

Neural Field Dynamics on the Folded Three-Dimensional Cortical Sheet and Its Forward EEG and MEG

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Abstract. Dynamic systems defined on the scale of neural ensembles are well-suited to model the spatiotemporal dynamics of electroencephalographic (EEG) and magnetoencephalographic (MEG) data. We develop a methodological framework, which defines the activity of neural ensembles, the neural field, on a sphere in three dimensions. Using Magnetic Resonance Imaging (MRI) we map the neural field dynamics from the sphere onto the folded cortical surface of a hemisphere. The neural field represents the current flow perpendicular to the cortex and thus allows the calculation of the electric potentials on the surface of the skull and the magnetic fields outside the skull to be measured by EEG and MEG, respectively. For demonstration of the dynamics, we present the propagation of activation at a single cortical site resulting from a transient input. Non-trivial mappings between the multiple levels of observation are obtained which would not be predicted by inverse solution techniques. Considering recent results mapping large-scale brain dynamics (EEG, MEG) onto behavioral motor patterns, this paper provides a discussion of the causal chain starting from local neural ensemble dynamics through encephalographic data to behavior.

1 Introduction

Non-invasive techniques such as functional Magnetic Resonance Imaging (fMRI), ElectroEncephaloGraphy (EEG) and MagnetoEncephaloGraphy (MEG) provide entry points to human brain dynamics for clinical purposes, as well as the study of human behavior and cognition. Each of these imaging technologies provides spatiotemporal information about the on-going neural activity in the cortex, in particular fMRI on the 10sec time scale and 1mm spatial scale, EEG and MEG on the 1msec and 1cm scales. Analysis techniques of experimental spatiotemporal data typically involve the identification of foci of activity such as single or multiple dipole localization (see [40] for an overview). More sophisticated techniques emphasize the pattern approach which aims at the identification of distributed sources or activity patterns. These remain somewhat invariant during the time course and typically minimize a postulated norm such as the Gaussian variance (Principal Component Analysis or PCA)[10,25,29] or non-Gaussian statistical

independence (Independent Component Analysis or ICA)[33] of which the latter may also be derived from a Bayesian framework[28]. Signal Source Projection or SSP provides a decomposition into patterns of activity which are physiologically or anatomically meaningful, by these means, however, restricting the possible solution space to the experimenters expectations. Most ambitious techniques wish not only to decompose the spatiotemporal dynamics into meaningful patterns, but also identify equations which govern the dynamics of these patterns [3,4,18,30,31,39]. Unfortunately, the successful application of these techniques has been typically limited to special cases in which the majority of the observed dynamics has already been well understood [18]. Spatiotemporal activity propagation of electro- and magnetoencephalographic signals has been represented by discretely coupled oscillator models (see chapter on source modeling in [40]) representing dipole sources. Spatially and temporally continuous models, so-called neural fields, were formulated by Wilson-Cowan [41,42], Nunez [35] and Amari[1] in the 70s. With improving imaging techniques and the development of MEG these types of models experienced a renaissance [8,19,32,37,43]. These models are typically based on coupled neural ensembles in a spatially continuous representation using integral equations involving a time delay via propagation. Jirsa & Haken [19] generalized and unified the earlier models by Wilson-Cowan [41,42] and Nunez [35] and demonstrated that they describe the same system. The modeling on these different levels of organization has been phenomenological, i.e. only partially taking into account the specific neurobiological nature of the measured signal and its underlying mechanism of generation. Each level of description has been tackled separately, never in unison with other fields of research, and typically applying strong simplifications. For example, Steyn-Ross et al.[38] explain a hysteresis phenomenon called 'biphasic response' in the clinical human EEG during anesthesia. Their underlying neural model is based upon Liley's work [32] using a spatially uniform activity distribution in one dimension with a connectivity distribution which falls off exponentially, independent of the cortical location. Similarly Jirsa et al. [21] also applied a one-dimensional model allowing, however, for varying spatial structure in activity distributions. Here, by applying the neural field equations to a bimanual coordination situation, they predicted the spatiotemporal dynamics observed in the MEG and confirmed these experimentally. A set of equations, governing human bimanual coordination [13] and known in the literature since 1985, was derived from these neural field equations. This connection between spatiotemporal brain dynamics to behavioral dynamics has become possible through the notion of functional units [19,21,11] serving as interfaces between neural and behavioral signals. Despite these successes, the simplifications made in these approaches do not take into consideration a more detailed physiological and anatomical interpretation of the identified mechanisms, e.g. how an active area may be identified when a spatially uniform activity distribution is assumed [38], resulting in an effectively zero-dimensional, thus point like model and hence brain.

