Chapter 13
Commentary by Zoltán Somogyvári and Péter Érdi

Forward and Backward Modeling: From Single Cells to Neural Population and Back

Zoltán Somogyvári and Péter Érdi

Abstract Some aspects of forward and backward neural modeling are discussed, showing, that the neural mass models may provide a "golden midway" between the detailed conductance based neuron models and the oversimplified models, dealing with the input–output transformations only. Our analysis combines historical perspectives and recent developments concerning neural mass models as a third option for modeling large neural populations and inclusion of detailed anatomical data into them. The current source density analysis and the geometrical assumption behind the different methods, as an inverse modeling tool for determination of the sources of the local field potential is discussed, with special attention to the recent results about source localization on single neurons. These new applications may pave the way to the emergence of a new field of micro-electric imaging.

13.1 Modeling Population of Neurons: The Third Option

Structure-based bottom-up modeling has two extreme alternatives, namely **multi-compartmental** simulations, and simulation of **networks** composed of simple elements. There is an obvious trade-off between these two modeling strategies. The first method is appropriate to describe the electrogenesis and spatiotemporal propaga-

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tion of the action potential in single cells, and in small and moderately large networks based on data on detailed morphology and kinetics of voltage- and calcium-dependent ion channels. The mathematical framework is the celebrated Hodgkin–Huxley model [19] supplemented with the cable theory [34, 35]. The construction of neural simulation softwares such as NEURON [17, 18], and GENESIS [5] contributed very much to make the emerging field of computational neuroscience is able to make realistic bottom up neural simulations. The second approach grew up from the combination of the McCulloch–Pitt neuron models and the of the Hebbian learning rule, and offers a computationally efficient method for simulating large network of neurons where the details of single cell properties are neglected. A classical example of using two-level neural network models by combining activity and synaptic dynamics as a model of generating ordered neural pattern by a self-organizing algorithm is [47], and a newer one for invariant pattern recognitions in the same spirit [4].

As concerns single cell modeling, there is a series of cell models with different level of abstraction. While multi-compartmental models take into account the spatial structure of a neuron, neural network techniques are generally based on integrate-and-fire models. The latter is a spatially homogeneous, spike-generating device. For a review of 'spiking neurons' see [13]. As is well known, neural network theory, incorporating biologically non-plausible learning rules became a celebrated subclass of machine learning discipline called *artificial neural network*. Modeling population of neurons emerged as a compromise between "too microscopic" and "too macroscopic" descriptions [10].

13.2 Mesoscopic Neurodynamics

13.2.1 Statistical Neurodynamics: Historical Remarks

There is a long tradition to try to connect the 'microscopic' single cell behavior to the global 'macrostate' of the nervous system analogously to the procedures applied in statistical physics. Global brain dynamics is handled by using continuous (neural field) description instead of the networks of discrete nerve cells. Both deterministic, field-theoretic [1, 15, 37, 46] and more statistical approaches have been developed. [10] introduced a modular and therefore hierarchical framework of neural field models, as the series of K models from K0 to KIII. This series of more and more complex neural mass models has been reached the level of behavioral analysis with the KIII sets. Later, [25] extended the K sets theory to the next (KIV) level to account for the interaction between cortical areas as well. One of us (PE) participated in the application of KIV system for hippocampus-related problems [26, 27].

This way, the otherwise pure statistical handling of neural populations gains new anatomical details.

Francesco Ventriglia constructed a neural **kinetic theory** of large-scale brain activities that he presented in a series of somewhat overlooked papers [41–44]. His statistical theory is based on two entities: spatially fixed neurons and spatially propagating impulses. Neurons might be excitatory or inhibitory and their states are characterized by their subthreshold membrane potential or inner excitation, threshold level for firing, a resting level of inactivity state, maximum hyperpolarization level, absolute refractoriness period and a synaptic delay time. Under some conditions they emit impulses. Neurons are grouped in populations, state of the neurons in the population is described by the population's probability density function. Impulses move freely in space (in the numerical implementation some rule should be defined due to treat the effects due to spatial discretization), and might be absorbed by neurons chaining their inner excitation. Impulses are distributed in velocity–space according to the corresponding probability density function.

