lambda = [A_1; A_2; ...;$ \mathbf{A}_{m}]. The transfer function $S(\Psi)$ of Ψ is taken to have a sigmoidal shape in most works (e.g., Atay and Hutt, 2005; Breakspear et al., 2006; Coombes, 2010; Jirsa and Haken, 1996; Pinotsis et al., 2012). The temporal differential operator $\mathbf{P} = [\mathbf{D}_1; \mathbf{D}_2; ...; \mathbf{D}_m]$ accounts for m time constants that characterize the m different neural masses. Note that the number of variables n can differ with the class of neural mass $i : i \in \mathbb{N}$, [1, m] so that $n : n_i$. The square matrix \mathbf{V}_{loc} of order $\sum_{i=1}^{m} n_i$ connects state variables Ψ to transfer among the *m* different neural masses. Hence, the local transfer matrix V_{loc} can be constructed, for example, such that the *m* neural masses are simply connected via the first state variable $\{\varphi_{n=1}\}_{i}$ of each neural mass *i*. Using the FitzHugh–Nagumo temporal dynamics for describing *m* neural masses the network structure is then expressed by non-zero entries for odd columns and rows in V_{loc} (i.e., connecting the first state variable of each mass). Another example is the Jansen-Rit model (Jansen and Rit, 1995; Spiegler et al., 2011) that describes the temporal evolution of postsynaptic potentials $\forall_i : n_i = 1, \Phi_i = \{\varphi_1\}_i$ caused among three interacting neural masses $\Psi = [\Phi_1; \Phi_2; \Phi_3] : m = 3$, namely, pyramidal cells (i = 1) with feedback loops mediated by excitatory and inhibitory interneurons (i = 2 and i = 3, respectively) by a second-order ordinary differential operator U = 2, **P** : $D_i = \lambda^2 + 2b_i\lambda + b_i^2$ with $b_1 = b_2 = 1$ and $b_3 = 1 / 2$. The vector $\Xi = (\epsilon_1, \epsilon_2, \epsilon_3)^{\top}$ then describes the extrinsic synaptic input on all three neural masses, the state operator $\mathbf{\Lambda} = \mathbf{0}_{3 \times 1}$ since $\forall_i : n_i = 1$, the postsynaptic potentials φ_{n_i} are transferred according to a sigmoid function $S(\varphi_{n_i}) = 1 / (1 + \xi \exp(-\varphi_{n_i})) : \xi = \exp(3.36)$, and the transfer matrix V_{loc} describes the four couplings between the three neural masses by the nonzero entries $V_{2,1} = 5V_{1,2} / 4 = 4V_{3,1} = -13V_{1,3} / 44 = 12.285$ (see Appendix A for further details).

Note that the description for a local neural mass model Eq. (3) neglects the spatial extent (i.e., only time dependent) and rather represents a discrete representation of the neural tissue (i.e., *m* neural masses). However, considering the extent of a neural tissue, such as the whole cortex in the spatial domain, Ω , Eq. (2) leads to a generalized *neural field* description by the following system of delay-integro-differential equations

$$\begin{split} \mathbf{P}(d/dt)\mathbf{\Psi}(x,t) &= \mathbf{\Xi}(x,t) - \mathbf{\Lambda}(\mathbf{\Psi}(x,t)) + S(\mathbf{V}_{\text{loc}}\mathbf{\Psi}(x,t)) \\ &+ \mathbf{V}_{\text{hom}} \int_{\Omega} dy \ W_{\text{hom}}(\Delta(x,y)) \ S(\mathbf{V}_{\text{loc}}\mathbf{\Psi}(y,t-\Delta(x,y)/c_1)) \\ &+ \mathbf{V}_{\text{het}} \int_{\Omega} dy \ W_{\text{het}}(x,y) \ S(\mathbf{V}_{\text{loc}}\mathbf{\Psi}(y,t-\Delta(x,y)/c_2)), \end{split}$$

$$\end{split}$$

$$(4)$$

where, in addition to Eq. (3), the integral terms in Eq. (4) connect the state variables among the local networks in the k-dimensional space $\Omega : \Omega \subset \mathbb{R}^k$ with $k = \{1, 2, 3\}$, the locations x, $\gamma \quad \Omega = [-L, N]$ L] and the spatial extension L of the neural field. If connections are translationally invariant with respect to the distance $\Delta(x, y)$ between two neural masses at x and y we call it homogeneous $W_{\text{hom}}(\Delta(x, y))$, otherwise heterogeneous $W_{\text{het}}(x, y)$. The latter $W_{\rm het}(x, y)$ typically is global concerning the whole brain, whereas the former $W_{\text{hom}}(\Delta(x, y))$ represents intracortical, that is a local connection type. In general, the extent of the homogeneous connectivity, $W_{\text{hom}}(\Delta(x, y))$, is assumed to be small compared to the spatial extension L of the neural field. The parameters c_1 and c_2 account for the propagation velocities through the homogeneous and heterogeneous paths respectively. The square matrices $V_{\rm hom}$ and $V_{\rm het}$ are of the same order than $\boldsymbol{V}_{\text{loc}}$ and describe the coupling schemes for homogeneous and heterogeneous connectivities, respectively. For instance, the homogeneous paths connect all neural masses at different locations (see, David et al., 2005, for an example of a hierarchical coupling scheme developed for the Jansen-Rit model), while the heterogeneous paths are established by pyramidal cells in layer V of the cortex projecting onto glutamatergic spiny stellate cells in layer IV (Thomson and Bannister, 2003).

The neural field Eq. (4) can be transferred without loss of generality into the framework of a network of neural masses Eq. (3) by adequately sampling the spatial domain Ω . The connectivities $W_{\text{hom}}(\Delta(x, y))$ and $W_{\text{het}}(x, y)$ are sampled on the field geometry (i.e., integral terms in Eq. (4)) and pooled with the coupling schemes, \mathbf{V}_{hom} and \mathbf{V}_{het} , respectively. While for a one-dimensional space the sampling procedure of the connectivity functions is well-defined (i.e., with a Dirac comb), for higher dimensional geometries k > 1 several methods are available, such as the Delaunay triangulations (de Berg et al., 2008). However, irrespective of the discretization procedure the space Ω is sampled with a finite number of points *l* so that Eq. (4) results in

$$\hat{\mathbf{P}}(d/dt)\hat{\mathbf{\Psi}}(t) = \hat{\mathbf{\Xi}}(t) - \hat{\mathbf{\Lambda}}\left(\hat{\mathbf{\Psi}}(t)\right) + \sum_{\nu=0}^{2} U_{\nu} S\left(\mathbf{V}_{\mathsf{loc}}\hat{\mathbf{\Psi}}(t-\mathbf{K}/c_{\nu})\right),$$
(5)

where the number of elements in the column vectors $\hat{\mathbf{P}} = [\mathbf{P}_1, \mathbf{P}_2, ..., \mathbf{P}_l]$, $\hat{\mathbf{\Psi}} = [\mathbf{\Psi}_1, \mathbf{\Psi}_2, ..., \mathbf{\Psi}_l]$, $\hat{\mathbf{\Xi}} = [\mathbf{\Xi}_1, \mathbf{\Xi}_2, ..., \mathbf{\Xi}_l]$, $\hat{\mathbf{\Lambda}} = [\mathbf{\Lambda}_1, \mathbf{\Lambda}_2, ..., \mathbf{\Lambda}_l]$, **K** and the order of the square matrices \mathbf{U}_v is $l \sum_{i=1}^m n_i$. Local (v = 0), homogeneous (v = 1) and heterogeneous connectivities (v = 2) are described in the sampled spatial domain Ω by the coupling matrix

described in the sampled spatial domain Ω by the coupling matrix and the distance vector, \mathbf{U}_{ν} and \mathbf{K} , respectively, where the speed for local propagation is $c_0 = \infty$. In other words, \mathbf{U}_{ν} and \mathbf{K} code the space-time structure of the connectivity over the space Ω in $\hat{\mathbf{\Psi}}$.

Note that each neural mass in the network could be considered to take up space depending on the spatial sampling of a lattice, or as a point, without spatial extent. In the first case, a neural mass model is specific to a spatial scale of description, whereas in the latter case it is not. In general, a neural mass can be defined by common input and output behavior of neurons, regardless of whether the averaging (e.g., of action potentials) takes place over time, space, or both. However, within the scope of this work we do not restrict ourselves to a specific definition about neural mass models.

The delay-differential system (Eq. (5)) reduces to a system of ordinary differential equation, that is, the network of neural masses (Eq. (3)) if $\forall_{\nu} : c_{\nu} = \infty$.

In addition to the spatial domain, also the discretization of the time *t* is needed for numerical integration, which essentially transfers the differential equations (i.e., Eqs. (1) to (5)) into a set of difference equations dependent on the numerical integration method (for example, Euler's method and its modifications, such as the Runge–Kutta methods). In the scope of this work we focus on the spatial discretization of the homogeneous connectivity $W_{\text{hom}}(\Delta(x, y))$ in the neural field Eq. (3), since the heterogeneous connectivity $W_{\text{het}}(x, y)$ of living human beings is, for the present state-of-the-art, obtained by diffusion-

weighted MRI tractography procedures with an already coarser spatial resolution, describing discrete connections between brain regions (Cammoun et al., 2012).

Homogeneous connectivity

The homogeneous connectivity $W_{hom}(\Delta(x, y))$ between neurons or neural ensembles is usually specified in the literature as isotropic and dependent only on the distance $r = \Delta(x, y)$ between two sites x and y. Mathematically, this describes a symmetric function $W_{hom}(r) = W_{hom}(-r)$ implying that the expectation value is zero $\int_{-\infty}^{\infty} r W_{hom}(r) dr = 0$. In the literature, the homogeneous connectivity $W_{hom}(\Delta(x, y))$ is usually described by the Gaussian distribution function (e.g., Amari, 1977; Atay and Hutt, 2005; Freestone et al., 2011; Markounikau et al., 2010) or the Laplace distribution function (e.g., Jirsa and haken, 1996; Nunez, 1974; van Rotterdam et al., 1982; Wilson and Cowan, 1973). In this work we consider both descriptions of the homogeneous connectivity $W_{hom}(\Delta(x, y))$ by the following expression

$$W_{\hom,\zeta}(z) = \eta \sum_{u=1}^{R} \beta_{u,\zeta} \exp\left(-\gamma_{u,\zeta} \left(z^{\mathsf{T}} z\right)^{1/\zeta}\right),\tag{6}$$

where z = |x - y| is a column vector with *k* entries. The superscript \top denotes the transpose operator. The homogeneous connectivity consists of $R : R \in \mathbb{N}$ distribution kernels with the synaptic weight $\beta_{u,\zeta} : \beta_{u,\zeta} \in \mathbb{R}$ (i.e., excitatory $\beta_{u,\zeta} > 0$, inhibitory $\beta_{u,\zeta} < 0$) and the spreading $\gamma_{u,\zeta}$ for each distribution that are in total scaled by η (e.g., with respect to R; see Appendix B for more information). If the shape parameter is $\zeta = 1$ or $\zeta = 2$, then the kernel is a sum of Gaussian or a sum of Laplace distributions, respectively (see Fig. 1). Note that $\sqrt{z^{\top}z} = ||z||_2$ is the Euclidean norm on \mathbb{R}^k and Eq. (6) can be rewritten as follows

$$W_{\text{hom},\zeta}(r) = \eta \sum_{u=1}^{R} \beta_{u,\zeta} \exp\left(-\gamma_{u,\zeta} r^{2/\zeta}\right),\tag{7}$$

where $r = \Delta(x, y) = ||z||_2$. The homogeneous connectivity function $W_{\text{hom}}(z)$ is consequently a radial function $W_{\text{hom}}(z) : \mathbb{R}^k \to \mathbb{R}$ on the physical space $\Omega \subseteq \mathbb{R}^k$ (see *k*-Dimensional case section in Appendix B).

In the following, we illustrate our approach to assess the sampling approximation by using a single exemplary building block, that is, R = 1 of the homogeneous connectivity $W_{\text{hom},\zeta}(z)$ for both cases, Gaussian $\zeta = 1$ and Laplace distributions $\zeta = 2$. The decay is $\gamma_{1,1} = \gamma_{1,2}^2 / 4$ and $\gamma_{1,2} = \sqrt{2} / \sigma$, with the standard deviation σ . The integral $\int_{-\infty}^{\infty} W_{\text{hom},\zeta}(z) dz$ of the homogeneous connectivity function is normalized to unity with $\eta\beta_{1,1} = (\gamma_{1,1} / \pi)^{k/2}$ and $\eta\beta_{1,2} = \sqrt{\pi} \eta\beta_{1,1}/\Gamma((1+k)/2)$ for the Gaussian and the Laplacian kernel, respectively, where $\Gamma(\lambda) = \int_{0}^{\infty} y^{\lambda - 1} \exp(-y) dy$ is the gamma function (see *k*-Dimensional case section in Appendix B for more details). However, the procedure can be directly applied to a sum of Gaussian, a sum of Laplace distributions and a sum of both including excitation as well as inhibition. Note that we refer $W_{\text{hom},\zeta}(z)$ and $W_{\text{hom},\zeta}(r)$, respectively, to the case R = 1 in the rest of this paper without further indication.

Sampling the homogeneous connectivity

Let the metric $r = \Delta(x, y)$ of the radial function Eq. (7) for the homogeneous connectivity $W_{\text{hom},\zeta}(r)$ be periodically captured along a basis v for the given k-dimensional Euclidean space Ω with a constant interval ϱ , the *Petersen–Middleton theorem* then informs about the requirements for an exact sampling procedure, that is, sampling lattice vwith a minimum sampling interval ϱ (Petersen and Middleton, 1962). This theorem extends the well-known *Whittaker–Kotel'nikov–Shannon sampling theorem* (e.g., Shannon, 1949) to k-dimensional Euclidean spaces. According to the mentioned sampling theorems, the spatial



Fig. 1. $W_{\text{hom},\zeta}(r)$ in (A) radial *r* and (B) frequency domain *q*.

spectra of the homogeneous connectivity function $W_{\text{hom},\zeta}(r)$ must be compact for preserving the information through a spatial discretization. An approximate reconstruction can be obtained under the condition that the spectrum is compact enough within the bound q_c

$$\widetilde{W}_{\hom,\zeta}(q,k) \approx 0 \,\forall q > q_c,\tag{8}$$

where $W_{\text{hom},\zeta}(q, k)$ is the *k*-dimensional Fourier transform. Sampling a basis *v* of the *k*-dimensional space Ω (i.e., *v* is a set of *k* basis vectors) periodically by ϱ gives the sampling lattice. A sampling lattice that uses a minimum number of vertices *l* to achieve exact reproduction of a bandlimited radial function, such as the homogeneous connectivity $W_{\text{hom},\zeta}(r)$ is, for instance, the hexagonal lattice in two dimensions and the body-centered cubic lattice in three dimensions (Petersen and Middleton, 1962). The sampling interval (or the edge length) $\varrho \subseteq \Delta(x, y)$ between to cortical location sites *x* and *y* must be at least twice the spectrum cutoff q_c at a finite spatial frequency

$$\varrho \le \frac{1}{2q_c}.\tag{9}$$

Decomposing the homogeneous connectivity, as described in Eq. (6), into an infinite number of waves we obtain

$$\tilde{W}_{\hom,\zeta}(s,k) = (2\pi)^{-k/2} \int_{\Omega \in \mathbb{R}^k} dz \ W_{\hom,\zeta}(z) \exp\left(j s^\top z\right), \tag{10}$$

where *j* is the imaginary number $(j^2 = -1)$ and *s* is the spatial frequency vector of the *k*-dimensional spatial frequency basis that is orthogonal to *v* (Petersen and Middleton, 1962). Since the homogeneous connectivity, Eq. (6), is radial on \mathbb{R}^k , see Eq. (7), the Fourier transform is radial, that is, $q = ||s||_2$ (more details are provided in *k*-Dimensional case section in Appendix B), and for both example building blocks the Fourier transform is specified by

$$\tilde{W}_{\text{hom},\zeta}(q,k) = \eta \beta_{1,\zeta} \nu_{1,\zeta} \times \begin{cases} \exp\left(-\frac{q^2}{4\gamma_{1,\zeta}}\right) & \zeta = 1\\ \\ \left(\gamma_{1,\zeta}^2 + q^2\right)^{\frac{k+1}{2}} & \zeta = 2 \end{cases}$$
(11)

with the scaling $v_{1,\zeta}$

$$\nu_{1,\zeta} \stackrel{\underline{\forall k}}{=} \begin{cases} \left(2\gamma_{1,\zeta}\right)^{-k/2} & \zeta = 1\\ \\ 2^{k/2} \frac{\gamma_{1,\zeta}}{\sqrt{\pi}} \Gamma\left(\frac{k+1}{2}\right) & \zeta = 2 \end{cases}$$
(12)

As it is apparent from Eq. (11) that Eq. (6) is not strictly bandlimited, the homogeneous connectivity $W_{\text{hom},\zeta}(z)$ cannot be perfectly reconstructed from an finite sequence of samples *l*. Under these circumstances, it is highly important to deliberate on the spatial frequency bound q_c , Eq. (9), that allows by implication to assess the approximation of the homogeneous connectivity.

For estimating the approximation spatial frequency bound q_c we define two measures that assess: (i) the magnitude of a frequency response, and (ii) the ratio of the spatial frequencies of interest to all spatial frequencies of the homogeneous connectivity. The combination of both measures gives an estimate of the captured spatial frequencies and the corresponding magnitude of response for a spatial frequency bound q_c . By applying the sampling theorem to the magnitude measure and to the spatial frequency measure we obtain an assessment of the spatial frequency bound q_c , or alternatively the sampling interval ϱ , depending on the standard deviation σ of the local homogeneous connectivity functions $W_{\text{hom},\zeta}(z)$.