In the present paper we develop a framework which overcomes these simplifications and allows a quantitative comparison between experimental data and

theoretical modeling. The neural model used here is based on Jirsa & Haken [19] which allows the connection to the behavioral dynamics through the concept of a functional input or output unit [11]. We form a synthesis of methodologies in order to systematically relate scales of organization from neural ensembles through EEG and MEG to behavioral dynamics (for strategic aspects of our approach, see the trilogy [26]). The conceptual steps are the following: We define a spatiotemporal neural field dynamics on a spherical geometry. This dynamics is mapped under the constraint of area preservation onto the folded cortical hemisphere. Here the propagation of neural activity generates the forward solutions of EEG and MEG under the spatial constraint of the skull and its return currents. For the simplest cortical architecture, we choose the experimental condition of an induced stimulus on the cortical surface and map the neural field dynamics on the different levels of organization: 1. cortex on a sphere; 2. unfolded cortex; 3. folded cortex; and 4. folded cortex in the skull generating EEG and MEG.

Our paper is organized as follows: First, we review the neural field dynamics of Jirsa & Haken, its physiological and anatomical basis and its connection to behavioral observations. Second, we elaborate the methodologies involved in traversing scales of organization from the level of neural ensemble to EEG and MEG. Third, we discuss the example of neural field dynamics after an induced stimulus. Finally, we provide a discussion and an outlook to future work.

2 Methods

2.1 Neural Field Dynamics

A neural field theory describes wave propagation along a continuous sheet composed of excitatory and inhibitory neural ensembles [19]. The first principles are based on conversion operations relating the local rates of action potentials (pulses) and dendritic currents (waves)[9]. When averaged over the ensemble, their relation follows a sigmoidal nonlinearity. Here, the main variable, the neural field, is the ensemble average of dendritic currents $\psi(x, t)$ generated at location x and time t . Action potentials travelling along axons with a velocity v may cause substantial time delays via propagation and are incorporated into the model. The distribution of the intracortical fibers, and thus the local connectivity, is homogeneous [2], whereas the distribution of the corticocortical fibers is not (estimates are that forty percent of all possible corticocortical connections are realized for the visual areas in the primate cerebral cortex [7]). For these reasons an inhomogeneous interareal connectivity has to be allowed resulting in a translationally variant connectivity function $f(x, X) \neq f(x - X)$. External input $p_j(x, t)$ is realized such that afferent fibers make synaptic connections. Then the neural field dynamics may be written as

$$\psi(x, t) = \int_{\Gamma} dX f(x, X) \cdot S\left[\psi(X, t - \frac{|x - X|}{v}) + \sum_j p_j(X, t - \frac{|x - X|}{v})\right], \quad (1)$$

where Γ represents the closed two-dimensional surface. Similar neural field systems of Jirsa-Haken type may be derived as special cases such as the Wilson-Cowan model [41,42] in terms of pulse activities and the Nunez model [35,36] in terms of wave activities. Both models may be mapped onto each other by applying known conversion operations [19]. The neural field equation (1) can be transformed into a partial differential equation for a homogeneous connectivity function $f(x, X) = f(|x - X|)$ such as $e^{-|x-X|/\sigma}$. Then the nonlinear partial differential equation reads in one dimension

$$\ddot{\psi} + (\omega_0^2 - v^2 \Delta) \psi + 2\omega_0 \dot{\psi} = (\omega_0^2 + \omega_0 \frac{\partial}{\partial t}) \cdot S[\psi(x, t) + p(x, t)] \quad (2)$$

where $\omega_0 = v/\sigma$. In case of a general connectivity function, an integral representation has to be maintained.