We extended [2, 16] this theory by using **diffusion theory** in two different senses. Both the dynamical behavior of neurons in their state-space and the movement of spikes in the physical space have been considered as diffusion processes. The state-space in the model consists of the two-dimensional space coordinate $\mathbf{r}$ for both neurons and spikes, a membrane potential coordinate u for all types of neurons, and an intracellular calcium-concentration coordinate χ for pyramidal neurons only. Both cell types, the inhibitory and excitatory ones are described by ionic conductances specific to neuronal type. Instead of fixed firing threshold a soft firing threshold is realized by voltage-dependent firing probability. Absorbed spikes induce time-dependent postsynaptic conductance change in neurons, expressed by the alpha-function.

We also realized in Budapest the importance of the existence of the database on connectivity in the cat cerebral cortex published in 1995, [36] and the necessity to include time delays. While our simulations of the activity propagation in hippocampus slices was based on the usual statistical assumptions, the first simulations by incorporating real connectivity data was done (well, with some time delay) by Tamás Kiss [23]. We (he) also took into account the axonal time delay. To calculate the the synaptic current a new term $\varepsilon_s(\mathbf{r}, u, \chi, t)$ has been added:

$$\gamma_{s's} = \gamma_{s's}^{old} + \frac{\overline{\gamma'_{s's}}}{\tau'_{s's}} \int_0^\infty dt' \int_{\Omega(\mathbf{r}')} \kappa(\mathbf{r}, \mathbf{r}') \cdot a_{s's}(\mathbf{r}, t - t_d - t') \cdot t' \cdot \exp\left(1 - \frac{t'}{\tau'_{s's}}\right), \tag{13.1}$$

where the $\kappa(\mathbf{r}, \mathbf{r}')$ function determines the source and target cortical area between which information exchange occurs. Activity produced by the source population influences the target population after t_d time delay giving account of signal propagation delay in fibers.

The method and results were published in his master thesis written in Hungarian [23], (not necessarily the best marketing strategy). We made early not well-published

(it is our fault) studies also on the disconnection syndromes, and simulated what it is now called *connectopathy* [8].

Statistical neurodynamics has at least two different features, as statistical mechanics. First, in neurodynamics "mean-field" approach is not enough, we should see both global and local dynamics. Our model gave the possibility to simulate the statistical behavior of large neural populations, and synchronously to monitor the behavior of an average single cell. Second, both statistical and specific cortical connections exist, model frameworks should describe their combination. In the project described in our last paper in the topic [24] both features were incorporated. As it was already written in [9], p. 272: "I think, each research group has bedroom secrets. The story with our "*population model*" is ours, and I think I should not blab it out."

Viktor Jirsa [20] classified the **mesoscopic models** into the following categories:

- Infinite Propagation Speed,Arbitrary Connectivity
- Finite Propagation Speed,Arbitrary Connectivity
- Infinite Propagation Speed, Symmetric, and Translationally Invariant Connectivity
- Infinite Propagation Speed, Symmetric and Translationally Variant Connectivity
- Finite Propagation Speed, Symmetric, and Translationally Invariant Connectivity
- Finite Propagation Speed,Asymmetric and Translationally Variant Connectivity

A general framework for neural field models with local and global connections also with time delay was given by him [21]. This model framework became the scientific basis of the Virtual Brain Project [45].

13.3 Forward and Inverse Modeling of the Neuro-Electric Phenomena

As we have seen in the previous paragraphs, that a strong branch of the modeling tradition in the neuroscience follows the bottom-up approach on the tracks of Hodgkin and Huxley. Starting from the biophysical mechanisms of the ion channels one can built neuron models on arbitrary levels of complexity. Then, connecting the neurons into networks, implementing connections from the basic synaptic dynamics up to the advanced activity dependent learning methods, one can study the emerging network dynamics. In the next step, as we will see here, solving the forward problem of the Poisson-equation, an artificial LFP can be synthesized and compared to the observed phenomena during electrophysiological measurements.