Magnitude measure

The homogeneous connectivity function $W_{\text{hom},\zeta}$ is typically a lowpass filter with the maximum spatial frequency response at $|\tilde{W}_{\text{hom},\zeta}(0)|$ that decreases with frequency (see Eq. (6) and Fig. 1). Let the approximation spatial frequency bound $q_c = q_{\text{dB}}$ be assigned to a specific magnitude ratio as follows

$$G_{\zeta}(q_{\rm dB},k) = 10\log_{10}\left(\frac{\tilde{W}_{\rm hom,\zeta}^2(q_{\rm dB},k)}{\tilde{W}_{\rm hom,\zeta}^2(0,k)}\right) \rm dB, \tag{13}$$

it appears that the magnitude ratio measure $G_{\zeta}(q_{dB}, k)$ in decibel (dB) is simply scaled by the dimensionality k of the space Ω (see k-Dimensional case section in Appendix B) as follows

$$G_{\zeta}(q_{\mathrm{dB}},k) = \chi G_{\zeta}(q_{\mathrm{dB}},k=1), \tag{14}$$

with the scaling

$$\chi = \begin{cases} 1 & \zeta = 1 \\ \frac{k+1}{2} & \zeta = 2 \end{cases}$$
(15)

The spatial frequency $q_{\rm dB}$ for both building blocks of the connectivity function is then

$$\frac{q_{dB}^{2}}{\zeta_{1,\zeta}^{\xi}} \quad \underline{\forall k} \begin{cases} -\frac{\log(10) \ G_{\zeta}(q_{dB}, 1)}{5 \ dB} & \zeta = 1\\ 10^{-G_{\zeta}(q_{dB}, 1)/(20 \ dB)} - 1 & \zeta = 2 \end{cases}$$
(16)

for the Gaussian (i.e., $\zeta = 1$) and for the Laplace distribution kernel (i.e., $\zeta = 2$). Note that the magnitude measure G_{ζ} (q_{dB} , k) is independent of the dimensionality k for the Gaussian kernel, that is, G_1 (q_{dB} , $\forall k$) = G_1 (q_{dB} , 1) but not for the Laplacian distribution kernel (see Appendix B). In the latter case, the spatial frequency q_{dB} is simply determined by the magnitude decay G_2 (q_{dB} , 1) of the one-dimensional Laplacian distribution kernel (see Eq. (16)). The dimensional corrected magnitude criteria for the Laplacian distribution kernel are given in Table 1 for a selection of values. For instance, the -3.01 dB-criterion in dimension k = 1 is equivalent to the -4.515 dB and -6.021 dB-criterion in dimension k = 2 and k = 3, respectively. The case $G_{\zeta}(q_{\rm dB}, k) \approx -3$ dB is a widely used measure of the bandwidth of a filter defined by the so-called 3 dB-*cutoff frequency* $q_{-3 \text{ dB}}$ at which the maximum response decreases by $\frac{1}{\sqrt{2}}$ (e.g., Freestone et al., 2011). In general, such a magnitude measure is not appropriate if high spatial frequencies of low power (i.e., $q > q_{\rm dB}$) contain information to capture. On that account we introduce a spatial frequency measure in the following section.

Spatial frequency measure

The range of spatial frequencies of interest $[0, q_{\alpha}]$: $q_c = q_{\alpha}$ is defined as the cumulative of the Fourier transform $\tilde{W}_{\text{hom},\zeta}(q, k)$ of the homogeneous connectivity function $W_{\text{hom},\zeta}(r)$ containing $(1 - \alpha) \times 100 \%$ of all frequencies

$$\int_{0}^{q_{\alpha}} \mathrm{d}q \, \tilde{W}_{\mathrm{hom}}(q,k) = (1-\alpha) \int_{0}^{\infty} \mathrm{d}q \, \tilde{W}_{\mathrm{hom}}(q,k), \tag{17}$$

where $\alpha \in [0, 1]$. The amount of spatial frequencies that are not captured by the integration is specified by α and is given for both building blocks of the connectivity function by

$$\alpha_{\zeta}(q_{\alpha},k) = 1 - \begin{cases} \operatorname{erf}\left(\frac{q_{\alpha}}{2\sqrt{\gamma_{1,\zeta}}}\right) & \zeta = 1\\ \frac{1}{2^{k-2}} \frac{\Gamma(k)}{\Gamma^{2}\left(\frac{k}{2}\right)} \frac{q_{\alpha}}{\gamma_{1,\zeta}} \ {}_{2}F_{1}\left(\frac{1}{2},\frac{k+1}{2};\frac{3}{2};-\frac{q_{\alpha}^{2}}{\gamma_{1,\zeta}^{2}}\right) & \zeta = 2 \end{cases}$$
(18)

with the Gaussian error function erf (λ) and the Gaussian hypergeometric function $_2F_1(\cdot,\cdot;\cdot;\cdot)$, where $\Gamma(\lambda) = \int_0^\infty y^{\lambda-1} \exp(-y) \, dy$ is the gamma function. The spatial frequency measure $\alpha_{\zeta}(q_{\alpha}, k)$ is independent of the dimensionality k for the Gaussian distribution kernel, that is, $\alpha_1(q_{\alpha}, \forall k) = \alpha_1(q_{\alpha}, 1)$, where $\alpha_{\zeta}(q_{\alpha}, k)$ is dependent on k for the Laplacian distribution kernel. However, in the latter case, $\alpha_2(q_{\alpha}, k)$ can be specified for any dimension k based on the first two

$$\alpha_2(q_\alpha, 1) = 1 - \frac{2}{\pi} \tan^{-1} \left(\frac{q_\alpha}{\gamma_{1,2}} \right), \tag{19}$$

$$\alpha_2(q_{\alpha}, 2) = 1 - \frac{q_{\alpha}}{\sqrt{\gamma_{1,2}^2 + q_{\alpha}^2}}.$$
(20)

The series expansion for k > 2 can be found in *k*-Dimensional case section in Appendix B. The spatial frequency measure α_{ζ} (q_{α} , 3) for the three-dimensional Laplacian kernel reads

$$\alpha_2(q_{\alpha},3) = \alpha_2(q_{\alpha},1) - \frac{2}{\pi} \frac{\gamma_{1,2} q_{\alpha}}{\gamma_{1,2}^2 + q_{\alpha}^2}.$$
 (21)

The spatial frequency content measure $\alpha_{\zeta}(q_{\alpha}, k)$, Eqs. (18) to (21), rates the amount of uncovered spatial frequencies due to a given spatial frequency of interest q_{α} dependent on the *k*-dimensionality of a Euclidean space $\Omega \in \mathbb{R}^k$ in the case of the Laplacian distribution kernel, that is, $\zeta = 2$. Since the radius $r = ||z||_2 : z \in \Omega$ of the homogeneous connectivity function $W_{\text{hom},\zeta}$ carries the *k*-volume of the Euclidean space Ω with it and thus the radial frequency $q = ||s||_2$: $r \leftrightarrow q$ as well, through the *k*-dimensional Fourier transform (i.e.,

 $s \leftrightarrow z$), the spatial frequency content measure α_2 (q_α , k) needs to be corrected if we wish to consider equivalent spatial frequencies of interest q_α regardless of dimension k, such as given by Eq. (16). Along these lines, we solve Eq. (19) for $q_\alpha / \gamma_{1,2}$ that we fix for all dimensions k (note that $\gamma_{1,2}$ is independent of k), introduce it then in Eq. (20), and use the series expansion of the spatial frequency measure α_2 (q_α , k + 2), given in k-Dimensional case section in Appendix B, to obtain the corrected spatial frequency content measure for the relevant physical spaces

$$\alpha_2(q_\alpha, 2) = 2\sin^2\left(\frac{\pi}{4}\alpha_2(q_\alpha, 1)\right) \tag{22}$$

$$\alpha_2(q_{\alpha}, 3) = \alpha_2(q_{\alpha}, 1) - \frac{1}{\pi} \sin(\pi \alpha_2(q_{\alpha}, 1)).$$
(23)

based on a given amount of uncovered spatial frequencies α_2 (q_α , 1) for the one-dimensional case. The dimensional corrected spatial frequency criteria are given in Table 1 for a selection of values. For instance, the 5 %-criterion in dimension k = 1 is equivalent to the 0.3083 % and 0.0205 % criteria in dimensions k = 2 and k = 3, respectively.

Combined measure and sampling assessment

The magnitude measure allocates the magnitude decay to a frequency and the frequency measure allocates the amount of not captured frequencies to a bandwidth. Since the spatial bandwidth can be specified by using the magnitude measure the amount of not captured spatial frequencies can be allocated to a decay by inserting Eqs. (16) into (18) with $q_{\alpha} = q_{\alpha} = q_{dB}$, and we obtain

$$\alpha_1(G_1(q_c, 1), \forall k) = 1 - \operatorname{erf}\left(\sqrt{\frac{-\log(10) \ G_1(q_c, 1)}{20 \ \mathrm{dB}}}\right)$$
(24)

for the Gaussian distribution kernel (i.e., $\zeta = 1$) and

$$\alpha_2(G_2(q_c, 1), 1) = 1 - \frac{2}{\pi} \tan^{-1} \left(\sqrt{10^{-G_2(q_c, 1)/20} \, \mathrm{dB}} - 1 \right)$$
(25)

$$\alpha_2(G_2(q_c, 1), 2) = 1 - \sqrt{1 - 10^{G_2(q_c, 1)/(20 \text{ dB})}}$$
(26)

$$\alpha_2(G_2(q_c, 1), 3) = \alpha_2(G_2(q_c, 1), 1) - \frac{2}{\pi} \frac{\sqrt{10^{-G_2(q_c, 1)/(20 \text{ dB})} - 1}}{10^{-G_2(q_c, 1)/(20 \text{ dB})}}$$
(27)

for k = 1, k = 2 and k = 3 of the Laplacian distribution kernel (i.e., $\zeta = 2$). Using Eq. (14) the frequency measure α_2 ($G_2(q_c, 1)$, k) with respect to the criterion for the one dimensional case, Eqs. (24) to (27), can be rewritten as α_2 ($G_2(q_c, k)$, k). Furthermore, in order to sample the maximum spatial frequency of interest q_α we apply the sampling theorem Eqs. (9) to (18) with $\varrho_{\zeta} = \varrho$ and $q_c = q_{\alpha}$

$$\alpha_{\zeta}(\varrho_{\zeta},k) \geq 1 - \begin{cases} \operatorname{erf}\left(\frac{1}{4\sqrt{\gamma_{1,\zeta}}}\varrho_{\zeta}\right) & \zeta = 1\\ \frac{\Gamma(k)}{\Gamma^{2}\left(\frac{k}{2}\right)}\frac{2^{1-k}}{\gamma_{1,\zeta}}\varrho_{\zeta}} {}_{2}F_{1}\left(\frac{1}{2},\frac{k+1}{2};\frac{3}{2};-\frac{1}{4\gamma_{1,\zeta}^{2}}\varrho_{\zeta}^{2}\right) & \zeta = 2 \end{cases}$$

$$(28)$$

Table 1

Shift of magnitude and frequency measure, $G_2(q_{dB}, k)$ and $\alpha_2(q_{\alpha}, k)$, for the Laplacian kernel $W_{hom,2}$ ($z \in \mathbb{R}^k$) on k-dimensional spaces. Eq. (14) specifies f and Eqs. (22) to (23) g.

k = 1	$G_2(q_{dB}, k) = f(G_2(q_{dB}, 1))$ in dB			$\alpha_2 (q_{lpha}, k) = g(\alpha_2 (q_{lpha}, 1))$ in %			
	-20	- 3.01	-1	5	10	20	80
2	-30	-4.515	- 1.5	0.308	1.231	4.894	69.098
3	-40	-6.021	-2	0.021	0.164	1.290	61.290

and then to capture the bandwidth spanned by q_c we equate Eq. (28) with Eqs. (24) to (27)

$$2\gamma_{1,\zeta}^{\zeta/2} \varrho_{\zeta} \Big(G_{\zeta}(q_{c}, 1) \Big) \leq \begin{cases} \sqrt{-\frac{5 \text{ dB}}{\log(10)G_{\zeta}(q_{c}, 1)}} & \zeta = 1\\ \frac{1}{\sqrt{10^{-G_{\zeta}(q_{c}, 1)/(20 \text{ dB})} - 1}} & \zeta = 2 \end{cases}$$
(29)

Taking the standard deviation $\sigma_{\zeta} = \sigma$ into account that both connectivity kernels (i.e., Gaussian and Laplacian) have in common through the normalization, that is, $\gamma_{1,1} = \gamma_{1,2}^2 / 4$ and $\gamma_{1,2} = \sqrt{2} / \sigma$ (see Appendix B), Eq. (29) gives then the lower bound for the ratio of standard deviation σ_{ζ} to sampling interval ϱ_{ζ} for a magnitude decay $G_{\zeta}(q_c, 1)$ as follows

$$\frac{1}{\sqrt{2}} \frac{\sigma_{\zeta}}{\varrho_{\zeta}} \leq \begin{cases} \sqrt{-\frac{\log(10)G_{\zeta}(q_c,1)}{5 \text{ dB}}} & \zeta = 1\\ 2\sqrt{10^{-G_{\zeta}(q_c,1)/(20 \text{ dB})} - 1} & \zeta = 2 \end{cases}$$
(30)

Consequently, both parameters, standard deviation σ_{ζ} and the sampling interval ϱ_{ζ} can be written as a function of G_{ζ} (q_c , 1) and the other, ϱ_{ζ} and σ_{ζ} , respectively. Furthermore, the magnitude decay $G_{\zeta}(q_c, 1)$, in Eq. (27), measures the homogeneous connectivity $W_{\text{hom},\zeta}(z)$ in one-dimensional spaces and can be specified for k-dimensions using Eq. (14). For the rest of this paper, the standard deviation σ_{ζ} (G_{ζ} (q_c , k)) and the sampling interval ϱ_{ζ} (G_{ζ} (q_c , k)) will refer to Eq. (30). Using the series expansion of the spatial frequency measure α_2 (q_α , k + 2), given in k-Dimensional case section in Appendix B, it can be shown that the relation in Eqs. (29) and (30) holds for any dimensional Laplacian distribution kernels. Based on the lower bound for the ratio of standard deviation σ_{c} to sampling interval ρ_{ζ} in Eq. (30) we can relate the magnitude decay $G_{\zeta}(q_{\zeta}, k)$ (or the spatial frequency content $\alpha_{\zeta}(\rho_{\zeta}, k)$) of the Gaussian distribution (i.e., $\zeta = 1$) to the Laplacian distribution kernel (i.e., $\zeta = 2$) for comparison. Assuming that both kernels are characterized by the same standard deviation $\sigma = \sigma_{\zeta}$ and are periodically sampled using the same step size $\rho = \rho_{\zeta}$, (i) the magnitude measure G_1 (q_c , k) = $G_1(q_c, 1), \forall k \text{ renders } G_2(q_c, k)$

$$G_2(q_c,k) \stackrel{\forall k}{=} -\xi \chi \, \log \left(1 - \xi^{-1} \, G_1(q_c,k)\right),\tag{31}$$

with $\xi = \frac{20 \text{ dB}}{\log(10)}$ and $\chi = \frac{k+1}{2}$, and (ii) the spatial frequency measure α_2 (ϱ , k) describes α_1 (ϱ , k) = α_1 (ϱ , 1), $\forall k$ by

$$\begin{aligned} \alpha_{2}(\varrho,k) &\stackrel{\forall k}{=} 1 - \frac{2}{\sqrt{\pi}} \frac{\Gamma(\frac{k+1}{2})}{\Gamma(\frac{k}{2})} \quad \text{erf}^{-1}(1 - \alpha_{1}(\varrho,k)) \\ & \times {}_{2}F_{1}\left(\frac{1}{2}, \frac{k+1}{2}; \frac{3}{2}; - \text{erf}^{-1}(1 - \alpha_{1}(\varrho,k))^{2}\right) \end{aligned}$$
(32)

with

$$\alpha_2(\varrho, 1) = 1 - \frac{2}{\pi} \tan^{-1} \left(\operatorname{erf}^{-1}(1 - \alpha_1(\varrho, 1)) \right)$$
(33)

$$\alpha_{2}(\varrho, 2) = 1 - \frac{\text{erf}^{-1}(1 - \alpha_{1}(\varrho, 1))}{\sqrt{\text{erf}^{-1}(1 - \alpha_{1}(\varrho, 1))^{2} + 1}}$$
(34)

$$\alpha_{2}(\varrho, 3) = \alpha_{2}(\varrho, 1) - \frac{2}{\pi} \frac{\operatorname{erf}^{-1}(1 - \alpha_{1}(\varrho, 1))}{\operatorname{erf}^{-1}(1 - \alpha_{1}(\varrho, 1))^{2} + 1}$$
(35)

for the relevant physical spaces. The series expansion for α_2 (q_α , k + 2), given in k-Dimensional case section in Appendix B, can be used to determine the relation in higher dimensional space, that is, k > 3. Applying Eqs. (22) and (23) to Eqs. (34) and (35), respectively, and then solving

both for α_2 (ρ , 1) gives Eq. (33). In other words, matching frequency content criteria α_2 (ρ , 1) with the dimensionality k of the underlying space by Eqs. (22) and (23), reduces the relation of the frequency content of Gaussian and Laplacian distribution in k-dimensional space, Eq. (32), to the one-dimensional case, Eq. (33).

Cortex model

As a concrete example for a geometrical approximation we use here a triangulated cortical surface Cortex_reg13.mat that is included in the Virtual Brain software package, available at http://thevirtualbrain.org/ app/ (version 1.0). This surface composes the cortical geometry of 16,384 vertices and 32,760 triangles. Periodic boundaries determine the two hemispheres composed by 8192 vertices each. Each vertex covers nearly 16 mm² of the cortical sheet. Here, we are not discussing the geometric sampling procedures that are used for this cortex model. However, if the sampling is regular (e.g., regular triangulation) the edges characterize the basis of the sampling lattice (e.g., two vectors in the hexagonal sampling lattice). In general, it is worth mentioning that the cortical surface may not be regularly sampled from empirical data, such as from anatomical MRI because of irregular shape, finite size or finite number of voxels. That means that the length of edges ρ (i.e., distances between two vertices) of the resulting surface mesh may rather differ than be the same. This issue has to be taken into account for developing a dynamical system on top of such a discrete geometrical structure, in particular when the aim is to investigate spatiotemporal patterns.