Functional units represent interfaces between the neocortex and non-cortical (input and output) signals and include subcortical structures such as the projections of the cerebellum on the cortex or specific functional areas such as the motor cortex. Until now the spatial localizations of functional units have been identified with the spatial structure generated by time dependent input signals, open to observation in the EEG/MEG (e.g. see [27]). In the case of a finger movement this spatial structure corresponds to a dipolar mode in the EEG/MEG located over the contralateral motor cortex. Anatomically these areas are obviously defined via their afferent and efferent fibers connecting to the cortical sheet. As such we will treat these in the spirit of this paper, a realistic treatment of brain signals, architecture and its resulting EEG/MEG. We define the j -th functional input unit $p_j(x, t)$ (see [11] for a detailed treatment) by its location $\beta_j(x)$ on the folded cortical sheet and a time dependent peripheral signal $r_j(t)$ (such as a finger movement)

$$p_j(x, t) = \beta_j(x) \int_{t_0}^t f(t - \tau) N(r_j(\tau)) d\tau \quad (3)$$

where t_0 is the initial time point, $f(t - \tau)$ a convolution and N a nonlinear function, the latter both to be determined from experimental data as shown in [11]. There, a read-out procedure of EEG/MEG has been developed such that finger movements may be reconstructed directly from encephalographic data. Equivalently, the read-out procedure may be viewed as a rule for how neural currents drive the finger movement represented as an oscillator. This idea served as the basis for connecting brain and behavioral dynamics in [21] and allowed the derivation of the phenomenological behavioral HKB equations from neural fields. Along the same lines a functional output unit may be constructed,

$$\bar{\psi}_j(t) = \int_{\Gamma} dx \beta_j(x) \psi(x, t), \quad (4)$$

where $\beta_j(x)$ defines the spatial location of the output unit in the cortical sheet and $\bar{\psi}_j(t)$ is the signal sent to the periphery, e.g. driving finger movements[11].

2.2 Neural Field Dynamics on a Sphere

The neural field equation (1) is defined in two dimensions with spherical boundary conditions. For a homogeneous, exponentially decaying connectivity function the corresponding partial differential equation may be determined:

$$\left(\frac{\partial^2}{\partial t^2} + 2\omega\frac{\partial}{\partial t} + \omega_0^2 - v^2\Delta\right)^{3/2}\psi = (\omega_0^3 + \omega_0^2\frac{\partial}{\partial t}) \cdot S[\psi(x,t) + p(x,t)] \quad (5)$$

The details of the differential operators on the lhs of (5) depend on the spatial decay of the connectivity. However, these details are not significant for large scale pattern formation as shown by Haken [14]. Each cortical hemisphere is represented in a spherical geometry and its dynamics is defined by (1), or (5) respectively. The two spheres interact by two means: through calossal pathways connecting the two spheres and through afferent fibers (crossing and non-crossing) from the periphery. Subcortical regions such as the brainstem are not included. Should heterogeneous fiber pathways be included also, then the integral representation given by (1) is used and two types of pathways distinguished: 1. The calossal fiber system from one sphere to another is treated in a manner equivalent to peripheral afferents. 2. Other heterogeneous pathways are included in the connectivity function $f(x, X)$. Note that heterogeneous pathways contribute strongly to the dynamics on all scales of organization; even local changes of connectivity have recently been shown to result in a major reorganization of brain activity [22,23].

2.3 Unfolding of the Cortical Sheet and Its Spherical Representation

In order to equate the distribution of neural fields with actual cortical structure a mapping between the spherical surface and the cortical surface is required. Several steps are undertaken to complete this mapping. All of the described procedures were performed using the Freesurfer software package developed by Dale and colleagues [5,6]. The first step is the segmentation of the brain structure and the definition of the gray-white matter boundary within each hemisphere. This step allows for the description of the cortical surface by a mesh defined by a set of vertices and polygons. The second step involves the inflation of the cortical surface to produce a closed surface that has minimal folding but also minimizes any distortion in the relative location between cortical locations (see middle of figure 1). This step eliminates the difficulty of visualizing cortical activity within sulci. The final step is to transform this shape onto a spherical representation while maintaining as much of the spatial relation as possible by preserving the metric properties of the surface while minimizing the local curvature. With this procedure, any point on the folded cortex can be addressed using any number of coordinate systems via its isometric location on the neural sphere. Both transformations, forward and backward, are well defined and their product yields the identity. Figure 1 gives an impression of this process by showing the three surfaces with again the curvature of the gray-white matter boundary color coded in red and blue and a spherical coordinate grid in green with the line of zero

longitude in white. The resulting meshes are extremely dense typically involving on the order of 150,000 vertices for the representation of a single hemisphere. For the purpose of computational frugality we decimated this tessellation to a more manageable number of vertices and corresponding polygons, 4512 and 9022 respectively.