While the role of the modeling is less obvious in the top-down approach, it will be shown in this section, that models and modeling have an indispensable role, when we want to understand the measured electric signals by decomposing them into their sources. Here the model means a set of constrains and prior assumptions about the sources which implicitly or explicitly adopted by each method, to find a unique solution to source determination problem.

13.3.1 Micro-Electric Imaging

An average neuron in the cortex receives 10–15 thousand synapses from other neurons. While many fine details are known about the properties of individual synapses, and there is a progress on understanding brain connectivity [40], the spatio-temporal transmembrane current patterns, resulting from the summation of a huge number of individual synaptic inputs on a whole neuron, are almost entirely unknown. The main reason for this large gap in our knowledge is the lack of a proper technique for measuring spatio-temporal inputs patterns on single neurons in behaving animals. While the output of a neuron is well recognizable in the extracellular potential measurements in the form of action potentials, the input that evoked the observed spike is unknown. Without knowing the input, deciphering the input–output transformation implemented by an individual neuron is hopeless.

The steadily improving **optical imaging** techniques provide extremely good spatial resolution, but they still have not reached the speed, signal-to-noise ratio, sampling frequency, aperture and miniaturization properties necessary to record action potentials and synaptic input patterns on whole neurons in behaving animals.

On the other hand, the number of channels, together with the spatial resolution, have dramatically increased recently in the widely used multi-electrode arrays (MEA), and further improvements are expected [3, 6, 22]. This relatively low cost technique is applicable to freely behaving animals as well. Traditionally, only the spike timings are used from these extracellular (EC) potential recordings, but recent improvements significantly increased the spatial information content of these measurements. Thus, new techniques of data analysis are needed to exploit this new information.

We conclude that the rapid development of MEA techniques and the set of new analysis methods, directly designed to exploit the spatial information content of MEA recordings, may help to create a new emerging field to be called **micro-electric imaging**. Similar to the macroscopic imaging techniques, the different tasks of this field are: forward modeling, source reconstruction, anatomical area and layer determination, correlation and causality analysis while a specific task on this microscopic field is membrane potential and synaptic current reconstruction.

During the last few decades, a large variety of mathematical source reconstruction algorithms or imaging techniques have been developed for macroscopic neural electro-magnetic measurements, such as EEG and MEG. For a review, see [14]. However, on micro scales, only the traditional current source density (CSD) method has served the aim of identifying the neural transmembrane sources underlying the observed EC potential [30, 31]. The traditional CSD works well if the full 3-dimensional potential distribution is known with the spatial resolution comparable to the size of the sources. Definitely, current sources on single neurons cannot be analyzed this way, since 3D data cannot be collected by electrode systems without large tissue damage. Lacking this full 3D data, the CSD analysis based on 2D and 1D MEA measurements intrinsically requires the adoption of assumptions about homogeneity of the source density in the unknown dimensions. This homogeneity assumption can

be a good approximation in the case of large population activities, but it is certainly not valid for single cell sources. Thus, we can conclude, that the (implicit) source model of the traditional 1D CSD analysis is an infinite homogeneous laminar source.

13.3.2 Source Reconstruction on Single Neurons

An alternative approach for CSD estimation is based on the inverse of the forward solution. To our knowledge, the first inverse CSD method was developed and applied to LFP data of olfactory bulb by Walter J. Freeman in 1980 [11, 12]. The inverse method was not applied to LFP data since, till it was rediscovered in recent years and applied to extracellular action potentials by [38] and local field potentials by [32].