In our particular case the mesh that describes an individual cortical surface is based on a set of anatomical MRI scans. The mesh is obtained by extracting a high-resolution surface from MRI, and sampling the high-resolution surface down to a manageable number of vertices for simulating brain dynamics on a state-of-the-art computer system. The downsampling procedure achieves a balance between surface curvature preservation and mesh regularity. By neglecting the errors that are associated with the imaging technique, the sampling of the cortical surface from the MRI scanned volume can be characterized by the probability density $q(\sigma)$ of lengths between the edges of the mesh. For our particular example, the histogram in Fig. 2 characterizes the edge lengths ϱ . The number of bins n_{bins} in the histogram is calculated according to $n_{\text{bins}} = \exp (0.626 + 0.4 \log(n_o - 1))$, where $n_o = 49,140$ is the total number of edges ρ (Otnes and Enochson, 1972). In addition to Fig. 2, the edge length distribution is characterized using the statistical moments (see Table 2). The distribution fairly reveals to be unimodal and asymmetric (or more precisely, positively skewed). The range of edge lengths has nearly the order of magnitude of 1 cm (see Table 2). This indicates that the spatial dynamics are sampled differently, depending on the position in the cortical mesh by using a homogeneous connectivity function $W_{\text{hom}}(z)$ (with the same order of spatial spreading σ).

Regarding a specific probability density of the edges, $p(\varrho)$, and a specific spreading of homogeneous connectivities, σ_{ζ} , the amount of spatial frequencies $\alpha_{\zeta}(\varrho, k)|_{\sigma_{\zeta}}$ that is not covered due to the sampling can be characterized in terms of mean

$$E\left(\alpha_{\zeta}(k)\Big|_{\sigma_{\zeta}}\right) = \int \alpha_{\zeta}(\varrho,k)\Big|_{\sigma_{\zeta}} p(\varrho) \,\mathrm{d}\varrho, \tag{36}$$

and variance

$$\operatorname{Var}\left(\alpha_{\zeta}(\varrho,k)\Big|_{\sigma_{\zeta}}\right) = \int \left(\alpha_{\zeta}(\varrho,k)\Big|_{\sigma_{\zeta}}\right) - \operatorname{E}\left(\alpha_{\zeta}(\varrho,k)\Big|_{\sigma_{\zeta}}\right)^{2}(\varrho) \,\mathrm{d}\varrho. \tag{37}$$

These two measures are used here to assess the approximation of a neural field as a network of neural masses for the geometric model of the cortical surface with an unimodal compact probability density of edges (see Fig. 2).



Fig. 2. Edge length distribution characterizes the cortex model.

Results

The magnitude G_{ζ} (q_{dB} , k) and the frequency measure α_{ζ} (q_{α} , k) allow for the assessment of the approximation of the homogeneous connectivity function $W_{\text{hom},\zeta}$ (z). The spatial cutoff frequency q_c of the homogeneous connectivity is measured (see, for example, Fig. 3) as a function of the magnitude decay G_{ζ} (q_c , k) and the amount of uncovered spatial frequencies α_{ζ} (q_c , k) for both building blocks, namely, Gaussian and Laplacian distributions (i.e., $\zeta = 1$ and $\zeta = 2$) with the standard deviation σ_{ζ} : (i) to determine the sampling width ϱ_{ζ} for discretizing $W_{\text{hom},\zeta}$ (z), using the Petersen–Middleton theorem (see Eqs. (8) and (9)); or (ii) to parameterize the homogeneous connectivity for a given discrete geometry (see, for example, the cortex model presented in the Cortex model section). The measures are independent of the dimension k for the Gaussian kernel and are specific to a dimension k for the Laplacian kernel.

In the case of the Laplacian distribution function, criteria for both measures, $G_2(q_c, 1)$ and $\alpha_2(q_c, 1)$, can be matched with the dimension by the relations in Eqs. (14), (22) and (23). A given criterion G_2 $(q_c, 1)$ for the magnitude decay $G_2(q_c, k) = (k + 1) G_2(q_c, 1) / 2$ (see Eq. (14) and Table 1) gives, for higher dimensions k, lower proportions α_{ζ} (q_c , k) of the spatial frequencies q that are not covered with the cutoff frequency q_c (see Table 3). A given criterion α_{ζ} (q_c , 1) for the frequency content α_{ζ} (q_c , k) (relation is given with Eqs. (22) and (23) as well as Table 1) indicates a higher magnitude decay $G_{\mathcal{E}}(q_c, k)$ of the Laplacian kernel with increasing dimensionality *k* (see Table 3). However, applying the dimensional corrected criteria to the sampling assessment, $\sigma_{\zeta}(G_{\zeta}(q_c, k))$ and $\varrho_{\zeta}(G_{\zeta}(q_c, k))$ (using Eqs. (25) to (27) for α_2 (q_c , 1)) reduces the k-dimensional sampling problem to the one-dimensional sampling problem (see Tables 4 to 6). Applying the same criteria to any dimension k, that is, G_2 (q_c , $k = G_2(q_c, 1)$ and $\alpha_2(q_c, k) = \alpha_2(q_c, 1)$, the sampling assessment misleadingly indicates an improvement with the dimensionality k of the Euclidean space $\Omega \in \mathbb{R}^k$ for the parameterization: (i) of the sampling procedure (i.e., sampling interval ρ_{ζ} and spatial spectrum cutoff q_c ; and (ii) of the Laplacian distribution kernels, that is, σ_2 (see

Та	ble	2

Statistics of	edge	lengths	ρ	of th	ıe	cortex	model
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Parameter	Value	Unit
Range Expectation	[0.6638, 7.7567] 3 9761	mm
Variance	1.1882	mm ²
Skewness Quantile_5 %	0.3667	1
Quantile—50 %	3.8979	mm
Quantile-95 %	5.9199	mm
Quantile—99 %	6.7165	mm

Tables 4 to 6, values in square brackets). Comparing the Gaussian distribution and the Laplacian distribution function by means of Eq. (31) reveals the reason for that. The compactness of the Laplacian (i.e., peak) near the origin is indicated by a faster decay within the range: $G(q_c, k) < G_2(q_c, k) < 0$, whereas the fat tails of the Laplacian distribution function are indicated by a slower decay within the range: $G_2(q_c)$ k < $G(q_c, k)$, with $G(q_c, k) = G_1(q_c, 1) = G_2(q_c, k)$. The transition $G(q_c, k)$ from the tails to the bounded part near the origin decreases with increasing dimension k, since the spatial frequencies of the Laplacian distribution kernel decay with the power of the dimension k by $\frac{k+1}{2}$. Consequently, the peak around zero z = 0 gets less pronounced and the tails get more pronounced with increasing dimension k (see Fig. 1). Typical values for $G(q_c, k)$ are: $G(q_c, k) = 0$ for all dimensions k and, in addition, $G(q_c, 2) = -9.937$ dB for k = 2, or $G(q_c, 3) = -21.827$ dB for k = 3. Consequently, it should be emphasized that a matching of measures to the dimensionality of an underlying space is crucial.

Applying the dimensional matched measures to the Gaussian and Laplacian distribution reduces any *k* dimensional sampling problem to the one-dimensional problem, as mentioned previously. Using the dimensional corrected criteria, the sampling assessment indicates that for the same spatial cutoff frequency q_c (or sampling width ϱ_{ζ}) and standard deviation σ_{ζ} more spatial frequencies are covered using a Gaussian compared to a Laplacian distribution function (see Tables 4 to 6). In other words, to cover the same proportion of spatial frequencies (i.e., $1 - \alpha_{\zeta}(q_c, 1)$), the ratio of standard deviation σ_{ζ} to sample width ϱ_{ζ} has to be greater for the Laplacian, $\zeta = 2$, compared to the Gaussian distribution kernel, $\zeta = 1$ see Eqs. (32) to (35).

Overall, the sum of Gaussian distributions is better to approximate, that is, with fewer samples than the sum of Laplacian distributions for any dimensional spaces. To assess the spatial approximation of a neural field (see Eq. (4)) as a network of neural masses (see Eq. (5)), Eqs. (24) to (27) and Eq. (30) can be used, which are brought together in Fig. 3 and Supplementary data in Fig. S1 for k = 2 and k = 3.

The approximation of the neural field as a network of neural masses can be approached from different perspectives to: (i) consider biological evidence in the model; (ii) model a specific measurement; or, (iii) define a dynamical model on top of a discrete cortical geometry. The sampling approximation is examined from these three points of view in the following sections by considering three approximation criteria: $\alpha_{\xi} (q_c, 1) = 0.05$, $G_{\xi} (q_c, 1) = -20$ dB and $G_{\xi} (q_c, 1) =$ -3 dB. For all three criteria, the matching, $G_2 (q_c, k)$ and $\alpha_2 (q_c, k)$, is given in Table 1, and the relation between the magnitude $G_{\xi} (q_c, k)$ and the spatial frequency measure $\alpha_{\zeta} (q_c, k)$, Eqs. (24) to (27), is listed in Table 3 for the two different kernels: Gaussian, $W_{\text{hom},1}(z)$, and Laplacian, $W_{\text{hom},2}(z)$, distribution.

From biophysical considerations to a network of neural masses

Intracortical and short-range corticocortical connections (linking adjacent cortices) in humans are described in the literature with a range up to several mm (e.g., Burkhalter and Bernardo, 1989; Schüz and Braitenberg, 2002). Considering such short-range connections we use here, for a demonstration of our approach, a standard deviation of $\sigma_{\zeta} = \sigma = 1$ mm for both homogeneous connectivity distribution functions, the Gaussian as well as Laplacian distribution. Note that this choice is in line with the homogeneous connectivity parameterization in modeling studies, such as of the visual cortex of cats (Markounikau et al., 2010), the auditory cortex of rats (Pinotsis et al., 2012), or multi-unit recordings (Freestone et al., 2011). Using Eq. (29), or alternatively Fig. 3, the maximum sampling interval ρ_{ζ} is determined by the given standard deviation $\sigma_{\zeta} = 1$ mm, the amount of uncovered spatial frequencies α_{ζ} (q_c , k) and the magnitude decay $G_{\zeta}(q_c, k)$ of $W_{\text{hom},\zeta}(z)$ given in Table 3. Overall, for this parameter case, a network of neural masses should be spatially



Fig. 3. Spatial frequency content α and magnitude G of (A) $W_{\text{hom},1}(z, \sigma): z \in \mathbb{R}^k$, $\forall k$ and (B) $W_{\text{hom},2}(z \in \mathbb{R}, \sigma)$ dependent on sampling (ϱ, q_c). $G_2(1)$ can be corrected by $\chi = \frac{k+1}{2}$.

sampled with a maximum sampling width in the order of submillimeters that covers spatial frequencies in the order of $q_c = 1 \text{ mm}^{-1}$. The specific values are given in Table 4.

Regarding the dimensional matched criteria (see Table 1), the sampling of both kernels is comparable for $G_{\zeta}(q_c, 1) = -3$ dB, whereas the sampling of the Laplacian distribution kernel (i.e., $\zeta = 2$) should be almost two times and nine times finer-grained for $G_{\zeta}(q_c, 1) = -20$ dB and $\alpha_{\zeta}(q_c, 1) = 5$ % compared to the Gaussian kernel (i.e., $\zeta = 1$).

Applying the same criteria to any dimension *k*, that is, $G_{\zeta}(q_c, k) = G_{\zeta}(q_c, 1)$ and $\alpha_{\zeta}(q_c, k) = \alpha_{\zeta}(q_c, 1)$ (see Table 4, values in square brackets), the spatial sampling of both kernels is comparable for all

criteria used here, except for α_{ζ} (q_c , k) = 5 % in the two-dimensional case (i.e., k = 2), where the sampling of the Laplacian distribution kernel (i.e., $\zeta = 2$) should be almost two times finer-grained compared to the Gaussian kernel.

Note that the relations are inverse for the spatial cutoff frequency q_{c} , using Eq. (9), also owing to the broader spectrum of the Laplacian compared to the Gaussian distribution (see Fig. 1).

From measurements to a network of neural masses

All measurements have their peculiarities and limitations, such as accuracy and precision of a quantity (i.e., potential) in space and/or

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Relation of magnitude $G_{\zeta}(c_{\zeta}(q_c, k), k)$ [$G_{\zeta}(\alpha_{\zeta}(q_c, 1), k)$] in dB and frequency measure $\alpha_{\zeta}(G_{\zeta}(q_c, k), k)$ [$\alpha_{\zeta}(G_{\zeta}(q_c, 1), k)$] in %.

$W_{\mathrm{hom},\zeta}(z):z\in$	$\equiv \mathbb{R}^k$	$\alpha_{\zeta} \left(G_{\zeta} \left(q_{c} , k ight) , k ight)$ in %		$G_{\zeta}(\alpha_{\zeta}(q_c, k), k)$ in dB	
ζ	k	$\overline{G_{\zeta}\left(q_{c},k\right)}=-3\mathrm{dB}$	$G_{\zeta}(q_c, k) = -20 ext{ dB}$	$lpha_{\zeta}\left(q_{c},k ight)=5\%$	
1	$\forall k$	40.510	3.188	- 16.683	
2	1	63.594	20.483	-44.214	
2	2	54.580 [45.880]	11.425 [5.132]	-66.321 [-30.330]	
2	3	50.594 [34.622]	8.417 [1.385]	-88.429 [-25.643]	

Table 4 Maximum sampling interval ρ_{ζ} for $W_{\text{hom},\zeta}(z)$ with $\sigma_{\zeta} = 1$ mm. Uncorrected intervals, $[\rho_{\zeta}(G_{\zeta}(q_{c}, 1))]$ and $[\rho_{\zeta}(\alpha_{\zeta}(q_{c}, 1))]$ are in brackets.

$W_{\hom,\zeta}(z): z \in \mathbb{R}^k$		$\varrho_{\zeta}\left(G_{\zeta}\left(q_{c},k\right)\right)$ in mm	$\varrho_{\zeta}(\alpha_{\zeta}(q_c,k))$ in mm	
ζ	k	$G_{\zeta}\left(q_{c},1 ight)=-3\;\mathrm{dB}$	$G_{\zeta}\left(q_{c},1 ight)=-20\;\mathrm{dB}$	$lpha_{\zeta}\left(q_{c},1 ight)=5\%$
1	$\forall k$	0.6006	0.2330	0.2551
2	1	0.5493	0.1179	0.0278
2	2	0.5493 [0.6935]	0.1179 [0.1853]	0.0278 [0.1162]
2	3	0.5493 [0.8128]	0.1179 [0.2404]	0.0278 [0.1924]

time. All the measurements that we address here apply to the brain. Along these lines we consider the brain as a continuous physical process which generates uncertainty at a finite rate that is empirically observable. In order to describe a measurement one may simply use the limitations (e.g., noise) to construct a model regardless of the source of uncertainty. Here we are using the examples of functional MRI, ECoG, EEG and MEG to demonstrate how to set up a dynamical model and how to assess the approximations. For this purpose, we directly infer the cutoff frequency q_c from the limitation of the measurements (e.g., noise level) and use Eq. (9) to determine the sampling width $\rho = \rho_{\zeta}$ as a constant value for the distances of location sites in the network of neural masses (i.e., regular sampling). Of course, limitations may vary with specific experimental set-ups and should condition a specific modeling. In the case of EEG and MEG, for instance, the distances of the finite measuring sites to the neural substrate involve volume conduction of the head and thus a variety of sources and uncertainty that limits, or rather characterizes an observation. Since in the scope of this paper we do not analyze concrete recordings we refer instead to findings indicated in the literature, such as spatial resolution and noise level of an addressed brain measurement entity.

Considering the spatial resolution of ECoG and EEG, the minimum appropriate value for the standard deviation σ_{ζ} of the homogeneous connectivity function, $W_{\text{hom},\zeta}(z)$, can be specified dependent on the proportion of uncovered spatial frequencies $\alpha_{\zeta}(q_c, k)$ and the magnitude decay $G_{\zeta}(q_c, k)$ by using Eq. (29), or alternatively Fig. 3 combined with the criteria in Table 3. In general, the minimum appropriate standard deviation σ_{ζ} depends on the approximation criterion characterized by $\alpha_{\zeta}(q_c, 1)$ and $G_{\zeta}(q_c, 1)$.

Freeman et al., (2000) describe the inflection point above noise level in a spatial spectrum as an optimal criterion for a low pass spatial filter to remove noise. This inflection point is indicated at $q_c = 0.4 \text{ mm}^{-1}$ for the ECoG (Freeman et al., 2000), which corresponds to a minimum sampling width of $\varrho_{\zeta} \leq 1.25$ mm. The spatial resolution of functional MRI techniques is comparable to ECoG (Petridou et al., 2013; Yoo et al., 2004). Overall, for a spatial grid modeling based on ECoG and functional MRI, a standard deviation (or spreading) σ_{ζ} of the homogeneous connectivity $W_{\text{hom},\zeta}(z)$ in the order of several mm up to cm is necessary to explain the spatial correlations.

Regarding the dimensional matched criteria (see Table 1), the standard deviation of both kernels is comparable for G_{ζ} (q_c , 1) = -3 dB whereas the standard deviation of the Gaussian distribution kernel (i.e., $\zeta = 1$) can be set two times and nine times smaller for G_{ζ} (q_c , 1) = -20 dB and α_{ζ} (q_c , 1) = 5 % compared to the Laplacian kernel (i.e., $\zeta = 2$). For the Gaussian distribution kernel (i.e., $\zeta = 1$) the standard deviation σ should be at least in the

order of several mm, where for the Laplacian distribution kernel σ should be in the order of cm (see Table 5).

Applying the same criteria to any dimension k, that is, $G_{\zeta}(q_c, k) = G_{\zeta}(q_c, 1)$ and $\alpha_{\zeta}(q_c, k) = \alpha_{\zeta}(q_c, 1)$ (see Table 5, values in square brackets), the standard deviation of both kernels is comparable for almost all magnitude criteria $G_{\zeta}(q_c, 1)$, except for $\alpha_{\zeta}(q_c, k) = 5\%$ in the two-dimensional case (i.e., k = 2), where the standard deviation of the Gaussian distribution kernel (i.e., $\zeta = 1$) can be set two times smaller compared to the Laplacian distribution kernel (i.e., $\zeta = 2$).