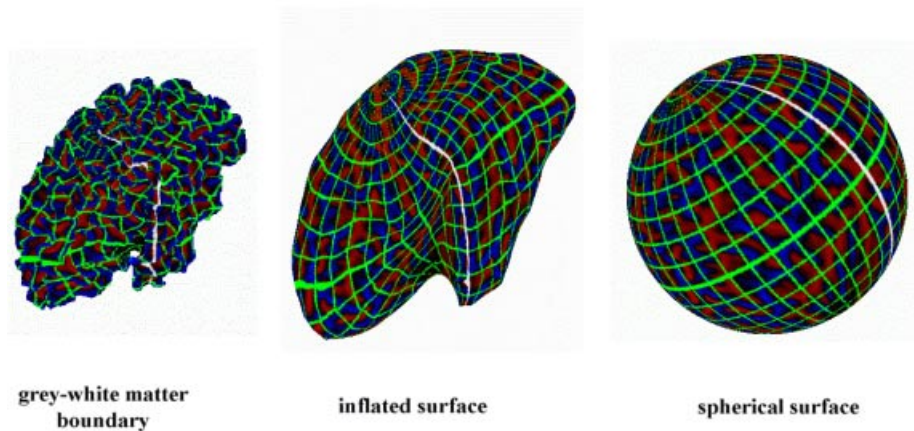


Fig. 1. Inflating the surface representing the gray-white matter boundary and mapping onto a sphere. From right to left the sequence shows how a spherical coordinate grid gets folded into the fissures.

2.4 Representation of Neural Fields on the Folded Cortex

In the previous section we described how each hemisphere was expanded and warped onto a sphere. As a result of this transformation, each sampled vertex on the folded cortical surface has a corresponding vertex located on the surface of a sphere. In addition to this one-to-one mapping between the vertices defining both the surface of the cortex and a sphere, the connectivity of the polygons (i.e. how the vertices are connected) remains constant across this transformation. As a result, a description of activity on the surface of the spherical hemisphere is automatically mapped onto the surface of the cortical representation. The task, therefore, simplifies the mapping of the activity onto the surface of an irregularly sampled sphere. This is a simple matter because the neural field is continuous across the sphere on which it is generated and therefore can be sampled at any arbitrary point. The mesh vertices of the cortical sphere are easily converted to spherical coordinates and the value at the corresponding location of the neural field sphere is assigned. For graphical presentation, the field distribution over

the cortical surface can be represented as a set of color values scaled between the maximum and minimum field strength. Changes in this color representation over time then give a temporal depiction of how the field dynamics unfold on the actual cortical surface. However, in order to calculate the forward solution using these current densities we need the addition of information about the direction of current flow at each vertex location and each point in time.

The generation of local field potentials within the cortex is dominated by activity in ensembles of pyramidal cells, which are oriented perpendicular to the cortical surface. It is possible therefore to model the direction of instantaneous current flow in a small cortical region as a normal vector on the mesh surface. The orientation of the vector gives the direction of current flow and the length of the vector gives the current strength. For the purpose of mapping neural activations onto the representation of the cortical surface a vector oriented normal to the polygon surface was computed for each mesh vertex. These vectors were then normalized to a length of one and scaled by the amount of neural activation at each time point. Because the direction of current flow is given by the orientation of the cellular generators, orientation of these vectors does not change over time (see following section 2.5 for details). Instantaneous current flow is always represented by vectors oriented orthogonal to the cortical surface while the propagation of current flow across the cortical surface is modelled as changes in the absolute and relative strengths of these vectors over time.

