Journal of Biological Physics **22:** 101–112, 1996.

Derivation of a Field Equation of Brain Activity

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(Received: 16 April 1996; accepted: 23 April 1996)

Abstract. We present a nonlinear field theory of the brain under realistic anatomical connectivity conditions describing the interaction between functional units within the brain. This macroscopic field theory is derived from the quasi-microscopic conversion properties of neural populations occurring at synapses and somas. Functional units are treated as inhomogeneities within a nonlinear neural tissue.

Key words: Brain dynamics, Neural ensembles, Nonlinear field theory, Partial differential equations, Synergetics

1. Introduction

The brain operates as an open complex physical system which exhibits spatio-temporal behavior. A necessary condition for this pattern-forming character of the brain is a nonlinear dynamics and a spatial interconnection. The functional behavior of the brain is encoded in these spatio-temporal structures and can be extracted from the dynamics of the macroscopic quantities measured by the EEG and MEG [10–12, 16]. According to synergetics [13–15] this extraction contains all the relevant information about the spatio-temporal behavior of the brain and has, in general, a small number of degrees of freedom. This idea has been formalized to the *order parameter concept* based on circular causality: the order parameters are determined and created by the cooperation of microscopic quantities, but at the same time the order parameters govern the qualitative behavior of the whole system. Based on this approach phenomenological models were set up in the past for different experiments in order to find evolution equations that describe the experimentally observed macroscopic dynamics [9, 10]. On the quasi-microscopic level, ensembles of neurons are gathered together in units, which tend to behave as single entities.

The present paper aims at bridging the gap between a quasi-microscopic and a macroscopic description. We define a mathematical description of the input–output behavior, the conversion operations, at the synapses and the somas of neurons in an ensemble. Here the idea of separation of time scales and spatial scales is utilized such that a spatio-temporal description is obtained relevant for the macroscopic level obtained from EEG and MEG measurements. This description is reduced to a one-variable field equation given as a non-linear partial differential equation. Here

the brain is considered as a nonlinear medium with specific dispersive properties. Functional units like the auditory cortex area are assumed to interact as inhomogeneities with this medium. The coupling between these inhomogeneities and the neural sheet is nonlinear and given by the field equation. The geometry of the brain, given by the dimension and the boundary conditions of the brain, is an open question and non-trivial. Fuchs et al. successfully used the geometry of a closed sphere in the case of EEG measurements of α-waves [11]. Nunez proposes two geometries: a closed sphere and a closed one-dimensional loop [2]. Here we use a one-dimensional description for reasons of simplicity. The expansion to higher dimensions is obvious.

2. Anatomical and Physiological Considerations

As is well known, the elementary unit of which the nervous system is composed is the neuron which is divided into three basic components [8]: the dendrites, the cell body and the axon. The dendrites act as the receptive side of the neuron and provide a large surface area for the synapses. There are mainly two kinds of synapses [6, 7]: Excitatory synapses release transmitters that, on contact with the postsynaptic membrane, create currents depolarizing the postsynaptic cell. Inhibitory cells release transmitters that tend to hyperpolarize the postsynaptic cell or to increase the conductance of the postsynaptic membrane to chloride, thereby diminishing the effects of the depolarizing currents generated by the excitatory synapses. It is believed in general that in the cortex, all the synapses that a given neuron makes release the same neurotransmitters (Dale's principle) [7]. Today, most investigators agree that for the analysis of cortical function, it is safe to assume that excitatory and inhibitory neurons can be categorized according to the types of transmitters they release at their synaptic endings. Here we want to deal with the two main cell categories: Pyramidal neurons and stellate neurons. Anatomically it is realized that the axons of pyramidal neurons are always involved with excitatory synapses and the axons of stellate neurons with inhibitory neurons. Thus we can assume that excitatory neurons only have excitatory synapses and inhibitory neurons only inhibitory synapses. In a simplified manner synapses can be viewed as small batteries which convert the inputs from other neurons by initiating electric currents on the dendrites which are spatially integrated at the cell body. By Kirchoff's law these currents are linearly summed up and cause a resulting current. If the resulting current at the cell body exceeds a certain threshold, it will be converted into a pulse train along the axon without attenuation. Pools of neurons in local neighborhoods tend to share activity and thus can be regarded as the quasi-microscopic entities that perform spatially coherent behavior. The EEG measures macroscopic quantities which mainly correspond to summed dendritic potentials [8] and the MEG measures macroscopic quantities mainly corresponding to summed dendritic currents [3]. The cortical neurons are connected via intracortical fibers over short distances which can be excitatory or inhibitory,

Table I.