Note that for the Gaussian distribution kernel the standard deviation is in the range that we considered in From biophysical considerations to a network of neural masses section for all three criteria.

Regarding EEG, Freeman et al. (2003, Chap. 4.4) indicate the inflection point in the spatial spectrum at which EEG would be sampled above the noise level (i.e., oversampling) with $q_c = 0.04 \text{ mm}^{-1}$. Because Freeman et al. (2003) recommend a 3 to 5 times higher sampling rate than that limit, we use here a spatial cutoff frequency of $q_c = 0.05 \text{ mm}^{-1}$ that corresponds to a maximum sampling width of $\varrho = 10 \text{ mm}$, using Eq. (9). Note that the resolution of EEG is comparable to MEG (Hämäläinen et al., 1993; Malmivuo and Suihko, 2004). The cortical lattice that covers the activity on the scalp is coarser compared to the intracranial grid for ECoG by the factor of 10. As a consequence, the connectivity kernels $W_{\text{hom},\zeta}(z)$ that are able to describe the spatial correlations have standard deviations σ in the order of several cm (see Table 6) and thus outside the range for intracortical and short-range corticocortical connections (see From biophysical considerations to a network of neural masses section).

Considering the dimensional matched criteria (see Table 1), the standard deviation of both kernels is comparable for $G_{\zeta}(q_c, 1) = -3$ dB, whereas the standard deviation of the Gaussian distribution kernel (i.e., $\zeta = 1$) can be set two times and nine times smaller for $G_{\zeta}(q_c, 1) = -20$ dB and $\alpha_{\zeta}(q_c, 1) = 5\%$ compared to the Laplacian kernel (i.e., $\zeta = 2$).

Applying the same criteria to any dimension k, that is, $G_{\zeta}(q_c, k) = G_{\zeta}(q_c, 1)$ and $\alpha_{\zeta}(q_c, k) = \alpha_{\zeta}(q_c, 1)$ (see Table 6, values in square brackets), the standard deviation of both kernels is comparable for most of the magnitude criteria $G_{\zeta}(q_c, 1)$, except for $\alpha_{\zeta}(q_c, k) = 5\%$ in the two-dimensional case (i.e., k = 2), where the standard deviation of the Gaussian distribution kernel (i.e., $\zeta = 1$) can be set two times smaller compared to the Laplacian distribution kernel (i.e., $\zeta = 2$).

From a geometric model of the cortex to a network of neural masses

Given a surface model (i.e., k = 2) of the cortical geometry (see Cortex model section) the minimum standard deviation σ_{ζ} of the

Table 5

Minimum standard deviation σ_{ζ} of $W_{\text{hom},\zeta}$ (*z*) for ECoG and functional MRI with the maximum frequency $q_c = 0.4 \text{ mm}^{-1}$ and the optimal sampling width $\varrho_{\zeta} = 1.25 \text{ mm}$. Uncorrected standard deviations, [σ_{ζ} (G_{ζ} (q_c , 1))] and [σ_{ζ} (α_{ζ} (q_c , 1))] are in brackets.

$W_{\hom,\zeta}(z): z \in \mathbb{R}^k$ $\sigma_\zeta(G_\zeta(q_c,k)) \text{ in mm}$		$\sigma_{\zeta}(\alpha_{\zeta}(q_c, k))$ in mm			
ζ	k	$G_{\zeta}(q_c, 1) = -3 \text{ dB}$	$G_{\zeta}\left(q_{c},1 ight)=-20\;\mathrm{dB}$	$lpha_{\zeta}\left(q_{c},1 ight)=5\%$	
1	$\forall k$	2.081	5.365	4.900	
2	1	2.275	10.607	44.923	
2	2	2.275 [1.803]	10.607 [6.747]	44.923 [10.757]	
2	3	2.275 [1.538]	10.607 [5.199]	44.923 [6.496]	

Table 6

Minimum standard deviation σ_{ζ} of $W_{\text{hom},\zeta}(z)$ for EEG and MEG with the maximum frequency $q_c = 0.05 \text{ mm}^{-1}$ and the optimal sampling width $\varrho_{\zeta} = 10 \text{ mm}$. Uncorrected standard deviations, $[\sigma_{\zeta} (G_{\zeta} (q_c, 1))]$ and $[\sigma_{\zeta} (\alpha_{\zeta} (q_c, 1))]$ are in brackets.

$W_{\hom,\zeta}(z): z \in \mathbb{R}^k$		$\sigma_{\zeta} \left(G_{\zeta} \left(q_{c} , k \right) \right)$ in mm		$\sigma_{\zeta}(\alpha_{\zeta}(k))$ in mm
ζ	k	$\overline{G_{\zeta}\left(q_{c},1\right)}=-3 \text{ dB}$	$G_{\zeta}(q_c, 1) = -20 ext{ dB}$	$lpha_{\zeta}\left(q_{c},1 ight)=5\%$
1	$\forall k$	16.651	42.919	39.199
2	1	18.204	84.853	359.386
2	2	18.204 [14.420]	84.853 [53.975]	359.386 [86.053]
2	3	18.204 [12.303]	84.853 [41.591]	359.386 [51.969]

homogeneous connectivity function $W_{\text{hom},\zeta}(z)$ can be specified due to the given characteristic edge length ϱ using the approximation criteria $G_{\zeta}(q_c, 1)$ and $\alpha_{\zeta}(q_c, 1)$ in Table 3 and Eq. (29) or Fig. 3. Here, we use the expectation value of the edge lengths in the geometric model, $E(\varrho = 3.98 \text{ mm})$ for demonstration (see Table 2 and Fig. 2). That spatial limit corresponds to a maximum spatial cutoff frequency of $q_c = 0.13 \text{ mm}^{-1}$. In general, the edge lengths are in the range of spatial resolution of EEG and MEG (see From measurements to a network of neural masses section). This is consequently also the case for the spatial frequencies q. Overall, the standard deviations of the homogeneous connectivity functions $W_{\text{hom},\zeta}(z)$ are in the order of $W_{\text{hom},\zeta}(z)$. The specific values for the standard deviations considering the expectation value of the edge lengths in the model $E(\varrho) = 3.98 \text{ mm}$ are listed in Table 7.

The standard deviation of both kernels is comparable for the magnitude decay criteria, except for the dimensional uncorrected criterion, G_{ζ} (q_c , 2) = -20 dB (see Table 7, values in square brackets), where the standard deviation of the Gaussian distribution kernel (i.e., $\zeta = 1$) can be set two times smaller compared to the Laplacian distribution kernel (i.e., $\zeta = 2$).

Regarding the criterion for the spatial frequency measure, the standard deviation of the Gaussian distribution kernel (i.e., $\zeta = 1$) is nine times and two times smaller for the dimensional corrected criterion, $\alpha_{\zeta} (q_c, 2) = 5$ %, and for the uncorrected criterion, $\alpha_{\zeta} (q_c, 2) = 0.308$ % (see Table 1), compared to the Laplacian kernel (i.e., $\zeta = 2$).

Given the dimensional matched values for the minimum standard deviation σ_{ζ} for both connectivity kernels $W_{\text{hom},\zeta}(z)$ in Table 7, the discretization of a neural field as a network of neural masses on the two-dimensional geometry of the cortex model (see Cortex model section) is assessed for all used criteria by considering the proportion of covered spatial frequencies $\alpha_{\zeta} (\varrho, k)|_{\sigma_{\gamma}}$ using the specific probability density of the edge lengths $p(\varrho)$ (Eqs. (36) and (37)). In this way, α_{ζ} (ρ , k) $|_{\sigma_{\zeta}}$ should indicate the given spatial frequency content α_{ζ} (q_c , k) for dimension k = 2 of all criteria, G_{ζ} $(q_c, 1)$ and α_{ζ} $(q_c, 1)$. The values of α_{ζ} $(\varrho, k)|_{\sigma_{\zeta}}$ are listed in Table 8. Indeed, $\alpha_{\zeta}(\varrho, k)|_{\sigma_{\zeta}}$ reflects $\alpha_{\zeta}(q_c, k)$ (for conversions, see Tables 1 and 3), although with high variations due to the irregularity of the cortical mesh. To capture, for instance, $(1 - \alpha_{\zeta} (q_c, k)) \times 100$ % = 85 % of all spatial frequencies of the homogeneous connectivity, $W_{\text{hom},\zeta}(z)$, that is, $G_1(q_c, 2) \approx -14.5 \text{ dB}$ and $G_2(q_c, 2) \approx -43.85 \text{ dB}$ for $\zeta = 1$ and $\zeta = 2$, respectively, the minimum standard deviation of a Gaussian and a Laplacian kernel is $\sigma_1 \ge 14.55$ and $\sigma_2 \ge 140.01$ mm, respectively, for this cortex model.

As an example we sample the model of the cortical geometry (i.e., space $\Omega \in \mathbb{R}^2$) using the Gaussian homogeneous function $W_{\text{hom},1}(z)$ with three different standard deviations $\sigma = 15 \text{ mm}$, $\sigma = 25 \text{ mm}$

and $\sigma = 41$ mm. To obtain the connectivity of each vertex with its neighborhood on the triangular mesh, the shortest path along the edges to a neighbor is considered to sample the homogeneous connectivity function. The resulting homogeneous connectivity matrices $\mathbf{U}_1(\sigma)$ are shown in Fig. 4. The matrices are of size $(l \times l)$, where lis the number of vertices (here l = 16,384). The increase of connectivity spreading reduces the sparseness of the matrix. Since $\mathbf{U}_1(\sigma)$ condenses the couplings between two location sites on the twodimensional space of the cortical surface, the spatial structure of the surface Ω and the connectivity kernel is coded, but not well presented in a two-dimensional array of location sites. However, at least the hemispheres can be distinguished by the two large clusters that appear with increasing standard deviation σ .

Discussion

In this paper an approach is presented with the aim to assess the translation of neural field models into a network of neural masses. A translation is often inevitable, in particular with the aim to incorporate discrete information on heterogeneous connections established by white matter fibers (i.e., connectome). For this reason it is crucial to assess the translation of a spatiotemporal dynamic model in a digital scheme for integration. The work presented in this paper extends previous studies on two-dimensional neural fields, such as Bojak et al. (2010) and Freestone et al. (2011) in three points: (i) the spatial sampling approximation (e.g., spatial cutoff frequency) can be assessed using two measures, magnitude and frequency measure (ii) that are applicable on any dimensional physical space (iii) for two widely used classes of connectivity probabilities, namely, Gaussian and Laplacian probability functions.

In the case of neural field models, the homogeneous connectivity (i.e., intracortical connections) has to be sampled in space. For this case we applied two measures to quantify the sampling quality. The sampling is complicated due to the fact that the geometry of the human cerebral cortex shows a highly folded surface that varies across subjects. We applied our approach to a model of a cortical surface derived from experimental data. We focused on the spatial sampling aspect rather than the neural mass and its spatial and/or temporal consolidation. In other words, a neural mass model that may be specific to a certain spatial extent and to a given measurement should be specified after the space has been sampled.

Considering the work of Bojak et al. (2010), the two measures presented here can be used to assess the maximum reliable spatial frequency in their mean field simulations for EEG and MEG. Freestone et al. (2011) mention, for instance, that the spatial cutoff frequency becomes a design choice for the desired level of smoothness in their

Table 7

Minimum standard deviation σ_{ζ} of $W_{\text{hom},\zeta}(z)$ for the two-dimensional cortex model, k = 2, with the mean edge length $\varrho_{\zeta} = E(\varrho) = 3.98$ mm and the maximum frequency $q_c = 0.13 \text{ mm}^{-1}$. Uncorrected standard deviations, $[\sigma_{\zeta}(G_{\zeta}(q_c, 1))]$ and $[\sigma_{\zeta}(\alpha_{\zeta}(q_c, 1))]$ are in brackets.

$W_{\mathrm{hom},\zeta}\left(z ight):z\in\mathbb{R}^{k}$		$\sigma_{\zeta}\left(G_{\zeta}\left(q_{c},k ight) ight)$ in mm		$\sigma_{\zeta}(\alpha_{\zeta}(q_c,k))$ in mm
ζ	k	$G_{\zeta}(q_c, 1) = -3 ext{ dB}$	$G_{\zeta}\left(q_{c},1 ight)=-20\;\mathrm{dB}$	$lpha_{\zeta}\left(q_{c},1 ight)=5\%$
1	2	6.627	17.082	15.601
2	2	7.245 [5.739]	33.771 [21.482]	143.036 [34.249]

Table 8 Mean and standard deviation of the dimensional corrected approximation error $\alpha_{\zeta}(\varrho, k)|_{\sigma_c}$ in % of the cortex model using σ_{ζ} and q_c from Table 7.

$W_{\mathrm{hom},\zeta}\left(z ight)$	$G_{\zeta}(q_c, 1) = -3 \mathrm{dB}$	$G_{\zeta}(q_c, 1) = -20 \text{ dB}$	$lpha_{\zeta}\left(q_{c} ext{, 1} ight)=5\%$
$\begin{array}{c} \zeta = 1 \\ \zeta = 2 \end{array}$	$\begin{array}{c} 38.374 \pm 12.775 \\ 62.035 \pm 8.272 \end{array}$	$\begin{array}{c} 4.548 \pm 4.890 \\ 20.321 \pm 5.163 \end{array}$	$\begin{array}{c} 6.326 \pm 6.040 \\ 0.330 \pm 0.178 \end{array}$

approximated field using Gaussian radial basis functions. The approach presented here could be used to specify the spatial cutoff frequency for the homogeneous connectivity in the neural field as well as spatial cutoff frequency for the radial basis functions in their data-driven framework of neural field modeling (Freestone et al., 2011 use a -3 dB-cutoff criterion). Furthermore, the widely used Laplacian distribution for describing the homogeneous connectivity (e.g., Jirsa and Haken, 1996; Nunez, 1974; van Rotterdam et al., 1982; Wilson and Cowan, 1973) behaves in a specific way depending on the dimension of the considered physical space (see the discussion in Comparison of Gaussian and Laplaican connectivities section as well as Figs. 3 and S1). For that reason, a magnitude criterion, such as the -3 dB-cutoff criterion can be misleading, especially when comparing the approximation on different spaces. Therefore, it is essential to match the measures and thus the criteria to the dimension of the underlying space. Using the spatial frequency measure introduced here (see Spatial frequency measure section), the cutoff criterion can be defined as a proportion of spatial frequencies that are to be captured. In addition to the widely used magnitude measure, the spatial frequency measure gives additional information and improves the assessment of the approximation. Both measures and the criteria therefore can be easily applied to any dimensional spaces for both widely used homogeneous connectivity functions by matching the measures to the dimension. In fact, the matching reduces the sampling task of both homogeneous connectivity functions in higher dimensional spaces to the one-dimensional sampling case.

To go more into detail, two specific criteria are applied to assess the sampling of the homogeneous connectivity in space. The limitations of our approach are discussed in Sampling the connectivity in space section. The approximation of the homogeneous connectivity with the aim to create a computational model can be tackled with different intentions. The three scenarios we went through are discussed in Computational models section. The impact of sampling the homogeneous connectivity is discussed in Bandwidth-limiting effect of sampling on the homogeneous connectivity section. An alternative approach of approximation and assessment of the homogeneous connectivity is discussed in An alternative approximation of the homogeneous connectivity section. Finally, the two distributions that are used in the scope of this work to describe the homogeneous connectivity are compared in Comparison of Gaussian and Laplaican connectivities section.

Sampling the connectivity in space

In order to sample a signal or a function in a domain, the basic theorem that needs to be satisfied is the Nyquist-Shannon sampling theorem (Shannon, 1949) and its extension to higher dimensional Euclidean spaces, the Petersen-Middleton theorem (Petersen and Middleton, 1962). In our case the characteristics of the functions that are used to describe the homogeneous connectivity are complicating the sampling procedure in addition to the already complex spatial geometry of the cortex. In fact, we are dealing with two models of different scales derived from different sources. On the one hand we have the geometric model of the cortex derived from structural measurements, and on the other hand we have the probability distribution describing intracortical connections derived from biophysical techniques and considerations. The local connectivity is usually approximated as a continuous function, that is symmetric and translationally invariant in physical space. This continuity characteristic is basically the reason why the Petersen-Middleton sampling theorem is not satisfiable, and a sampling is not perfect. In order to perform an adequate sampling of the homogeneous connectivity we introduce two measures for (i) the decay of magnitude, and (ii) the proportion of covered spatial frequency components to the uncovered ones. Criteria are obtained by applying the measures to the connectivity distribution function and then to the Petersen-Middleton sampling theorem. This procedure leads to the main result of this work (see, for example, Fig. 3) that permits to assess and to set up the sampling of the Gaussian and Laplacian distribution functions. In addition to the magnitude measure we also measure the content of spatial frequencies because the magnitude measure implies that the spatial frequencies outside the maximum response (cutoff) do not convey additional information. This is so far not clear for the brain due to the nonlinear characteristics of brain activity (Buzsáki, 2006; Freeman, 2000; Nunez, 1995). In the discussion, up to here, we assumed that the underlying physical space is either continuous, or the available discrete geometric cortex model is well sampled. In particular, the procedure implied that the sampling is periodically along the basis of the considered space, in other words, that the space is sampled with a fixed step size, forming an optimal lattice (e.g., a two-dimensional hexagonal sampling lattice; Petersen and Middleton, 1962). In practice, the extraction and sampling of the cortex from structural brain data (i.e., MRI) is complicated because of the folding of the cortical sheet in sulci and gyri. However, the sampling of the physical space is beyond the scope of this work, and we assume that the cortex model is well constructed. In this paper we demonstrate our approach by using the example of an irregular cortical



Fig. 4. Homogeneous connectivity matrix \mathbf{U}_1 ($R = \zeta = 1$) aggregates $W_{\text{hom}}(z, \sigma, R, \zeta)$, sampling the cortex model Ω (see Cortex model section) with (A) $\sigma = 15$ mm, (B) $\sigma = 25$ mm, and (C) $\sigma = 41$ mm.

grid (from anatomical MRI; see Cortex model section and From a geometric model of the cortex to a network of neural masses section). Due to the irregular spatial grid, the criterion is applied to the mean value of the edge lengths, and the sampling of the homogeneous connectivity distributions is then assessed by taking all edges into account (see Table 8). In this way, the approximation error can be considered as the upper bound regarding a basis of the sampling lattice with respect to the applied criterion to specify the distribution function.