2.5 Forward EEG and MEG from the Neural Field Dynamics

At this stage we have a representation of the current distribution in three-dimensional space $x \in \mathcal{R}^3$ and its evolution over time t . To make a comparison with experimental data the forward solutions of the scalar electric potential $V(x)$ on the skull surface and of the magnetic field vector $\mathbf{B}(x)$ at the detector locations have to be calculated. Here it is useful to divide the current density vector $\mathbf{J}(x)$ produced by neural activity into two components. The volume or return current density, $\mathbf{J}^v(x) = \sigma(x)\mathbf{E}(x)$, is passive and results from the macroscopic electric fields $\mathbf{E}(x)$ acting on the charge carriers in the conducting medium with the macroscopic conductivity $\sigma(x)$. The primary current density is the site of the sources of brain activity and is approximately identical to the neural field $\psi(x, t)$, because, although the conversion of chemical gradients is due to diffusion, the primary currents are determined largely by the cellular-level details of conductivity. In particular, cell membranes, being good electrical insulators, guide the flow of both intracellular and extracellular currents and thus result in a current flow perpendicular to the cortical surface due to the perpendicular alignment and elongated shape of pyramidal neurons. In the quasistatic approximation of the Maxwell equations, the electric field becomes $\mathbf{E} = -\nabla V$ where ∇ is the Nabla-operator $(\dots \partial/\partial x \dots)^T$. The current density \mathbf{J} is

$$\mathbf{J}(x) = \psi(x, t)\mathbf{n}(x) + \sigma(x)\mathbf{E}(x) = \psi(x, t)\mathbf{n}(x) - \sigma(x)\nabla V(x) \quad (6)$$

where $\mathbf{n}(x)$ is the cortical surface normal vector at location x .

The forward problem of the EEG and MEG is the calculation of the electric potential $V(x)$ on the skull and the magnetic field $\mathbf{B}(x)$ outside the head from a given primary current distribution $\psi(x, t)\mathbf{n}(x)$. The sources of the electric and magnetic fields are both, primary and return currents. The situation is complicated even more by the fact that the present conductivities such as the brain tissue and the skull differ by the order of 100. Following the lines of Hämäläinen et al. [15,16] and using the Ampère-Laplace law, the forward MEG solution is obtained by the volume integral

$$\mathbf{B}(x) = \frac{\mu_0}{4\pi} \int (\psi(X, t)\mathbf{n}(X) + V(X)\nabla'\sigma(X)) \times \frac{X}{|X|^3} dv' \tag{7}$$

where dv' is the volume element, ∇' the Nabla-operator with respect to X and μ_0 the magnetic vacuum permeability. The forward EEG solution is given by the boundary problem

$$\nabla \cdot (\sigma(x)\nabla V(x)) = \nabla \cdot (\psi(x, t)\mathbf{n}(x)) \tag{8}$$

which is to be solved numerically for an arbitrary head shape, typically using boundary element techniques as presented in [15,16]. In particular, these authors showed that for the computation of neuromagnetic and neuroelectric fields arising from cortical sources, it is sufficient to replace the skull by a perfect insulator, and, therefore, to model the head as a bounded brain-shaped homogeneous conductor. Three surfaces S_1, S_2, S_3 have to be considered at the scalp-air, the skull-scalp, and the skull-brain interface, respectively, whereas the latter provides the major contribution to the return currents. The three-dimensional geometry of these surfaces may be obtained from MRI scans.

3 Results

To illustrate the simultaneously ongoing dynamics on the different levels of organization we choose a simple example of induced wave propagation along the cortical sheet. The connectivity is spatially homogeneous and has an exponential fall-off. Only one functional unit, the stimulus input, is defined just posterior to the central fissure, otherwise the neural sheet is completely homogeneous and isotropic. For visualization purposes, only one hemisphere is shown in the following.

At time $t = 0$ a stimulus signal $r(t)$ is sent to the cortical sheet through afferent fibers via synaptic connections defined by $\beta(x - x_0) = e^{-|x-x_0|}$. The time course $r(t)$ is an exponential increase until $t=160\text{ms}$, then followed by an exponential decrease and is plotted on the bottom of figure 2. The stimulus excites the neural sheet at site A , $x = x_0$, and initiates wave propagation by means of a circular traveling wave front undergoing attenuation in space and in time. The time courses of the neural ensembles at site A and site B , which is more distant to the stimulus site, are shown. For several selected time points the spatiotemporal activity patterns on the sphere are plotted in the top row

of figure 2. Here and in the following the color code represents -MAX to MAX as black goes to white. In the rows below, the same neural activity patterns are represented on the unfolded cortex and on the folded cortex for the same time points after being mapped from the spherical representation following sections 2.3 and 2.4.