Times scales	
Synaptic delay	1 msec
Neuronal refractory time	1 msec
Inhibitory delay due to propagation	1 msec
Membrane time constant	10 msec
Excitatory delay due to propagation	100 msec
Spatial scales	
Spatial range of intracortical fibers	0.1 cm
Spatial range of corticocortical fibers	10 cm

but also via corticocortical fibers through the white matter over long distances [7]. The latter are exclusively excitatory. The spatial range of the dendritic trees is comparable to the intracortical connection range [7].

The ranges of physiological parameters vary a lot dependent on the cortex areas and types of fibers considered. We emphasize that here we only want to give an impression of the relation of the parameter scales to each other. Detailed discussions of parameter ranges can be found in [3, 5–7]. Synaptic delays and refractory times are of the order 1 msec, the neuronal membrane constant is in the range of several msec [6]. Corticocortical propagation velocities have a wide range from 0.2 m/sec [5] up to 6–9 m/sec [2]. Here we will use 1 m/sec as an average propagation velocity. The lengths of corticocortical fibers range from about 1 cm to 20 cm [2] which yields a broad range of delays of 10–200 msec. In Table I we give a survey of the parameter scales on which our subsequent discussion will be based.

Single neurons have two main state variables [8]: dendritic potentials (wave amplitude), which correspond to the synaptic activities, and the axon pulse frequency. The conversion of pulse frequency to current amplitude occurs at synapses, the dendritic wave amplitude is converted to a pulse frequency at the somas. In ensembles of cortical neurons activity densities are defined over spatial distributions of neurons. Here the pulse-to-wave conversion at the synapses is constrained to a linear small-signal range, whereas the wave-to-pulse conversion shows a sigmoidal behavior [8]. These two conversion operations for ensembles are shown in Figure 1.

3. Derivation of a Field Theory of the Brain

We mathematically formalize the conversion operations at the synapses and the somas of neural ensembles and derive from these a nonlinear partial differential field equation describing the spatio-temporal behavior of brain activity.

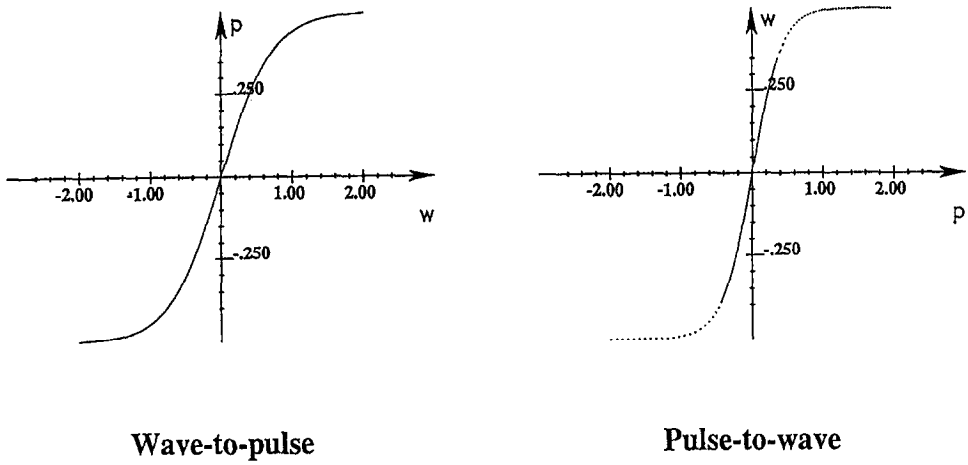

Figure 1. On the left, the wave-to-pulse conversion operation performed at the somas of neurons in an ensemble is shown. This conversion shows a sigmoidal behavior. On the right the same situation for the pulse-to-wave conversion performed at the synapses in a neuronal ensemble is shown. Here the conversion is constrained to a small signal range. The functional forms of these conversions presented here are only valid for neuronal ensembles and differ from the ones of single neurons.