Computational models

The measurements considered here (i.e., ECoG, EEG, MEG and functional MRI) are capable of gathering activity on various spatial scales ranging from neuronal ensembles to the whole brain (i.e., dependent on the number of measurement sites or sensors and sensor layout) with different temporal resolutions. All four measurement modalities contain less spatial information than the intracranial biophysical plausible configuration due to the distance of the sensors to the neural substrate in the case of the considered electrophysiological measurements (i.e., ECoG, EEG and MEG) or the spatial extent of the recording site (i.e., voxel size) in the case of fMRI. Functional MRI and ECoG recordings provide better spatial information than EEG or MEG (see From measurements to a network of neural masses section).

Due to these differences in scales of organization, brain network models can be defined specific to a type of measurement by considering its information content. The results presented here provide a guideline (see From measurements to a network of neural masses section) of how to do so with an emphasis on the right choice of model with parsimonious variables and parameters. For instance, in a situation where a parsimonious model captures well the recordings on the level of the measurement sites, a model to integrate multimodal data (e.g., for all four measurement modalities) needs to describe the spatiotemporal dynamics on a more detailed level (see, for instance, Bojak et al., 2010, and references therein), such as the neural substrate. In the scope of this work, we give guidance to set up a cortical mesh based on biophysical considerations and given anatomical and geometric constraints (see From biophysical considerations to a network of neural masses section and From a geometric model of the cortex to a network of neural masses section). Since in such a multimodal approach the described state is usually not directly accessible to the measurement (e.g., membrane potential for functional MRI) a link to each measurement has to be established. In addition to Eq. (5), a so-called observer system **Q** can be introduced that relates the hidden state $\hat{\Psi}$ to a certain measurement **M** as follows

$$\mathbf{M} = \mathbf{Q}\left(\hat{\Psi}, a\right) + \varepsilon, \tag{38}$$

where *a* parameterizes the observation and ε describes the noise processes, such as thermal noise associated with the measuring apparatus. The observer system Q has to take into account additional information on the physics of the sources, the media and the measuring apparatus. In the case of ECoG, EEG and MEG this comprises, for instance, the equivalent dipole model (Lopes da Silva and van Rotterdam, 1999; Schimpf et al., 2002), the geometry, permeability and permittivity of tissues (Haueisen et al., 1997, 2002) and the sensors (e.g., Hämäläinen et al., 1993). Further, functional MRI records change in metabolism and blood flow indicating energy consumption. These changes are indirectly related to changes in the activity of neurons or neural ensembles. For this reason, a hemodynamic model, such as the Ballon-Windkessel model (Friston et al., 2000, 2003) has to be used as observer system. A model that integrates ECoG, EEG, MEG and functional MRI contains redundancy as the observer system Q is low-pass filtering the state $\hat{\Psi}$ in space for EEG and MEG and in time for functional MRI.

To range this study in the area of neural field modeling, a selection of studies should be taken into consideration. For instance, Liley et al. (2002) specify the Laplacian distribution for the homogeneous connectivity with a standard deviation of $\sigma_2 = 35.355$ mm. Using our approach, this configuration corresponds to a sampling interval of $\rho_2 = 0.984 \text{ mm}$ on an optimal (e.g., hexagonal) two-dimensional lattice for capturing $(1 - lpha_2 \ (q_c \ , \ 1)) imes 100 \ \% = 95 \ \%$ of all spatial frequencies up to $q_c = 0.508 \text{ mm}^{-1}$. This model consequently can be ranged in a description on the level of ECoG and fMRI (see From measurements to a network of neural masses section) and allows for incorporating more macroscale brain measurements, such as EEG and MEG. Other neural field studies specify coarser standard deviations for the homogeneous connectivity, such as Nunez and Srinivasan (2006) : $\sigma_2 = 141.421$ mm, Robinson et al. (1997) : $\sigma_2 = 118.794$ mm, or Jirsa et al. (2002) : $\sigma_2 = 84.853$ mm, all using the Laplacian distribution. Again, applying the frequency measure α_{ζ} (q_c , k) (see Spatial frequency measure section), and considering these configurations on an optimal (e.g., hexagonal) two-dimensional lattice, $(1 - \alpha_2)(q_c)$ 1)) \times 100 % = 95 % of all spatial frequencies of the Laplacian connectivity function are covered with a sampling interval ρ_2 and a spatial cutoff frequency q_c : $\rho_2 = (3.935, 3.306, 2.361)$ mm and $q_c =$ (0.1271, 0.1513, 0.2118) mm⁻¹, listed in the order of the three studies. As a consequence, all three models can be ranged in a description on the level of EEG and MEG (see From measurements to a network of neural masses section). To complete, Markounikau et al. (2010) and Freestone et al. (2011) are using a Gaussian distribution; and Pinotsis et al. (2012) use a Laplacian distributed homogeneous connectivity with standard deviations in the range of mm for intracranial recordings, where all three models correspond to a description on the level of human intracranial connections From biophysical considerations to a network of neural masses section. For all these example cases, we assumed an optimal sampling. However, knowing the sampling lattice allows for assessing the approximation of neural fields as networks of neural masses and, moreover, for better interpreting the spatial pattern obtained from numerical simulations (e.g., with noise).

Bandwidth-limiting effect of sampling on the homogeneous connectivity

The finite step size ϱ of the spatial sampling is limiting the spatial frequencies by \hat{s} containing the continuous homogeneous connectivity kernel $W_{\text{hom}}(z)$. The maximum frequency \hat{s} can be specified according to the magnitude Eq. (13) and/or the spatial frequency measure Eq. (17). In order to discuss the bandwidth-limiting effect we transform the spectra of both kernels back into the spatial domain by

$$W_{\text{hom},\zeta}(z) = \frac{1}{\sqrt{2\pi}} \int_{-\hat{s}}^{\hat{s}} ds \ \tilde{W}_{\text{hom},\zeta}(s) \exp(jsz).$$
(39)

We obtain the following transfer function $K_{\text{hom},\zeta}(z) = \hat{W}_{\text{hom},\zeta}(z) / W_{\text{hom},\zeta}(z)$

$$K_{\text{hom},1}(z) = \frac{1}{\sqrt{2\pi}} \sum_{u=0}^{\infty} \frac{(-1)^u}{2^u (1+2u)u!} \left(\left(\frac{jz}{\sigma} + \sigma \hat{s}\right)^{1+2u} - \left(\frac{jz}{\sigma} - \sigma \hat{s}\right)^{1+2u} \right)$$
(40)

for the Gaussian distribution kernel $W_{\text{hom},1}(z)$ and

$$K_{\text{hom},2}(z) = \frac{1}{\pi} \tan^{-1} \left(\frac{\sigma \hat{s}}{\sqrt{2}} \right) + \frac{j}{2\pi} \sum_{u=1}^{\infty} \frac{|z|^u}{\sigma^u u! u} \left(\left(\sqrt{2} - j\sigma \hat{s} \right)^u - \left(\sqrt{2} + j\sigma \hat{s} \right)^u \right)$$
(41)



Fig. 5. Bandwidth-limitation effect on $W_{\text{hom},\zeta}(z)$: (A, C) Gaussian $\zeta = 1$ and (B, D) Laplacian distribution $\zeta = 2$.

for the Laplacian distribution kernel $W_{\text{hom},2}(z)$. The mathematical details are presented in Appendix C. In Fig. 5 we see that the shape of the Gaussian distribution $W_{\text{hom},1}(z)$ is preserved, where the Laplacian distribution $W_{\text{hom},2}(z)$ is modified by an oscillatory term. Generally, the sampling limitation of the bandwidth effects a reduction of the peak around z = 0 in both cases. In the case of the Laplacian distribution the peak is well-sampled simply for the limit $\hat{s} \rightarrow \infty$. In other words, for finite sampling width, ϱ , the peak of the Laplacian distribution is not preserved and an oscillatory term is added, especially for higher sampling spatial frequencies.

An alternative approximation of the homogeneous connectivity

Another approach to implement the homogeneous connectivity $W_{\text{hom},\zeta}(z)$ in the framework of a neural field or a network of neural masses is to specify the partial differential operator $C_{\zeta}(\partial/\partial x, \partial/\partial t)$ (Jirsa, 2009; Qubbaj and Jirsa, 2009). This alternative representation of the homogeneous connectivity function $W_{\text{hom},\zeta}(z)$ (including the propagation delays) as a power series of partial derivatives (i.e., with respect to time *t* and space *x*) allows to approximate $W_{\text{hom},\zeta}(z)$ as a finite number of terms that act on the state $\Psi(x, t)$ allows to compare both distribution functions. Using the *Green's function* method (e.g., Jirsa and Haken, 1996, 1997; Nunez, 1995) we can rewrite the system for the generalized neural field Eq. (4) as follows

$$\begin{aligned} \mathbf{P}(\partial/\partial t)\mathbf{\Psi}(x,t) &= \mathbf{\Xi}(x,t) - \mathbf{\Lambda}(\mathbf{\Psi}(x,t)) + \mathbf{V}_{\text{loc}} \ S(\mathbf{\Psi}(x,t)) \\ &+ \mathbf{V}_{\text{hom}} \ C_{\zeta}(\partial/\partial x, \partial/\partial t) \ S(\mathbf{\Psi}(x,t)), \end{aligned} \tag{42}$$

where the partial differential operator $C_{\zeta}(\partial/\partial x, \partial/\partial t)$ is given as a power series in $\partial/\partial x$ and $\partial/\partial t$ for the Gaussian $W_{\text{hom},1}(z)$ and Laplacian distribution function $W_{\text{hom},2}(z)$ (Eqs. (D.11) and (D.12), respectively) used here for specifying the homogeneous connectivity (see Eq. (B.11)). The details of the calculus and the power series of the partial differential operator can be found in Appendix D. Note that the partial differential operator for the Laplacian distribution $C_2(\partial/\partial x, \partial/\partial t)$ is in line with previous studies (Jirsa, 2009; Qubbaj and Jirsa, 2009). In general, both distribution functions can simply be determined rigorously as partial differential operator if infinite number of terms *v* are considered sup $\{v\} = \infty$. Expanding the power series C_{ζ} (λ_1 , λ_2) Eqs. (D.11) and (D.12) we obtain the following first four derivatives

$$C_1\left(\frac{\partial}{\partial x},\frac{\partial}{\partial t}\right) \approx \frac{1}{\sqrt{8\pi}} + \frac{\sigma^2}{\sqrt{32\pi}}\frac{\partial^2}{\partial x^2} + \frac{\sigma^3}{2\pi c_1}\frac{\partial^3}{\partial x^2 t} + \frac{\sigma^2}{\sqrt{32\pi}}\frac{\partial^2}{c_1^2} + \cdots$$
(43)

for the Gaussian distribution kernel $W_{\text{hom},1}(z)$ with $\sup\{v\} = 1$ and

$$C_2\left(\frac{\partial}{\partial x}, \frac{\partial}{\partial t}\right) \approx \frac{1}{2\pi} - \frac{\sigma}{2\pi c_1} \frac{\partial}{\partial x} + \frac{\sigma^2}{2\pi} \frac{\partial^2}{\partial x^2} + \frac{\sigma^2}{2\pi c_1^2} \frac{\partial^2}{\partial t^2} + \cdots$$
(44)

for the Laplacian distribution kernel $W_{\text{hom},2}(z)$ with $\sup\{v\} = 2$. However, the coefficients indicate the contribution of each term and thus indicate the convergence of the power series. The contribution can be assessed by applying the magnitude measure G(a), Eq. (13), described in Magnitude measure section, to the coefficient *a* of each derivate $(\partial^{u+w}) / (\partial x^w \partial t^u)$ in $C_{\zeta} (\partial/\partial x, \partial/\partial t)$, and then using a criterion, such as $G(a) \leq -20$ dB. In this way the approximation of the homogeneous connectivity $W_{\text{hom}}(z)$ can be assessed, dependent on the propagation speed c_1 and standard deviation σ . Fig. 6 shows the coefficients in the space spanned by the derivatives with respect to space and time $C_{\zeta}(\partial/\partial x, \partial/\partial t)$ up to order sup{u} = sup{w} = 6. The magnitude ratios G(a) of the coefficients (i.e., the gray scale) are showing the case $(c_1, \sigma) = (1, 0.4)$. From the characteristic spatiotemporal pattern of the coefficients we see that all even order derivatives exist with respect to space in C_{ζ} $(\partial/\partial x, \partial/\partial t)_{\zeta}$ but no odd derivatives. This is simply due to the fact that both distributions $W_{\text{hom},\zeta}(z)$ are even functions in space. Considering the changes in time we see that all derivatives of even and odd order exist with respect to time, except for the case of the Gaussian distribution where the derivatives for the spatial offset, that is, $(\partial/\partial x)^0$ are of even order. This is due to the fact that the propagation delay is defined by the spatial distances and the distances have no specific spatial pattern on Ω . Whereas for the case of the Gaussian distribution the coefficients of all existing derivatives are positive, the coefficients for the case of the Laplacian distribution are positive for even and negative for odd order derivatives with respect to time. In



Fig. 6. Coefficients of the differential operator $C_{\zeta}(\lambda_1, \lambda_2)$ for (A) the Gaussian $\zeta = 1$ and (B) the Laplacian distribution $\zeta = 2$. Coefficients are black framed squares, gray shaded for $(c_1, \sigma) = (1, 0.4)$, where $\lambda_1 = \partial/\partial x$, $\lambda_2 = \partial/\partial t$, and the \star denotes coefficients for which the ratio $|a| / \sup\{|a|\} > -20$ dB.

general, the power series converges faster with v and with increasing order of derivatives (v and u) for the Gaussian compared to the Laplacian distribution. In the case of the Gaussian distribution the coefficients drop off with higher order derivatives with respect to both, time and space. In the case of the Laplacian distribution the coefficients drop faster along the spatial and temporal offset $(\partial/\partial x)^0$ and $(\partial/\partial t)^0$, respectively, compared to the mixed derivatives (around $\partial^{u} / (\partial x^{u/2} \partial t^{u/2}))$. This is the reason why, for the example in Fig. 6, we need to expand at least seven terms $\sup\{v\} = 6$ of the power series for the Laplacian distribution to satisfy the criterion $G(a) \leq -20$ dB. For the Gaussian distribution two terms are sufficient to satisfy the -20 dB-criterion in our example. This approximation involves 4 and 13 derivatives, up to the order of 2 and 4 for the Gaussian and the Laplacian distribution, respectively (including the offsets). This approach also demonstrates that an approximation of the Gaussian distribution is less expensive than for the Laplacian distribution.

Following this alternative approximation of the homogeneous connectivity, the obtained partial differential equations can also be implemented in a digital scheme for integration. For this purpose, methods that control the step size of integration are available for an optimal sampling of the evolution in space and time. However, this approach might be restricted to study the homogeneous connectivity $W_{\text{hom}}(z)$ (i.e., spatially continuous) since the available empirical data (e.g., diffusion-weighted MRI tractography) characterize a heterogeneous connectivity (i.e., connectome) $W_{\text{het}}(z)$ as non-continuous with respect to the cortical neural sources and targets projected onto the cortical surface.

Comparison of Gaussian and Laplacian connectivities

Comparing both distribution functions, Gaussian $W_{\text{hom},1}(z)$ and Laplacian $W_{\text{hom},2}(z)$, we can see that the most salient difference is the peak around zero z = 0 (see in Fig. 1). Concerning a normalization of both connectivity kernels $W_{\text{hom},\zeta}(z)$ with respect to a joint standard deviation (see Appendix B), the Laplacian peak $W_{\text{hom},2}(z = 0)$ tops the Gaussian peak $W_{\text{hom},1}(z = 0)$ up to four-dimensional Euclidean space $z \in \Omega$. As we discussed earlier (in Bandwidth-limiting effect of sampling on the homogeneous connectivity section) it is not possible to sample the peak of the Laplacian around z = 0 (see Fig. 5).

The spatial Fourier spectrum of a Gaussian-distributed homogeneous connectivity in any *k* dimensional Euclidean space Ω is again characterized by a Gaussian because it is an eigenfunction of the Fourier transform. Consequently, magnitude decay and frequency content of the Gaussian distribution kernel, $G_1(q_c, k)$ and $\alpha_1(q_c, k)$, remain unchanged, independent of the dimension *k* of the space Ω . In contrast, because of the singularity at the origin (i.e., peak) and the fat tails of the Laplacian-distributed homogeneous connectivity, the Lorentzian shaped spatial spectrum of a one-dimensional Euclidean space decays with the power of increasing dimension *k* by $\frac{k+1}{2}$ (see Tables 4 to 6). In general, a radial function, that is, radially symmetric on $\Omega \in \mathbb{R}^k$ has a Fourier transform that decays faster than $a^{(k+1)/2}$ if integrable and bounded near the origin. Consequently, the fat tails of the Laplacian distribution kernel and thus the corresponding low spatial frequencies get more pronounced with increasing dimensionality k. That is why, the magnitude decay and the frequency content of the Laplacian distribution kernel, $G_2(q_c, k)$ and α_2 (q_c , k), are dependent on the dimension k of the space Ω . In other words, using the same criteria for different k dimensional spaces, such as $G_2(q_c, k) = -3$ dB and $\alpha_2(q_c, k) = 5$ % neglect the extent of the underlying space Ω . Suiting the criteria to the dimensionality of the spaces (using Eqs. (14), (22) and (23) as well as Table 1) allows to compare the sampling procedure of the Laplacian-distributed homogeneous connectivity independent of the dimensionality, assuming regular sampling lattices (e.g., hexagonal and body-centered cubic lattice in k = 2 and k = 3 dimensional spaces). That way, the magnitude decay and the spatial frequency content of the Laplacian distribution kernel are independent of the dimensionality k of the space Ω and reduce to the one-dimensional cases. With respect to both measures, the Gaussian is easier to sample than the Laplacian distribution function.