The first inverse method for the estimation of cell-electrode distance and the reconstruction of the CSD on single neurons was introduced in our own lab [38] in 2005. The source model applied here called counter current model was a line-source, parallel to the electrode and consists of one high negative (sink) current peak on a smooth background of positive counter currents (sources). This model is valid only until the negative peak of the extracellular spike, so this single cell CSD method is able to calculate the CSD only at the peak of the action potential. Since then, numerous inverse CSD methods have been developed in many other research groups as well. Pettersen et al. [32] developed inverse CSD solutions for LFP, generated by a cortical column. The corresponding source model consists of homogeneous discs, whose laminar distribution was described either as sum of thin discs or a spline interpolated continuous distribution. Later, Daniel Wójcik and his group used kernel methods for 1, 2 and 3D inverse solutions [28, 29, 33]. The source models here consist of 3D Gaussian blobs and ensures a smooth inverse solution.

The recent sCSD method [39], built on the basis of the counter current model, is able to reconstruct the full **spatio-temporal CSD dynamics** of single neurons during the action potentials. By the sCSD method, the EC observability of back propagating action potentials in the basal dendrites of cortical neurons, the forward propagation preceding the action potential on the dendritic tree and the signs of the Ranvier-nodes has been demonstrated for the first time (Fig. 13.1).

13.3.3 Anatomical Area and Layer Determination: Micro-Electroanatomy

Proper interpretation of single neuron CSD maps during in vivo application of MEAs requires precise identification of the anatomical structures, cortical and synaptic layers in which the EC potentials were recorded. Post-hoc histology can provide information on the position of the probes in the brain, but it would be advantageous if this information would be accessible during the experiment as well, and in some