In Section 2 we pointed out that there are two conversion operations in the neural tissue: the pulse-wave conversion at the synapses and the wave-pulse conversion at the somas. The term *pulse* describes action potentials and the term *wave* synaptic activities. Here we have a spatially distributed system consisting of four components: the two variables (wave and pulse) and the two converters (wave-pulse and pulse-wave). The variables pulse and wave are classified in two subvariables according to their excitatory or inhibitory character: excitatory pulse $E(\mathbf{x}, t)$ and inhibitory pulse $I(\mathbf{x}, t)$, excitatory wave $\psi_e(\mathbf{x}, t)$ and inhibitory wave $\psi_i(\mathbf{x}, t)$. We interprete these four quantities as deviations from a fixed physiological state and formalize them mathematically as

$$\begin{aligned} \psi_e(x,t) &= \int_\Gamma \mathrm{d}X f_e(x,X) H_e(x,X,t), \\ \psi_i(x,t) &= \int_\Gamma \mathrm{d}X f_i(x,X) H_i(x,X,t), \end{aligned} \tag{1}$$

$$\begin{aligned} E(x,t) &= \int_\Gamma \mathrm{d}X f_E(x,X) H_E(x,X,t), \\ I(x,t) &= \int_\Gamma \mathrm{d}X f_I(x,X) H_I(x,X,t). \end{aligned} \tag{2}$$

The functions $H_k(x, X, t)$ represent the output of a conversion operation and $f_k(x, X)$ the corresponding distribution function depending on the spatial connectivity. The considered surface area of the brain is denoted by Γ. In order to set up equations for the conversion output we make the following considerations (see Section 2):

- Excitatory neurons only have excitatory synapses, inhibitory neurons only inhibitory synapses.
- In ensembles of neurons the pulse-wave conversion at the synapses is linear, the wave-pulse conversion at the somas nonlinear and sigmoidal.
- The spatial distribution range of the dendrites and intracortical fibers is very short. Only the corticocortial connections cause a significant delay via propagation.
- External input is realized such that afferent fibers make synaptic connections.

These items lead to the following relations between conversion output and summed action potentials

$$H_e(x, X, t) = S\left(E\left(X, t - \frac{|x - X|}{v}\right)\right) \approx a_e E\left(X, t - \frac{|x - X|}{v}\right) \tag{3}$$

$$H_i(x, X, t) = S\left(I\left(X, t - \frac{|x - X|}{v}\right)\right) \approx a_i I\left(X, t - \frac{|x - X|}{v}\right) \tag{4}$$

and between conversion output and summed synaptic activities

$$\begin{aligned} H_E(x, X, t) \;=\; & S_e\left(\psi_e\left(X, t - \frac{|x - X|}{v}\right) - \psi_i\left(X, t - \frac{|x - X|}{v}\right) + \right. \\ & \left. + p_e\left(X, t - \frac{|x - X|}{v}\right)\right) \end{aligned} \tag{5}$$

$$\begin{aligned} H_I(x, X, t) \;=\; & S_i\left(\psi_e\left(X, t - \frac{|x - X|}{v}\right) - \psi_i\left(X, t - \frac{|x - X|}{v}\right) + \right. \\ & \left. + p_i\left(X, t - \frac{|x - X|}{v}\right)\right), \end{aligned} \tag{6}$$

where a_e and a_i are constant parameters, $p_j(X, t)$ external input to the neural sheet and S and S_j the sigmoid functions of a class j ensemble. The propagation velocity v is assumed to be fixed with a small variance. The distribution functions $f_E(x, X)$ and $f_I(x, X)$ are of short range and can be assumed to be δ-like. Inserting these into (2) we obtain

$$E(x,t) = \int_\Gamma \mathrm{d}X \delta(x-X) H_E(x,X,t)$$
$$= H_E(x,t) = S_e[\psi_e(x,t) - \psi_i(x,t) + p_e(x,t)] \tag{7}$$

$$I(x,t) = \int_\Gamma \mathrm{d}X \delta(x-X) H_I(x,X,t)$$
$$= H_I(x,t) = S_i[\psi_e(x,t) - \psi_i(x,t) + p_i(x,t)] \tag{8}$$