The motivation for using the Laplacian distribution in neural field theory is that Braitenberg and Schüz (1991) showed that the short-range intracortical fiber system of the mouse cortex shows a distribution with a connection probability which decays exponentially over the distance. This does not imply that it decays exponentially over all distances, in particular in the vicinity of z = 0, simply because of the finite number of measured points considering a certain distance to the soma. Furthermore, the somata are also taking up space, for instance, $\approx 15 \,\mu\text{m}$ in diameter in the human prefrontal cortex (Rajkowska et al., 1998). One could speculate that a Gaussian distribution (or even a third, different type of distribution) would also be suitable to explain such experimental data as gathered by Braitenberg and Schüz (1991). As Wilson and Cowan, (1973) mentioned, "It is possible that Gaussians would have been a more propitious choice." [compared to Laplacian distribution functions].

For comparing both, Gaussian and Laplacian distributions we fit the ratio of the standard deviation of the Gaussian to the Laplacian distribution $a = \sigma_{\zeta = 2} / \sigma_{\zeta = 1}$, using a method of least squares. The fitting procedure is described in Appendix E. For instance, for the one-dimensional case, the distributions are fitting best for a ratio of a = 0.703, considering all distances $z \in \mathbb{R}$. For fitting the tails of the distributions within the interval $\hat{z} \le z < \infty$, without taking the peaks into account (i.e., $\hat{z} > 0$), criteria for the lower bound \hat{z} can be applied, such as the magnitude criterion described in Magnitude measure section. See Appendix E for the ratios *a* that fit the tails using the -3 dB-criterion. In the case of fitting the whole range or using the magnitude criterion for fitting the tails the standard deviation of the Gaussian has to be decreased for fitting the Laplacian best (see also Fig. 1). In general, the fit is complicated by the fact that the Laplacian has fatter tails than the Gaussian distribution. This is also the case when using the amplitude of one of the distributions as a degree of freedom in addition to the spreading ratio *a*. Finally, if the Gaussian distribution is the homogeneous connectivity of choice, the correction(s) due to fitting to the Laplacian can be considered for assessing the approximation described in Sampling the homogeneous connectivity section, using Fig. 3.

Conclusion

Local connectivity contributes to the organization of the spatiotemporal large-scale brain dynamics. Before the full brain network modeling with local and global connectivity is carried into the applied domains, some ground truths need to be established. This has been the objective of the current article.

In general, a neural field needs to be approximated by a network of neural masses when

- inherent nonlinearities (e.g., transfer function S(φ) is sigmoidal) complicate solving the equation(s) and/or
- discrete connections (e.g., brain region connecting white matter fibers identified by diffusion-weighted MRI tractographic techniques) aimed to be integrated.

Where neural fields are spatially continuous descriptions of brain activity, networks of neural masses are discrete (e.g., point-like) descriptions in space.

An approximation of the neural field comprises a sampling in space, in particular of the local (homogeneous) connectivity (see Sampling the connectivity in space section). An approximation of the homogeneous connectivity function (i.e., $W_{\text{hom}}(z)$) can be assessed by

- the decay of the connectivity in space (see Magnitude measure section) and/or
- the amount of omitted spatial frequencies (see Spatial frequency measure section).

This holds for any dimensional Euclidean spaces.

The local connectivity is typically described by a sum of Gaussian or Laplace distributions. In this work an approximation is assessed using a single Gaussian or Laplace distribution, assuming a regular *k*-dimensional sampling lattice. However, the assessment approach presented here is in principle applicable to the sum of such distributions as well as to more complicated sampling schemes, using irregular sampling lattices. Moreover, this approach might be also applicable to other distributions, such as the gamma distribution (Hutt and Atay, 2005, 2007).

Here, the results show that the Gaussian distribution has a number of advantages over the widely used Laplacian distribution. For instance, in comparison to the Laplacian distribution, the Gaussian

- is easier to approximate (see Bandwidth-limiting effect of sampling on the homogeneous connectivity section to Comparison of Gaussian and Laplaican connectivities section) and/or
- requires fewer spatiotemporal derivatives (see An alternative approximation of the homogeneous connectivity section).

Finally, the present work gives guidance for modeling certain measurement modalities or integrating a number of them, such as ECoG, EEG, MEG and/or functional MRI, using given anatomical and geometric constraints or from scratch (see Computational models section).

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Appendix A. FitzHugh-Nagumo and Jansen-Rit model

To compare the exemplary implementation of the FitzHugh–Nagumo or the Jansen–Rit model in the general framework, Eq. (2) or Eq. (3) (see Material and methods section), the conventional formulation of both models is shown in this appendix.

FitzHugh-Nagumo model

The FitzHugh-Nagumo model has the following structure

$$\frac{d\varphi_1}{dt} = a_{11}\varphi_1 + a_{13}\varphi_1^3 + a_{21}\varphi_2 + \epsilon_1$$
(A.1)

$$\frac{\mathrm{d}\varphi_2}{\mathrm{d}t} = b_0 + b_{11}\varphi_1 + b_{21}\varphi_2 \tag{A.2}$$

with the parameters as follows: $a_{11} = a_{21} = c$, $a_{13} = -c / 3$, $b_0 = a / c$, $b_{11} = -1 / c$, $b_{21} = -b / c$, where a = 0.7, b = 0.8 and c = 3 (FitzHugh, 1961).

Jansen-Rit model

A general structure of the Jansen–Rit model (Jansen and Rit, 1995) is given by a set of nine coupled first-order ordinary differential equations:

Pyramidal cells

$$\frac{d^2\varphi_1}{d\bar{t}^2} + 2\frac{d\varphi_1}{d\bar{t}} + \varphi_1 = S\Big(V_{1,2}\varphi_2 + V_{1,3}\varphi_3\Big) + \epsilon_1$$
(A.3)

Excitatory interneurons

$$\frac{\mathrm{d}^2\varphi_2}{\mathrm{d}t^2} + 2\frac{\mathrm{d}\varphi_2}{\mathrm{d}t} + \varphi_2 = S(V_{2,1}\varphi_1) + \epsilon_2 \tag{A.4}$$

Inhibitory interneurons

$$\frac{d^2\varphi_3}{d\bar{t}^2} + 2b_3\frac{d\varphi_3}{d\bar{t}} + b_3^2\varphi_3 = b_3^2 S(V_{3,1}\varphi_1) + \epsilon_3$$
(A.5)

where the variables are normalized with respect to the characteristic constant of the model: time $\overline{t} = t a$: $a = 100 \text{ s}^{-1}$, potential $\varphi =$ $r y(\overline{t} / a)$: $r = 0.56 \text{ mV}^{-1}$. Since the original model distinguishes excitatory from inhibitory couplings with two different time constants a and *b*, and the excitatory time constant *a* is used here for normalization so that the parameter $b_3 = b / a$: $b = 50 \text{ s}^{-1}$ is the ratio of inhibition to excitation rate. The coupling factors are: $V_{1,2} = 2e_0rC_2A / a$, $V_{1,3} = -2e_0rC_4B / b$, $V_{2,1} = 2e_0rC_1A / a$ and $V_{3,1} = 2e_0rC_3A / a$, where $e_0 = 2.5 \text{ s}^{-1}$ is the potential for which 50 % firing rate is achieved, A = 3.25 mV and B = 22 mV determine the maximum amplitude of the excitatory and inhibitory postsynaptic potentials, and $C_1 = 5C_2 / 4 = 4C_3 = 4C_4$ (e.g., $C_1 = 135$ is used for alpha-like activity). Due to the normalizations the sigmoid function reads $S(\varphi) =$ Sigm $[\varphi r^{-1}] / (2e_0) = (1 + \xi \exp(-\varphi))^{-1}$ with $\xi = \exp(rv_0)$ and $v_0 = 6$ mV. In addition to the original formulation of the model, the structure presented here, Eqs. (A.3) to (A.5), also considers afferent input to both interneural populations (i.e., ϵ_1 and ϵ_3). The afferent input firing rate in the original version ϵ_2 is here normalized by $\epsilon_2 = p(\bar{t} / a) / (2e_0 C_2)$.

Appendix B. Homogeneous connectivity

Using the case of a single kernel R = 1 for the homogeneous connectivity $W_{\text{hom},\zeta}(z)$, Eq. (6) then reads

$$W_{\text{hom},\zeta}(z) = \eta \beta_{1,\zeta} \exp\left(-\gamma_{1,\zeta} \left(z^{\mathsf{T}} z\right)^{1/\zeta}\right) : \zeta = \{1,2\},\tag{B.1}$$

where *z* is a column vector with $z_{u \in k}$, $k = \{v \mid v \in \mathbb{N}\}$ entries. Converting *z* from Cartesian to *k*-spherical coordinates (e.g., Stein and Shakarchi, 2003, Appendix 2.4) by

$$z = r \begin{pmatrix} \sin \phi_{1} \sin \phi_{2} \cdots \sin \phi_{k-2} \cos \phi_{k-1} \\ \sin \phi_{1} \sin \phi_{2} \cdots \sin \phi_{k-2} \sin \phi_{k-1} \\ \vdots \\ \sin \phi_{1} \sin \phi_{2} \\ \cos \phi_{1} \end{pmatrix}$$
(B.2)

with the radial coordinate $r = ||z||_2 = \sqrt{z^\top z}$, $r : r \in \mathbb{R}_+$ and the angular coordinates $0 \le \phi_v \le \pi$ for $1 \le v \le k - 2$; $0 \le \phi_{k-1} \le 2\pi$, Eq. (B.1) reads

$$W_{\hom,\zeta}(r) = \eta \beta_{1,\zeta} \exp\left(-\gamma_{1,\zeta} r^{2/\zeta}\right). \tag{B.3}$$

This transform nicely shows the radial symmetry of the homogeneous connectivity Eq. (6). The k-dimensionality of z reduces to one-dimension using spherical coordinates.

We normalize a single distribution kernel as follows

$$\left(\eta\beta_{1,\zeta}\right)^{-1} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \exp\left(-\gamma_{1,\zeta} \left(z^{\top} z\right)^{1/\zeta}\right) dz_1 \cdots dz_k \tag{B.4}$$

$$\overset{k \ge 1}{=} s_{k-2}(1) \int_{0}^{n} \mathrm{d}\phi \, \sin^{k-2}(\phi)$$

$$\times \int_{0}^{\infty} \mathrm{d}r \exp\left(-\gamma_{1,\zeta}(r)^{2/\zeta}\right) r^{k-1},$$
(B.5)

(e.g., Stein and Shakarchi, 2003, Appendix 3.3) so that the area or *k*-volume under the homogeneous connectivity $W_{\text{hom},\zeta}(z)$ is unity, where $s_{k-2}(r) = \frac{2\pi^{k/2}r^{k-1}}{\Gamma(k/2)}$ is the surface of the *k*-sphere with the gamma

function $\Gamma(\lambda) = \int_{0}^{0} y^{\lambda - 1} \exp(-y) \, dy$. The variance of a single distribution kernel σ^2 is defined by

$$\sigma^{2k} = \int_{-\infty}^{\infty} \int_{-\infty} W_{\hom,\zeta}(z) \prod_{u=1}^{k} z_u^2 \, \mathrm{d}z_1 \cdots \mathrm{d}z_k. \tag{B.6}$$

In the case of the Gaussian distribution kernel, that is, $\zeta = 1$ the normalization reads in closed form

$$\eta\beta_{1,1} = \left(\frac{\gamma_{1,1}}{\pi}\right)^{k/2},\tag{B.7}$$

with

$$\gamma_{1,1} \stackrel{\forall k}{=} \frac{1}{2\sigma^2}.$$
(B.8)

In the case of the Laplacian distribution kernel, that is, $\zeta = 2$ the closed-form of the normalization reads

$$\eta\beta_{1,2} = \frac{\gamma_{1,2}^k}{2^k} \frac{\pi^{\frac{1-k}{2}}}{\Gamma(\frac{1+k}{2})},\tag{B.9}$$

with

$$\gamma_{1,2} \stackrel{\forall k}{=} \frac{\sqrt{2}}{\sigma}. \tag{B.10}$$

The decay $\gamma_{1,\zeta}$ of both kernels is independent of the dimensionality *k* of *z* but the kernels are scaled differently by $\eta\beta_{1,\zeta}$ so that Eq. (B.1) then reads

$$\frac{W_{\text{hom},\zeta}(z)}{\eta\beta_{1,\zeta}} = \begin{cases} \exp\left(-\frac{z^{T}z}{2\sigma^{2}}\right) & \zeta = 1\\ \exp\left(-\frac{1}{\sigma}\sqrt{2\,z^{T}z}\right) & \zeta = 2 \end{cases}, \tag{B.11}$$

with $\eta\beta_{1,\zeta}$ corresponding to Eqs. (B.7) to (B.10). Note that Eq. (B.11) gives the radial kernels by substituting $r^2 = z^{\top}z$.

In the following two sections the Fourier transform $W_{\text{hom},\zeta}(q, k)$, the total frequency content $\int_{0}^{\infty} dq \ \tilde{W}_{\text{hom},\zeta}(q, k)$ and the cumulative distribution $\int_{0}^{s_{\alpha}} ds \ \tilde{W}_{\text{hom},\zeta}(q, k)$ are listed for both kernels Eq. (B.1) (i.e., Gaussian and Laplacian distribution) that are necessary to obtain the two specific measures presented in Material and methods section, where $\tilde{W}_{\text{hom},\zeta}(q, 1) = \tilde{W}_{\text{hom},\zeta = 1}(s)$ with $q = ||s||_2$.

One-dimensional case

For the Gaussian distribution kernel Eq. (B.1) the Fourier transform is obtained by

$$\hat{W}_{\text{hom},1}(s) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} dz \ W_{\text{hom},1}(z) \exp(-jsz)$$
 (B.12)

$$=\frac{\eta\beta_{1,1}}{\sqrt{2\pi}}\int_{-\infty}^{\infty}dz\exp\left(-\gamma_{1,1},z^2-jsz\right)$$
(B.13)

$$=\frac{\eta\beta_{1,1}}{\sqrt{2\pi\gamma_{1,1}}}\exp\left(-\frac{s^2}{4\gamma_{1,1}}\right)\underbrace{\int_{-\infty+\frac{j^s}{2\sqrt{\gamma_{1,1}}}}^{\infty+\frac{j^s}{2\sqrt{\gamma_{1,1}}}}dy\exp\left(-y^2\right)}_{=\sqrt{\pi}},$$
 (B.14)

with $y = \frac{2\gamma_{1,1}z+js}{2\sqrt{\gamma_{1,1}}}$ and $dz = \sqrt{\gamma_{1,1}} dy$,

$$\tilde{W}_{\text{hom},1}(s) = \eta \beta_{1,1} \, \nu_{1,1} \exp\left(-\frac{s^2}{4\gamma_{1,1}}\right) \tag{B.15}$$

$$= \nu_{1,1} W_{\text{hom},1} \left(z = \frac{s}{2\gamma_{1,1}} \right) \tag{B.16}$$

where $v_{1,1} = (2\gamma_{1,1})^{-1/2}$ scales the spectrum of the Gaussian kernel.

The spatial frequency content measure Eq. (17) is defined with respect to all frequencies that are integrated in $\tilde{W}_{\text{hom},\zeta}(s)$, taking into account the symmetry of $\tilde{W}_{\text{hom},\zeta}: \tilde{W}_{\text{hom},\zeta}(-s) = \tilde{W}_{\text{hom},\zeta}(+s)$

$$\int_{0}^{\infty} ds \ \tilde{W}_{\text{hom},1}(s) = \frac{1}{2} \ \underline{\int}_{-\infty}^{\infty} ds \ \tilde{W}_{\text{hom},1}(s) \tag{B.17}$$

$$=\frac{\mu\beta_{1,1}\nu_{1,1}}{2}\int_{\infty}^{\infty}ds\exp\left(-\frac{s^2}{4\gamma_{1,1}}\right)$$
(B.18)

$$=\frac{\eta\beta_{1,1}}{\sqrt{2}}\underbrace{\int_{-\infty}^{\infty} dy \exp\left(-y^2\right)}_{=\sqrt{\pi}},$$
(B.19)

with $s = 2\sqrt{\gamma_{1,1}} y$ and $ds = 2\sqrt{\gamma_{1,1}} dy$, so that

$$\int_{0}^{\infty} ds \ \tilde{W}_{\text{hom},1}(s) = \sqrt{\frac{\pi}{2}} \eta \beta_{1,1}.$$
(B.20)

The cumulative distribution function for a maximum spatial frequency of interest s_{α} can be approximated by the Gauss error function erf (λ) as follows

$$\int_{0}^{s_{\alpha}} ds \ \tilde{W}_{\text{hom},1}(s) = \sqrt{2} \eta \beta_{1,1} \int_{0}^{\frac{w}{2\sqrt{\gamma_{1,1}}}} dy \exp\left(-y^{2}\right)$$
(B.21)

$$= \sqrt{\frac{\pi}{2}} \eta \beta_{1,1} \operatorname{erf}\left(\frac{s_{\alpha}}{2\sqrt{\gamma_{1,1}}}\right), \qquad (B.22)$$

with $s = 2\sqrt{\gamma_{1,1}} y$ and $ds = 2\sqrt{\gamma_{1,1}} dy$.

In the case of the Laplacian distribution kernel Eq. (B.1) the Fourier transform is obtained by

$$\tilde{W}_{\text{hom},2}(s) = \frac{\eta \beta_{1,2}}{\sqrt{2\pi}} \int_{-\infty}^{\infty} dz \exp\left(-\gamma_{1,2}|z| - jsz\right)$$
(B.23)

$$= \frac{\eta \beta_{1,2}}{\sqrt{2\pi}} \int_{-\infty}^{0} dz \exp\left(z\left(\gamma_{1,2} - js\right)\right) + \frac{\eta \beta_{1,2}}{\sqrt{2\pi}} \int_{0}^{\infty} dz \exp\left(-z\left(\gamma_{1,2} + js\right)\right)$$
(B.24)

$$=\eta\beta_{1,2}\nu_{1,2}\frac{1}{\gamma_{1,2}^2+s^2},$$
(B.25)

which is a Lorentzian function that is scaled by $v_{1,2} = \sqrt{\frac{2}{\pi}} \gamma_{1,2}$.