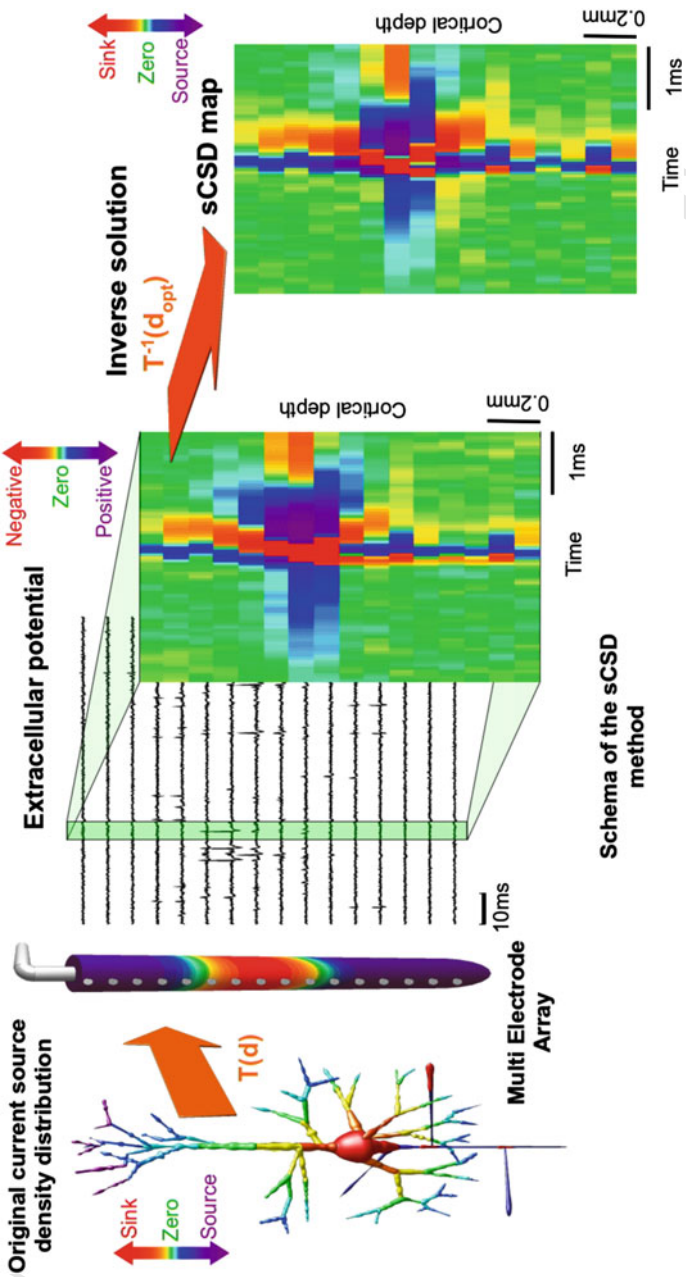

Fig. 13.1 The schema of the sCSD method: the *color-coded* current source density on the neuron determines the measured spatial potential pattern on the linear multi electrode array. This forward solution is expressed by the T(d) transfer matrix. The inverse solution, which we call sCSD method, starts from the measured EC potential of single neuron spikes. Then the application of the $T^{-1}(d)$ inverse transfer matrix yields the CSD distribution on the neuron. Modified from [39]

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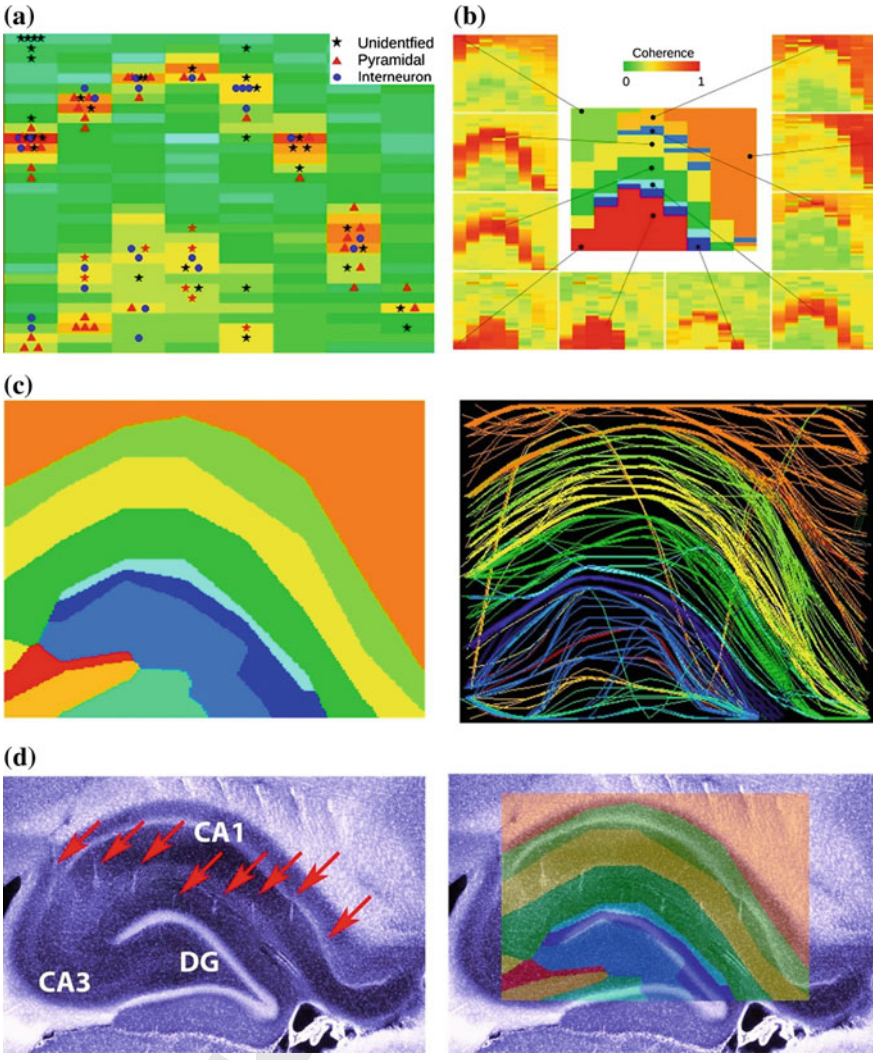