Replacing the variables $\psi_e(x,t), \psi_i(x,t)$ in (7), (8) according to (1) we obtain

$$E(x,t) = S_e \left[\int_\Gamma \mathrm{d}X f_e(x,X) H_e(x,X,t) - \right.$$
$$\left. - \int_\Gamma \mathrm{d}X f_i(x,X) H_i(x,X,t) + p_e(x,t) \right] \tag{9}$$

$$I(x,t) = S_i \left[\int_\Gamma \mathrm{d}X f_e(x,X) H_e(x,X,t) - \right.$$
$$\left. - \int_\Gamma \mathrm{d}X f_i(x,X) H_i(x,X,t) + p_i(x,t) \right]. \tag{10}$$

Inserting (3), (4) into (9), (10) the following retarded integral equations are obtained:

$$E(x,t) = S_e \left[\int_\Gamma \mathrm{d}X f_e(x,X) a_e E\left(X, t - \frac{|x-X|}{v}\right) - \right.$$
$$\left. - \int_\Gamma \mathrm{d}X f_i(x,X) a_i I\left(X, t - \frac{|x-X|}{v}\right) + p_e(x,t) \right]. \tag{11}$$

$$I(x,t) = S_i \left[\int_\Gamma \mathrm{d}X f_e(x,X) a_e E\left(X, t - \frac{|x-X|}{v}\right) - \right.$$
$$\left. - \int_\Gamma \mathrm{d}X f_i(x,X) a_i I\left(X, t - \frac{|x-X|}{v}\right) + p_i(x,t) \right]. \tag{12}$$

These equations describe the spatio-temporal behavior of summed action potentials in the brain and correspond to the phenomenological model by Wilson–Cowan [4] for the case that the time scale of the neural membrane is much smaller than the delay via propagation along corticocortical fibers.

In order to obtain the dynamics of synaptic activities we insert (3), (4) into (1) and obtain

$$\begin{aligned}\psi_e(x,t) &= \int_\Gamma \mathrm{d}X f_e(x,X) H_e(x,X,t) \\ &= a_e \int_\Gamma \mathrm{d}X f_e(x,X) E\left(X, t - \frac{|x-X|}{v}\right)\end{aligned} \tag{13}$$

$$\begin{aligned}\psi_i(x,t) &= \int_\Gamma \mathrm{d}X f_i(x,X) H_i(x,X,t) \\ &= a_i \int_\Gamma \mathrm{d}X f_i(x,X) I\left(X, t - \frac{|x-X|}{v}\right).\end{aligned} \tag{14}$$

Inserting (7) into (13) and (8) into (14) the system reads

$$\begin{aligned}\psi_e(x,t) = a_e \int_\Gamma \mathrm{d}X f_e(x,X) \cdot S_e \Big[&\psi_e\left(X, t - \frac{|x-X|}{v}\right) - \\ &- \psi_i\left(X, t - \frac{|x-X|}{v}\right) + p_e\left(X, t - \frac{|x-X|}{v}\right)\Big]\end{aligned} \tag{15}$$

$$\begin{aligned}\psi_i(x,t) = a_i \int_\Gamma \mathrm{d}X f_i(x,X) \cdot S_i \Big[&\psi_e\left(X, t - \frac{|x-X|}{v}\right) - \\ &- \psi_i\left(X, t - \frac{|x-X|}{v}\right) + p_i\left(X, t - \frac{|x-X|}{v}\right)\Big]\end{aligned} \tag{16}$$

These equations describe the spatio-temporal behavior of summed synaptic activities in the brain and correspond to the phenomenological model by Nunez [1].

As pointed out in Section 2 the EEG and MEG mainly measures macroscopic quantities generated by dendritic potentials and currents which correspond to synaptic activities. Thus we focus in the following on the evolution equations (15), (16). We specify the sigmoid function $S_j(n_j)$ as the logistic curve

$$S_j = \frac{1}{1+\exp(-\nu_j n_j + \nu_j \theta_j)} - \frac{1}{1+\exp(\nu_j \theta_j)}, \tag{17}$$

where θ_j denotes a fixed physiological state, usually the excitation threshold, and ν_j denotes the sensitivity coefficient of response of the corresponding neural subset. Since we interprete ψ_j as deviations from θ_j, we can set $\theta_j = 0$. We expand (17) into a Taylor series up to third order in n_j and obtain