The spatial frequency content measure Eq. (17) for the Laplacian distribution kernel is defined by the following integrals

$$\int_{0}^{s_{\alpha}} ds \ \tilde{W}_{\text{hom},2}(s) = \eta \beta_{1,2} \nu_{1,2} \int_{0}^{s_{\alpha}} ds \ \frac{1}{\gamma_{1,2}^2 + s^2}$$
(B.26)

$$= \eta \beta_{1,2} \frac{\nu_{1,2}}{\gamma_{1,2}} \tan^{-1} \left(\frac{s_{\alpha}}{\gamma_{1,2}} \right), \tag{B.27}$$

where for all spatial frequencies $s_{\alpha} \rightarrow +\infty$

$$\int_{0}^{\infty} ds \ \tilde{W}_{\text{hom},2}(s) = \eta \beta_{1,2} \ \frac{\pi \nu_{1,2}}{2\gamma_{1,2}}.$$
(B.28)

k-Dimensional case

Taking advantage of the radial symmetry of the homogenous connectivity kernels Eq. (B.3) the integrals of the *k*-dimensional Fourier transform

$$\tilde{W}_{\hom,\zeta}(s,k) = 2\pi^{-k/2} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} W_{\hom,\zeta}(z) \exp\left(-js^{\top}z\right) dz_1 \cdots dz_k, \quad (B.29)$$

can be reduced to

$$\tilde{W}_{\text{hom},\zeta}(q,k) = \frac{s_{k-2}(1)}{(2\pi)^{k/2}} \int_{0}^{\infty} W_{\text{hom},\zeta}(r) r^{k-1} dr \times \int_{0}^{\pi} \exp(-jrq\cos(\phi)) \sin^{k-2}(\phi) d\phi$$
(B.30)

$$=q^{-\frac{k-2}{2}}\int_{0}^{\infty} dr \ W_{\hom,\zeta}(r) \ r^{k/2} J_{\frac{k-2}{2}}(qr)$$
(B.31)

using spherical coordinates (see Eq. (B.2)), where $r = ||z||_2$ and $q = ||s||_2$ (Schaback and Wu, 1996; Stein and Shakarchi, 2003; Stein and Weiss, 1971). The surface of the *k*-dimensional sphere is $s_{k-2}(r) = \frac{2\pi k^{2}k^{k-1}}{\Gamma(k/2)}$. Note that the integral in Eq. (B.31) that includes the Bessel function of the first kind $J_{\frac{k-2}{2}}(qr)$ of order (k - 2) / 2 is the Hankel transform. Applying the radial connectivity kernels Eq. (B.3) in Eq. (B.31) with Eqs. (B.7) to (B.10) and using the Hankel transform (Poularikas, 2010, Tab. 9.2: Eqs. (9) and (10)), the radial Fourier spectrum is obtained for both kernels

$$\tilde{W}_{\text{hom},\zeta}(q,k) = \eta \beta_{1,\zeta} \nu_{1,\zeta} \begin{cases} \exp\left(-\frac{q^2}{4\gamma_{1,\zeta}}\right) & \zeta = 1 \\ \\ \frac{1}{\left(\gamma_{1,\zeta}^2 + q^2\right)^{\frac{k+1}{2}}} & \zeta = 2 \end{cases}$$
(B.32)

where the scaling $v_{1,\zeta}$ is

$$\nu_{1,\zeta} \stackrel{\forall k}{=} \begin{cases} \left(2\gamma_{1,\zeta}\right)^{-k/2} & \zeta = 1\\ \\ 2^{k/2} \frac{\gamma_{1,\zeta}}{\sqrt{\pi}} \Gamma\left(\frac{k+1}{2}\right) & \zeta = 2 \end{cases}$$
(B.33)

Please note that the Fourier spectra $W_{\text{hom},\zeta}(q, k)$ Eq. (B.32) with the scaling $\nu_{1,\zeta}$, see Eq. (B.33), incorporates the one-dimensional case, that is, k = 1 with s = q (see Eqs. (B.15) and (B.25)). Eq. (B.32) is therefore a closed-form expression of the Fourier transform of the connectivity kernel Eq. (B.1) for *k*-dimensional space *z*. Moreover, in the case of the Gaussian distribution kernel, that is, $\zeta = 1$, the shape of the spectrum is independent of the dimension *k*, simply the scaling $\nu_{1,1}$ depends on *k*, whereas, in the case of the Laplacian distribution kernel, that is, $\zeta = 2$, the shape and the scaling of the spectrum change with the dimensionality to the power of $\frac{k+1}{2}$ and to the power of $\frac{k}{2}$.

For the *k*-dimensional Gaussian distribution kernel both measures, magnitude measure $G_1(q_{dB}, k)$ and spatial frequency content measure $\alpha_1(q_{\alpha}, k)$, presented in Material and methods section are completely specified by the integral given in One-dimensional case section in Appendix B for the one-dimensional case, that is, k = 1, since the *k*-dependent scaling $\nu_{1,1}$ is canceled out (see Eqs. (13) and (17)).

For the *k*-dimensional Laplacian distribution kernel the dimensionality *k* simply scales the magnitude measure $G_2(q_{dB}, k)$ for the onedimensional case (i.e., k = 1) with the factor χ that is the power of the spectrum $\chi = \frac{k+1}{2}$ (see Eqs. (13) and (B.32)). Again, for both measures the *k*-dependent scaling $\nu_{1,2}$ is canceled out due to the ratio of spectral components. For the spatial frequency content measure $\alpha_2(q_\alpha, k)$ the cumulative of the spectrum of the *k*-dimensional Laplacian distribution kernel $\tilde{W}_{\text{hom},2}(q, k)$ is required (see Eq. (17)). The total area or the *k*-volume under the *k*-dimensional Laplacian distribution kernel $\tilde{W}_{\text{hom},2}(q, k)$ (Eq. (B.32)) is obtained, using Gradshteyn and Ryzhik (2007), Eq. 3.241–4¹¹

$$\frac{1}{\eta\beta_{1,2}\nu_{1,2}}\int_{0}^{\infty} \mathrm{d}q \ \tilde{W}_{\mathrm{hom},2}(q,k) \stackrel{\forall k}{=} \frac{2^{k}}{\gamma_{1,2}^{k}}\frac{\Gamma^{2}(\frac{k}{2})}{4\Gamma(k)}. \tag{B.34}$$

Note that this is a closed-form expression for *k*-dimensional space *z* since Eq. (B.34) incorporates the one-dimensional case, that is, k = 1 (Eq. (B.28)). The q_{α} -bounded area or *k*-volume under the Laplacian kernel Eq. (B.32) is obtained, using Gradshteyn and Ryzhik (2007), Eq. 3.254-1

$$\frac{1}{\eta\beta_{1,2}\nu_{1,2}} \int_{0}^{q_{\alpha}} \mathrm{d}q \ \tilde{W}_{\mathrm{hom},2}(q,k) \stackrel{\forall k}{=} \frac{q_{\alpha}}{\gamma_{1,2}^{k+1}} {}_{2}F_{1}\left(\frac{1}{2},\frac{k+1}{2};\frac{3}{2};-\frac{q_{\alpha}^{2}}{\gamma_{1,2}^{2}}\right), \quad (B.35)$$

where ${}_{2}F_{1}(\cdot,\cdot;\cdot;\cdot)$ denotes the Gaussian hypergeometric function. The one-dimensional case, that is, k = 1, Eq. (B.27) is incorporated in Eq. (B.35) because ${}_{2}F_{1}\left(\frac{1}{2},1;\frac{3}{2};-\frac{q_{\alpha}^{2}}{\gamma_{12}}\right) = \frac{\gamma_{12}}{q_{\alpha}} \tan^{-1}\left(\frac{q_{\alpha}}{\gamma_{12}}\right)$, that is therefore a closed-form expression for k dimensions. The effect of the dimensionality k on the spatial frequency content measure α_{2} (q_{α} , k) is dependent on the hypergeometric function. Using Bronstejn and Semendjajew (1996), Eq. 0.9.5–50. to solve the integral on the left-hand side of Eq. (B.35) gives a closed-form as follows

$$(k+1)\gamma_{1,2}^{2}\int_{0}^{q_{\alpha}} \frac{dq}{\left(\gamma_{1,2}^{2}+q^{2}\right)^{\frac{k+3}{2}}} = \frac{q_{\alpha}}{\left(\gamma_{1,2}^{2}+q^{2}_{\alpha}\right)^{\frac{k+1}{2}}} + k\int_{0}^{q_{\alpha}} \frac{dq}{\left(\gamma_{1,2}^{2}+q^{2}\right)^{\frac{k+1}{2}}}$$
(B.36)

which is a series that starts either from the k = 1 area

$$\int_{0}^{q_{\alpha}} \frac{dq}{\left(\gamma_{1,2}^{2} + q^{2}\right)} = \frac{q_{\alpha}}{\gamma_{1,2}^{2}} {}_{2}F_{1}\left(\frac{1}{2}, 1; \frac{3}{2}; -\frac{q_{\alpha}^{2}}{\gamma_{1,2}^{2}}\right)$$
(B.37)

$$=\frac{1}{\gamma_{1,2}}\tan^{-1}\left(\frac{q_{\alpha}}{\gamma_{1,2}}\right) \tag{B.38}$$

or from k = 2 volume

$$\int_{0}^{q_{\alpha}} \frac{dq}{\left(\gamma_{1,2}^{2} + q^{2}\right)^{\frac{3}{2}}} = \frac{q_{\alpha}}{\gamma_{1,2}^{3}} {}_{2}F_{1}\left(\frac{1}{2}, \frac{3}{2}; \frac{3}{2}; -\frac{q_{\alpha}^{2}}{\gamma_{1,2}^{2}}\right)$$
(B.39)

$$=\frac{q_{\alpha}}{\gamma_{1,2}^{2}\sqrt{\gamma_{1,2}^{2}+q_{\alpha}^{2}}}$$
(B.40)

for either odd or even number of dimension *k*. Note that Eq. (B.38) is equivalent to Eq. (B.27), simply unscaled. Compared to the closed-form expression Eq. (B.35), all higher dimensional q_{α} -bounded volumes, that is, k > 2 can be calculated, using Eq. (B.36), simply knowing the solution for the first and second dimension, Eqs. (B.38) and (B.40). In the case of Eq. (B.35) the hypergeometric function needs to be specified separately for each dimension *k*. Substituting Eqs. (B.34) and (B.35) or Eqs. (B.34) and (B.36) in Eq. (17), the spatial frequency content measure α_2 (q_{α} , *k*) for the *k*-dimensional Laplacian distribution kernel $W_{\text{hom},2}$ (*r*) is obtained

$$\alpha_2(q_{\alpha},k) = 1 - \frac{1}{2^{k-2}} \frac{\Gamma(k)}{\Gamma^2(\frac{k}{2})} \frac{q_{\alpha}}{\gamma_{1,2}} {}_2F_1\left(\frac{1}{2},\frac{k+1}{2};\frac{3}{2};-\frac{q_{\alpha}^2}{\gamma_{1,2}^2}\right)$$
(B.41)

$$\alpha_{2}(q_{\alpha}, k+2) = \alpha_{2}(q_{\alpha}, k) - \frac{4}{k} \left(\frac{\gamma_{1,2}}{2}\right)^{k} \frac{\Gamma(k)}{\Gamma^{2}\binom{k}{2}} \frac{q_{\alpha}}{\left(\gamma_{1,2}^{2} + q_{\alpha}^{2}\right)^{\frac{k+1}{2}}}$$
(B.42)

with

$$\alpha_2(q_\alpha, 1) = 1 - \frac{2}{\pi} \tan^{-1} \left(\frac{q_\alpha}{\gamma_{1,2}} \right) \tag{B.43}$$

$$\alpha_2(q_{\alpha}, 2) = 1 - \frac{q_{\alpha}}{\sqrt{\gamma_{1,2}^2 + q_{\alpha}^2}}.$$
(B.44)

Compared to Eq. (B.41), the spatial frequency content measure α_2 (q_α , k) can be calculated for all higher dimensional Laplacian

kernels k > 2 on the basis of the one-dimensional Eq. (B.43) and twodimensional kernel Eq. (B.44), using Eq. (B.42). Evaluating the difference between α_2 (q_α , k) and α_2 (q_α , k + 1) in addition to Eq. (B.42) we can conclude that the spatial frequency content measure α_2 (q_α , k) for the Laplacian distribution kernel generally decreases

with increasing dimensionality $\alpha_2 (q_{\alpha}, k) \ge \alpha_2 (q_{\alpha}, k+1) \forall q_{\alpha}, \forall k$. Finally, for higher dimensional (k > 2) Laplacian distribution kernels $W_{\text{hom},2}$ (r, k) the spatial frequency content measure $\alpha_2 (q_{\alpha}, k)$ for k = 1 and k = 2, respectively, can be used by correcting the dimensionality with Eq. (B.42).

For correcting the *k*-volume effect on the spatial frequency content measure α_2 (q_α , k) for the Laplacian distribution kernel $W_{\text{hom},2}$ (r, k) we set the spatial cutoff frequency $q_c = q_\alpha$ to be the same for all *k*-dimensional Euclidean spaces (note that $\gamma_{1,2}$ is independent of k). Solving Eq. (B.43) for $\frac{q_\alpha}{\gamma_{12}}$, and then plugging it in Eq. (B.44) gives the corrected spatial frequency content measure α_2 (q_α , 2) for dimension k = 2 as a function of the spatial frequency content measure α_2 (q_α , 1) in the k = 1-dimension case

$$\alpha_2(q_\alpha, 2) = 2\sin^2\left(\frac{\pi}{4} \ \alpha_2(q_\alpha, 1)\right). \tag{B.45}$$

Using Eq. (B.42) with Eq. (B.45) gives the corrected spatial frequency content measure α_2 (q_α , 3) for three-dimensional space, k = 3 based on the spatial frequency content measure α_2 (q_α , 1) in the k = 1-dimensional case

$$\alpha_2(q_{\alpha}, 3) = \alpha_2(q_{\alpha}, 1) - \frac{1}{\pi} \sin(\pi \, \alpha_2(q_{\alpha}, 1)). \tag{B.46}$$

In the scope of this work we are content with physical spaces up to dimension k = 3. However, the series expansion Eq. (B.42) can be used to correct the spatial frequency content measure α_2 (q_α , k) for higher dimensional spaces, if necessary.

Appendix C. Bandwidth-limitation

Applying the bandwidth limiting transform, Eq. (39), to the Fourier transform of the normalized Gaussian distribution function, Eq. (B.15), we obtain

$$\hat{W}_{\text{hom},1}(z) = \frac{1}{\sqrt{2\pi}} \int_{-\hat{s}}^{\hat{s}} ds \, \exp\left(-\frac{\sigma^2 s^2}{2} + jsz\right) \tag{C.1}$$

$$= \frac{1}{\sqrt{2\pi\sigma}} \exp\left(-\frac{z^2}{2\sigma^2}\right) \int_{-\hat{y}}^{\hat{y}} dy \, \exp\left(-y^2\right), \tag{C.2}$$

where $\sqrt{2}\sigma y = \sigma^2 s - jz$, $\sqrt{2}dy = \sigma ds$, $\pm \hat{y}\sqrt{2}\sigma = \pm \hat{s}\sigma^2 - jz$ and \hat{s} is the maximum spatial frequency. Please note that the expression before the integral in Eq. (C.2) is the Gaussian distribution function $W_{\text{hom},1}(z)$ (see Eq. (6)), which allows to introduce the transfer function $K_{\text{hom},1}(z) = \hat{W}_{\text{hom},1}(z) / W_{\text{hom},1}(z)$. We can write the integral in Eq. (C.2) as follows

$$2K_{\text{hom},1}(z) = \operatorname{erf}\left(\frac{jz + \sigma^2 \hat{s}}{\sqrt{2}\sigma}\right) - \operatorname{erf}\left(\frac{jz - \sigma^2 \hat{s}}{\sqrt{2}\sigma}\right). \tag{C.3}$$

Writing the error function as a power series (see Oldham et al., 2009, Chap. 40) we obtain Eq. (40)

$$K_{\text{hom},1}(z) = \frac{1}{\sqrt{2}\pi} \sum_{u=0}^{\infty} \frac{(-1)^u}{2^u (1+2u)u!} \left(\left(\frac{jz}{\sigma} + \sigma \hat{s}\right)^{1+2u} - \left(\frac{jz}{\sigma} - \sigma \hat{s}\right)^{1+2u} \right).$$
(C.4)

Applying the bandwidth limiting transform, Eq. (39), to the Fourier transform of the normalized Laplacian distribution function, Eq. (B.25), we can write

$$\hat{W}_{\text{hom},2}(z) = \frac{1}{\sqrt{8}\pi} \left(\int_{-\hat{s}}^{\hat{s}} ds_1 \frac{\exp(js_1 z_1)}{\sqrt{2} + j\sigma s_1} + \int_{-\hat{s}}^{\hat{s}} ds_2 \frac{\exp(js_2 z_2)}{\sqrt{2} - j\sigma s_2} \right), \tag{C.5}$$

where $s_1 = -s_2 = s$ and thus $z_2 = -z_1$ accounts for the absolute value z in Eq. (B.1). Considering then the fact that $z_1 = |z|$: $\forall z \ge 0$ and $-z_2 = |z|$: $\forall z \le 0$, Eq. (C.5) can be written as follows

$$\hat{W}_{\text{hom},2}(z) = \frac{1}{\sqrt{8\pi}} \int_{-\hat{s}}^{\hat{s}} ds \, \frac{\exp(js|z|)}{\sqrt{2} + j\sigma \, s} \tag{C.6}$$

$$= \frac{1}{\sqrt{2}\sigma} \exp\left(-\frac{\sqrt{2}|z|}{\sigma}\right) \frac{j}{2\pi} \int_{-\hat{y}}^{\hat{y}} \frac{dy}{y \exp(jy|z|)}, \quad (C.7)$$

where $\pm \sigma \hat{y} = \sqrt{-2} \pm \sigma \hat{s}$. Analogous to the calculation for the Gaussian we can introduce the transfer function $K_{\text{hom},2}(z) = \hat{W}_{\text{hom},2}(z) / W_{\text{hom},2}(z)$ since the exponential expression before the integral in Eq. (C.7) corresponds to the Laplacian distribution function $W_{\text{hom},2}(z)$ (see Eq. (6)) so that we obtain

$$K_{\text{hom},2}(z) = \frac{j}{2\pi} \int_{-y}^{y} \frac{dy}{y \exp(jy|z|)}.$$
 (C.8)

Using Gradshteyn and Ryzhik (2007), Eq. 3.352-3; Eq. (C.8) result in

$$K_{\text{hom},2}(z) = \frac{j}{2\pi} (\text{Ei}(j\hat{y} |z|) - \text{Ei}(-j\hat{y} |z|)), \tag{C.9}$$

where $\text{Ei}(\lambda) = -\int_{-\lambda}^{\infty} dy \exp(-y) / y$ is the exponential integral. We then write $K_{\text{hom},2}(z)$ as a power series (see Oldham et al., 2009, Chap. 37) and obtain Eq. (41)

$$K_{\text{hom},2}(z) = \frac{1}{\pi} \tan^{-1} \left(\frac{\sigma \, \hat{s}}{\sqrt{2}} \right) + \frac{j}{2\pi} \sum_{u=1}^{\infty} \frac{|z|^{u}}{\sigma^{u} u! u} \left(\left(\sqrt{2} - j\sigma \, \hat{s} \right)^{u} - \left(\sqrt{2} + j\sigma \, \hat{s} \right)^{u} \right).$$
(C.10)

The magnitude measure Eq. (15) and the spatial frequency measure Eq. (18) can be applied to the transfer functions $K_{\text{hom},\zeta}(z)$ by $\hat{s} = s_{\text{dB}}$, $\sigma = \sigma_{\text{dB}}$ and $\hat{s} = s_{\alpha}$, $\sigma = \sigma_{\alpha}$, respectively.