Fig. 13.2 Electroanatomy of the hippocampus. Somatic and synaptic layers are determined solely based on the recorded data. **a** Somatic layers were identified based on a high frequency (300 Hz) power map. **b** Synaptic layers were determined by coherence-based clustering. **c** The borders between layers and areas of the hippocampus is inferred by fusing the somatic map with the coherence-clusters. Our coherence-tracking algorithm visualizes the hippocampal anatomical structure clearly. **d** Comparison with histology. *Arrows* mark the paths of the 8 shanks of the electrode. From [3]

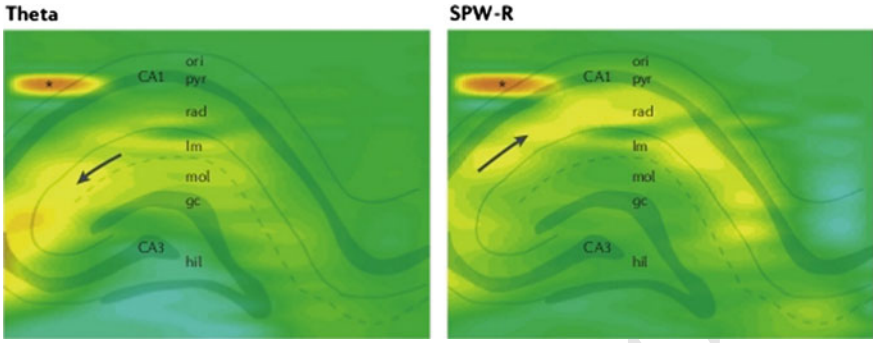

Fig. 13.3 Demonstration of different input patterns onto the same neuron. The same neuron (denoted by a *star*) is activated by different pathways and emits action potentials during theta and sharp-wave ripple oscillations. (Work of Z. Somogyvri and A. Bernyi, from [7], Fig. 6)

cases the post-hoc histology cannot be performed well. The methodology of micro-electroanatomy [3], which was able to determine and visualize anatomical structures and synaptic layers in the hippocampus and in the neocortex solely based on the recorded multi-channel LFP data was a recent attempt on that. This anatomical reconstruction serves as a good basis for investigation of different synaptic input pathways on the neurons (Fig. 13.2).

Our preliminary results, previewed in the Nature Reviews Neuroscience [7] have provided a new insight into hippocampal dynamics, showing that the same CA1 interneuron receives input on different pathways in different hippocampal states. More precisely, the input was found to be dominated by the entorhinal perforant path during theta oscillations, but the Schaffer-collateral input from CA3 was stronger during sharp-wave ripple (SPW-R) periods. Thus, we conclude, that new, high-channel-count MEA data, precise identification of synaptic layers and model-based source reconstruction technique make possible a systematic analysis of synaptic input patterns for different cell types in different subregions of the hippocampus (Fig. 13.3).

13.4 Conclusions

We reviewed some specific concepts, where density functions play important role and may provide novel approaches for inferring, modeling and understanding neural dynamics and functions. In the first section we have briefly reviewed the application of density functions in the neural mass models as a 'golden midway' between to too detailed microscopic and the too phenomenological macroscopic approaches. This historical point of view led us to the conclusion, that the anatomical knowledge on the brain connectivity structure should be included into the pure statistical treatment as well. Besides some early attempts for our own laboratory, we recognized a strong trend into this direction in the recent years.

On the other side, density functions have inevitable role in the inference of the neural currents from the extracellular potential measurements, known as current source density analysis. In the CSD analysis, the collective effect of the abundant number of individual synapses is described by an appropriate density function. We have shown, that the solution of this inverse problem depends on the geometrical and dynamical assumptions about the sources. Different CSD methods use different source models, defining their range of validity and applicability. Finally we showed, that a new and promising branch of CSD methods emerged as the density functions have been applied to single neurons, allowing the inference of input current source density patterns on single neurons.

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