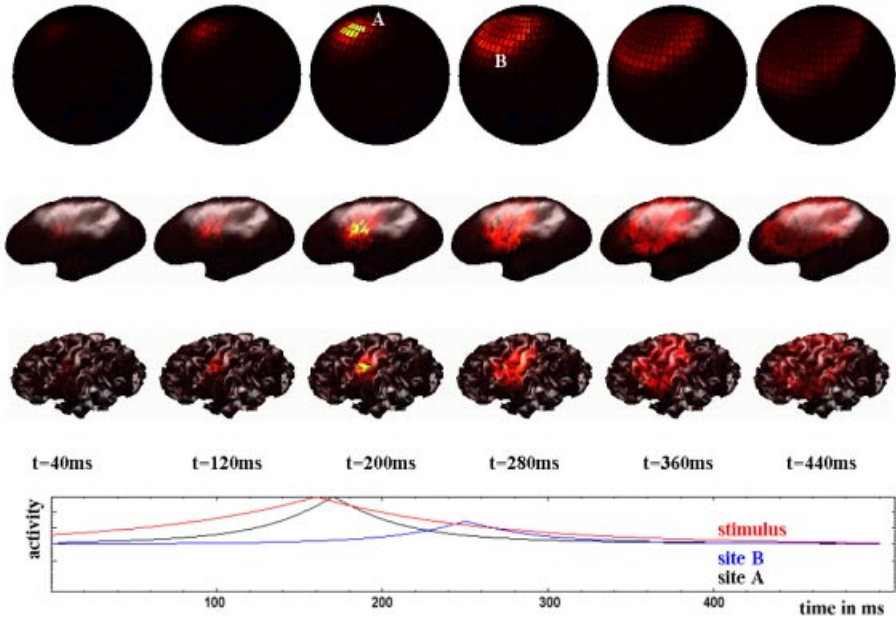


Fig. 2. The neural fields evoked by a transient stimuli distributed on the sphere (top row), inflated cortex (second row) and folded cortex (third row) for 6 separate time points. The bottom panel shows the time course of the stimulus (red line) and the activation pattern for two individual sites on the spherical surface.

For purposes of calculation of the forward EEG and MEG solutions, we use a single layer head model (skull-brain) as defined in 2.5 and a spherical head shape. The three-dimensional current distribution is defined on the folded cortical surface located within the skull as illustrated on the bottom in figure 3 (upper skull surface is not shown). The color coding on the cortical surface reflects the local curvature at the vertices with blue and red indicating convex and concave curvature, respectively. Note that the cerebellum is not part of these surfaces and has been removed. Adjacent is plotted the three cross sections of the voxel distributions showing the neural activity pattern color coded for $t=200\text{ms}$. The EEG and MEG detectors are placed directly on the spherical skull surface, infinitely close to each other. For the MEG we assume radial gradiometers measuring the

radial component of the magnetic field \mathbf{B} . We calculate the forward solutions of the EEG and MEG measured by these detectors following (7),(8) and plot the resulting EEG (top row) and MEG (second row) patterns for the selected times. Note that the visualization is in the spherical system, the nose pointing to the left, basically resembling the perspective shown in the picture on the bottom left of figure 3. In both patterns, EEG and MEG, a dipolar structure emerges with a maximum activity at around 280ms for the EEG and two maxima for MEG at around 200ms and 360ms. From figure 2 it is clear that the neural current distribution is damped and flattens out as time evolves. However, the propagation of the neural wave front along the cortical surface is such that the neuromagnetic forward solution not only undergoes a spatial reorganization from 360ms to 440ms, but also a temporal organization which does not map trivially on the neural field activity.