Appendix D. Partial differential form

In this appendix the partial differential operator that describes the homogeneous connectivity $W_{\text{hom}}(z)$ is derived. For that purpose, we use the Green's function method and follow the study of the Laplacian distribution for the homogeneous connectivity by Qubbaj and Jirsa (2009) and Jirsa (2009).

Considering the inhomogeneous part (i.e., right-hand side) of the delay-integro-differential equations, Eq. (4),

$$\mathbf{P}(d/dt)\mathbf{\Psi}(x,t) = \mathbf{\Xi}(x,t) - \mathbf{\Lambda}(\mathbf{\Psi}(x,t)) + S(\mathbf{V}_{\mathrm{loc}}\mathbf{\Psi}(x,t)) + \mathbf{V}_{\mathrm{hom}}H(x,t),$$
(D.1)

we can write the homogeneous connectivity term H(x, t) as follows

$$H(x,t) = \int_{\Omega} dy \ W_{\text{hom}}(\Delta(x,y)) \ S(\mathbf{V}_{\text{loc}} \boldsymbol{\Psi}(y,t-\Delta(x,y)/c_1)) \tag{D.2}$$

$$= \int_{\Omega} dy \int_{-\infty}^{\infty} dT \ I(\Delta(x,y), t-T) \ S(\mathbf{V}_{\mathsf{loc}} \Psi(y,T)), \tag{D.3}$$

where

$$I(\Delta(x,y),t-T) = W_{\text{hom}}(\Delta(x,y)) \ \delta(T-t+\Delta(x,y)/c_1), \tag{D.4}$$

with the Dirac's delta function $\delta(z)$. The function $I(\Delta(x,y), t - T)$ can then be formulated as

$$I(x-y,t-T) = \frac{1}{2\pi} \int_{-\infty}^{\infty} ds \int_{-\infty}^{\infty} d\omega \quad \tilde{I}(s,\omega) \exp(js(x-y) + j\omega(t-T)), \quad (D.5)$$

assuming that $\Delta(x, y) = ||x - y||_2$. Using the Fourier transforms, Eq. (D.1) can be written as follows

$$\frac{1}{2\pi} \mathbf{P}(d/dt) \int_{-\infty}^{\infty} ds \int_{-\infty}^{\infty} d\omega \quad \tilde{\mathbf{\Psi}}(s,\omega) \exp(jsx+j\omega t) \\
= \frac{1}{2\pi} \int_{-\infty}^{\infty} ds \int_{-\infty}^{\infty} d\omega \left(\tilde{\mathbf{\Xi}}(s,\omega) - \mathbf{\Lambda} \left(\tilde{\mathbf{\Psi}}(s,\omega) \right) + \tilde{S}(s,\omega) \right) \\
\times \exp(jsx+j\omega t) + \frac{1}{(2\pi)^2} \int_{\Omega} dy \int_{-\infty}^{\infty} dT \\
\times \int_{-\infty}^{\infty} ds \int_{-\infty}^{\infty} d\omega \tilde{I}(s,\omega) \exp(js(x-y) + j\omega(t-T)) \\
\times \int_{\infty}^{\infty} ds' \int_{-\infty}^{\infty} d\omega' \tilde{S}(s',\omega') \exp(js'y+j\omega'T),$$
(D.6)

where the variables $\Psi(x, t)$, $\tilde{\Xi}(x, t)$ and the functions $\tilde{I}(x, t)$, $\tilde{S}(x, t)$ denote the Fourier transform. Applying the fact that $(\partial/\partial t)^u \exp(j\omega t) = (j\omega)^u \exp(j\omega t)$ to the differential operator $\mathbf{P}(d/dt)$ and rearranging the terms, we obtain

$$\int_{-\infty}^{\infty} ds \int_{-\infty}^{\infty} d\omega \exp(jsx + j\omega t) \mathbf{P}(j\omega) \tilde{\mathbf{\Psi}}(s,\omega) = \int_{-\infty}^{\infty} ds \int_{-\infty}^{\infty} d\omega \exp(jsx + j\omega t) \left(\tilde{\mathbf{\Xi}}(s,\omega) - \mathbf{\Lambda} \left(\tilde{\mathbf{\Psi}}(s,\omega)\right) + \tilde{S}(s,\omega)\right) + \frac{1}{2\pi} \int_{-\infty}^{\infty} ds \int_{-\infty}^{\infty} d\omega \exp(jsx + j\omega t) \tilde{I}(s,\omega) \int_{-\infty}^{\infty} ds' \int_{-\infty}^{\infty} d\omega' \tilde{S}(s',\omega') \times \int_{\Omega} dy \exp(jy(s'-s)) \int_{-\infty}^{\infty} dT \exp(jT(\omega'-\omega)).$$
(D.7)

Note that the last two integrals on the right-hand side of Eq. (D.7) are equivalent to $2\pi \delta(s' - s)$ and $2\pi \delta(\omega' - \omega)$ for $L \to \infty$. Hence, Eq. (D.7) reduces to

$$\int_{-\infty}^{\widetilde{\sigma}} ds \int_{-\infty}^{\widetilde{\sigma}} d\omega \exp(jsx + j\omega t) \mathbf{P}(j\omega) \,\tilde{\mathbf{\Psi}}(s,\omega) = \int_{-\infty}^{\infty} ds \int_{-\infty}^{\widetilde{\sigma}} d\omega \exp(jsx + j\omega t) \left(\tilde{\mathbf{\Xi}}(s,\omega) - \mathbf{\Lambda} \left(\tilde{\mathbf{\Psi}}(s,\omega) \right) + \tilde{S}(s,\omega) \right) + 2\pi \int_{-\infty}^{\widetilde{\sigma}} ds \int_{-\infty}^{\widetilde{\sigma}} d\omega \exp(jsx + j\omega t) \tilde{I}(s,\omega) \,\tilde{S}(s,\omega)$$
(D.8)

or simply,

$$\mathbf{P}(j\omega)\,\tilde{\mathbf{\Psi}}(s,\omega) = \,\tilde{\mathbf{\Xi}}(s,\omega) - \mathbf{\Lambda}\Big(\,\tilde{\mathbf{\Psi}}(s,\omega)\Big) + \,\tilde{S}(s,\omega) \\ + 2\pi\,\mathbf{V}_{\mathrm{hom}}\,\tilde{I}(s,\omega)\,\tilde{S}(s,\omega). \tag{D.9}$$

We then write $\tilde{l}(s, \omega)$ as a power series in *s* and ω , and we multiply both sides of Eq. (D.9) by $\exp(jsx + j\omega t)$ and integrating over *s* and ω to obtain the partial differential form

$$\begin{aligned} \mathbf{P}(\partial/\partial t)\mathbf{\Psi}(x,t) &= \mathbf{\Xi}(x,t) - \mathbf{\Lambda}(\mathbf{\Psi}(x,t)) + S(\mathbf{V}_{\text{loc}}\mathbf{\Psi}(x,t)) \\ &+ \mathbf{V}_{\text{hom}}C_{\zeta}(\partial/\partial x,\partial/\partial t) \ S(\mathbf{V}_{\text{loc}}\mathbf{\Psi}(x,t)), \end{aligned} \tag{D.10}$$

where the partial differential operator $C_{\zeta} (\partial/\partial x, \partial/\partial t) = \tilde{I}(s, \omega)$ due to the fact that $(js)^{\nu} (j\omega)^{\mu} \exp(jsx + j\omega t) = (\partial/\partial x)^{\nu} (\partial/\partial t)^{\mu} \exp(jsx + j\omega t)$. Substituting the normalized homogeneous connectivity functions $W_{\text{hom},\zeta}(z)$ as defined by Eq. (B.1) in Eq. (D.4), and then using the Fourier transform to apply the relation $C_{\zeta} (js, j\omega) = \tilde{I}(s, \omega)$ we obtain

$$C_1(\lambda_1, \lambda_2) = \sum_{\nu=0}^{\infty} \sum_{u=0}^{2\nu} a_0(u, \nu) \ (a_1(u, \nu) + a_2(u, \nu) \ \lambda_1) \ \lambda_1^{2\nu-u} \ \lambda_2^u \qquad (D.11)$$

for the Gaussian distribution function $W_{\text{hom},1}(z)$ and

$$C_{2}(\lambda_{1},\lambda_{2}) = \sum_{\nu=0}^{\infty} \sum_{u=0}^{\nu} a(u,\nu) \ \lambda_{1}^{\nu-u} \ \lambda_{2}^{u}$$
(D.12)

for the Laplacian distribution function $W_{\text{hom},2}(z)$ with the coefficients

$$a(u,v) = \frac{1}{4\pi} \frac{\sigma^{v} v! (j^{2v} + j^{2u})}{c_{\perp}^{u} u! (v-u)!}$$
(D.13)

$$a_0(u,v) = \frac{1}{4\sqrt{2\pi}} \frac{\sigma^{2v}}{c_1^u u! (2v-u)!}$$
(D.14)

$$a_1(u,v) = \frac{(2v)! \left(1+j^{2u}\right)}{2^v v!} \tag{D.15}$$

$$a_2(u,v) = \sqrt{\frac{2}{\pi}} \frac{2^{\nu} v! \sigma \left(1 - j^{2u}\right)}{2\nu - u + 1}.$$
 (D.16)

The Fourier transform of the function $I(z, \tau)$ is given by

$$\tilde{I}(s,\omega) = \frac{1}{2\pi} \int_{-\infty}^{\infty} dz \int_{-\infty}^{\infty} d\tau \ I(z,\tau) \exp(-jsz - j\omega\tau)$$
(D.17)

and specified as follows

$$\tilde{I}_{1}(s,\omega) = \frac{1}{4\sqrt{2\pi}} \left(\exp\left(-b_{1}(s,\omega)^{2}\right) + \exp\left(-b_{2}(s,\omega)^{2}\right) \right) \\ + \frac{j}{2\sqrt{2\pi}} \left(F(b_{1}(s,\omega)) - F(b_{2}(s,\omega))\right)$$
(D.18)

for the Gaussian distribution function $W_{\text{hom},1}(z)$ as well as

$$\tilde{I}_{2}(s,\omega) = \frac{1}{2\pi} \frac{1 + j\omega\sigma/c_{1}}{(1 + j\omega\sigma/c_{1})^{2} + (\sigma s)^{2}}$$
(D.19)

for the Laplacian distribution function $W_{\text{hom},2}(z)$ where the coefficients $b_1(s, \omega)$ and $b_2(s, \omega)$ are defined by

$$b_u(s,\omega) = \frac{\sigma}{\sqrt{2}} \left(s - (-1)^u \omega / c_1 \right)$$
(D.20)

and $F(\lambda)$ is Dawson's integral (see Oldham et al., 2009, chap. 42)

$$F(\lambda) = \exp\left(-\lambda^2\right) \int_0^{\lambda} dy \, \exp\left(y^2\right) \tag{D.21}$$

$$= \frac{\sqrt{\pi}}{2} \lambda \sum_{u=0}^{\infty} \frac{(-1)^{u} \lambda^{2u}}{\Gamma(u+3/2)}$$
(D.22)

with the gamma function $\Gamma(\lambda) = \int_{0}^{\infty} y^{\lambda - 1} \exp(-y) dy$. We them write $\tilde{I}_{\zeta}(s, \omega)$, as a power series in *s* and ω which correspond to Eqs. (D.11) and (D.12) for $\zeta = 1$ and $\zeta = 2$, respectively,

$$I_{\zeta}(s,\omega) = C_{\zeta}(js,j\omega). \tag{D.23}$$

Appendix E. Fitting connectivity distribution functions

For finding the best-fitting parameters (a, b) we minimize the integral of square residuals between the Gaussian and the Laplacian. The fitting parameters are the amplitude *a* and spreading *b*. The integral of square residuals are given as follows $\hat{z} > 0$

$$Y(a,b,\hat{z}) = \int_{\hat{z}}^{\infty} dz \left(W_{\text{hom},1}(\sigma z) - a \ W_{\text{hom},2}(b\sigma z) \right)^2$$
(E.1)

$$=Y_{1}(\hat{z})+Y_{12}(a,b,\hat{z})+Y_{2}(a,b,\hat{z}), \tag{E.2}$$

with

=

$$Y_1(\hat{z}) = \int_{\hat{z}}^{\infty} dz \ W_{\text{hom},1}^2(\sigma z)$$
(E.3)

$$Y_{12}(a,b,\hat{z}) = -2a \int_{\hat{z}}^{\infty} dz \ W_{\text{hom},1}(\sigma z) W_{\text{hom},2}(\sigma z)$$
(E.4)

$$Y_{2}(a,b,\hat{z}) = -a^{2} \int_{\hat{z}}^{\infty} dz \ W_{\text{hom},2}^{2}(\sigma z).$$
(E.5)

Please note that Y_1 is independent of the fitting parameters *a* and *b*. Hence, we simply need to consider Y_{12} and Y_2 . Using the definition of the connectivity distributions Eq. (B.1) we can write Eq. (E.4) as follows

$$Y_{12}(a,b,\hat{z}) = -\frac{a}{\sqrt{\pi\sigma^2}} \int_{\hat{z}}^{\infty} dz \, \exp\left(-z^2/2 - \sqrt{2}bz\right)$$
(E.6)

$$= -\sqrt{\frac{2}{\pi}} \frac{a}{\sigma^2} \exp\left(b^2\right) \int_{\hat{z}/\sqrt{2}+b}^{\infty} dy \, \exp\left(-y^2\right), \tag{E.7}$$

where $y = z / \sqrt{2} + b$, $dy = dz / \sqrt{2}$, $y(\hat{z}) = \hat{z} / \sqrt{2} + b$ and $y(\infty) = \infty$. Writing the integral in Eq. (E.7) as complementary error function we obtain

$$Y_{12}(a,b,\hat{z}) = -\frac{a}{\sqrt{2}\sigma^2} \exp\left(b^2\right) \operatorname{erfc}\left(\hat{z}/\sqrt{2}+b\right). \tag{E.8}$$

Substituting the connectivity distributions Eq. $(\mathrm{B.1})$ in Eq. $(\mathrm{E.5})$ we obtain

$$Y_2(a,b,\hat{z}) = \frac{a^2}{2\sigma^2} \int_{\hat{z}}^{\infty} dz \exp\left(-\sqrt{8}bz\right) : b > 0$$
(E.9)

$$=\frac{a^2}{\sqrt{32}\sigma^2 b}\exp\left(-\sqrt{8}b\hat{z}\right).$$
(E.10)

In order to find the global minimum for *b* we substitute a = b in Eqs. (E.8) and (E.10). This has the effect that a change of the standard deviation σ by *a* is compensated by fixing the area under the Laplacian to unity. The parameter *a* describes then the ratio of the standard deviation of the Laplacian to the Gaussian distribution $a = \sigma_{\xi} = 2 / \sigma_{\xi} = 1$. We then calculate the derivative of $Y(a, \hat{z})$, Eq. (E.2) with respect to *b*

$$\frac{d}{da}Y(a,\hat{z}) = \frac{d}{da}Y_{12}(a,\hat{z}) + \frac{d}{da}Y_{2}(a,\hat{z})$$
(E.11)

$$= \frac{1}{\sqrt{32}\sigma^2} \left[-4\left(2a^2+1\right) \exp\left(a^2\right) \operatorname{erfc}\left(a+z/\sqrt{2}\right) + \left(1-\sqrt{8}az\right) \exp\left(-\sqrt{8}az\right) + 8a \exp\left(-z\left(\sqrt{8}a+z\right)/2\right)/\sqrt{\pi} \right].$$
(E.12)

Both connectivity functions are fitting for a given \hat{z} if Eq. (E.12) has at least a zero at which the derivative (with respect to a) is positive. The derivative of Eq. (E.12) is not shown here. Using the Nelder–Mead simplex method (Nelder and Mead, 1965) we identified the global minimum a = 0.703 for $\hat{z} = 0$. Note that for \hat{z} such criteria as the magnitude criteria described in Magnitude measure section can be used. Applying the -3 dB-criterion either to the Gaussian or to the Laplacian distribution we identified a global minimum a = 0.79 or a = 0.81.

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