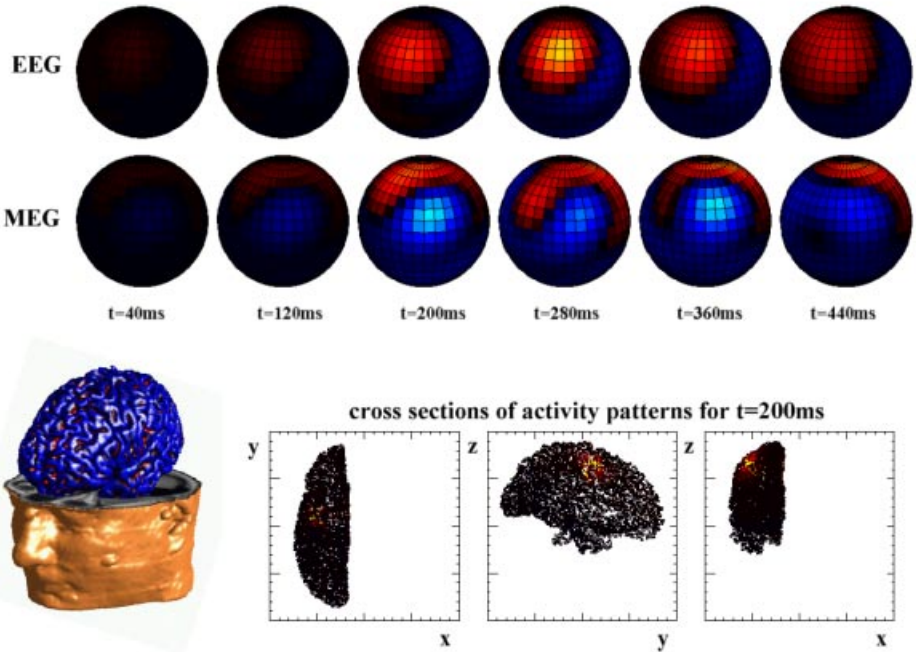


Fig. 3. The EEG (top row) and MEG (second row) forward solutions calculated at the same 6 time points as shown in figure2. The activation patterns are plotted on a spherical head model used in the forward calculation (10 cm diameter). The spherical head model is oriented such that the nose is to the left of the page and the left side of the head is facing the reader. The location of the left cortical hemisphere used here is given within both the head of the subject (bottom left) and within the spherical model of the head (three views on the bottom right).

Here we have presented the conceptual and methodological framework for the development of a theoretical model of human brain function and behavior that operates at multiple levels of description. Interconnected neural ensembles with homogeneous connection represent a neural level, while a network or systems level is defined by the interaction between heterogeneously connected cortical regions. An even broader level is defined by the computation of the spatiotemporal dynamics of EEG and MEG generated by the model and the connection of these data to behavior. For demonstration purposes we have presented the simplest of examples, the propagation of activation at a single cortical site resulting from a transient input. Even without the incorporation of heterogeneous connections however, it is evident that a simple stimulus produces elaborate dynamics on the folded cortical surface that translate into time varying patterns in the EEG and MEG which would not be predicted by inverse solution techniques. At the same time the distributions described on the spherical head model are still consistent with what has been described in the literature using, for example, simple tactile stimulation or the generation of a simple self paced motor response [27,11].

Elaboration of this model will proceed not only at the neural level or even at the macroscopic EEG and MEG level, but also at the behavioral level. That is, the goal is not to simply reproduce observed spatiotemporal data sets by activating specific cortical regions, but to describe and explain behavioral phenomenon via the dynamics within and between interconnected cortical and sub-cortical areas. For instance, several properties of spatiotemporal cortical activity, as measured by EEG and MEG, have been shown to accompany behavioral transitions in coordinative states [12,17,25,34]. At present the link between these specific neural events and the resulting behavioral dynamics is unknown in general, except for special cases such as rhythmic coordination [11]. This is despite the fact that much is known about the neural structures involved in producing coordinated movements and how they are connected to one another. Similar phenomena have been investigated using a one dimensional model of neural field dynamics [19,18,21] and it is expected that the application of the current model in its present and future forms will continue to provide insight into these and other behavioral phenomena.

It should be emphasized that the model presented here is not a form of inverse solution that defines putative neural sources associated with a particular experimental design and set of data. The mapping of neural fields onto the folded cortex and the calculation of the forward solution are performed for the purpose of connecting cortical dynamics with neurophysiological and behavioral results. The data that result from the model are purely a function of the dynamics of the defined system, and are not constrained by observed data. It is possible therefore, to define a single dynamical model that can explain several different phenomena that may arise by changing input/output patterns. That is, the same model may generate qualitatively different data given different types of inputs or different output constraints. Such a system may also explain changes in perceptual phenomena despite the constancy of a stimulus (so-called bistable

stimuli). This model then represents a powerful tool capable of representing the complexities that define human brain and behavior.

Acknowledgements

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