$$S_j(n_j) \approx \alpha_j n_j - \tfrac{4}{3}\alpha_j^3 n_j^3, \tag{18}$$

where $\alpha_j = \nu_j/4$. Here the sigmoid function is approximated by odd orders in n_j due to the choice $\theta_j = 0$. Increasing the distance to this inflexion point second-order terms of n_j will turn up which can be eliminated by a linear transformation. Next, we look at (16) in more detail. The time scale of the intrinsic dynamics of $\psi_i(x,t)$ is given by the synaptic decay time and the delay via propagation along intracortical fibers. We assume the connectivity functions to be of the following form:

$$f_i(x,X) = \frac{1}{2\sigma_i} e^{-|x-X|/\sigma_i} \approx \delta(x-X) \tag{19}$$

$$f_e(x,X) = \frac{1}{2\sigma_e} e^{-|x-X|/\sigma_e}, \tag{20}$$

where (19) takes into account that intracortical connections are mainly local. Here the spatial range of the distribution of the fibers defines a hierarchy in time scales. The excitatory synaptic activity $\psi_e(x, t-|x-X|/v)$ operates on a much slower time scale than the inhibitory synaptic activity $\psi_i(x, t-|x-X|/v)$. With (19) the evolution equation (16) of inhibitory synaptic activity reduces to

$$\psi_i(x,t) = a_i S_i[\psi_e(x,t) - \psi_i(x,t) + p_i(x,t)]. \tag{21}$$

Using (18) and taking only linear contributions of (21) into account we obtain the following behavior of the inhibitory synaptic activity:

$$\psi_i(x,t) \approx \frac{a_i\alpha_i}{1+a_i\alpha_i}(\psi_e(x,t) + p_i(x,t)). \tag{22}$$

Here the dynamics of $\psi_i(x,t)$ is expressed in terms of the leading order of the slowly varying quantities $\psi_e(x,t)$ and $p_i(x,t)$, which means that on this time scale the intrinsic dynamics of $\psi_i(x,t)$ is negligible. The higher order contributions of these quantities cause small modifications of the corresponding parameters and are neglected here. Inserting (22) into (15), we readily obtain for the dynamics of the excitatory synaptic activity:

$$\psi_e(x,t) = a_e \int_\Gamma \mathrm{d}X f_e(x,X) S_e\left(\tilde{\rho}\psi_e\left(X, t-\frac{|x-X|}{v}\right) + p\left(X, t-\frac{|x-X|}{v}\right)\right), \tag{23}$$

where

$$p(X,T) = p_e(X,t) - \frac{a_i\alpha_i}{1 + a_i\alpha_i} \cdot p_i(X,t) \tag{24}$$

and

$$\tilde{\rho} = 1 - \frac{a_i\alpha_i}{1 + a_i\alpha_i}. \tag{25}$$

Equation (23) represents a one-variable neural tissue equation which will serve as the starting point of the following analysis. We will follow the idea that the input signals to the neural sheet and output signals from the neural sheet can be understood as inhomogeneities which are embedded into the neural sheet. These inhomogeneities represent the localized areas in the brain that perform different functional tasks. The coupling of these inhomogeneities to the neural sheet is described by (23). This yields the following form of the stimulus $p(x,t)$:

$$p(x,t) = \beta(x)s(t), \tag{26}$$

where $\beta(x)$ defines the spatial properties and $s(t)$ the temporal behavior of the input signal. In the case of m signals at different locations with a different temporal behavior we obtain the following formulation:

$$p(x,t) = \sum_{i=1}^{m} p_i(x,t) = \sum_{i=1}^{m} \beta_i(x)s_i(t). \tag{27}$$

Expressing the time delay via propagation along the corticocortical fibers by a delta function $\delta(t - T - |x - X|/v)$ we can rewrite (23) as follows:

$$\psi_e(x,t) = \int_\Gamma \int_{-\infty}^{\infty} G(x - X, t - T) \cdot \rho(X,T)\,\mathrm{d}X\,\mathrm{d}T \tag{28}$$

with the Green's function

$$G(x - X, t - T) = \delta\left(t - T - \frac{|x - X|}{v}\right) \cdot \frac{1}{2\sigma_e} \mathrm{e}^{-|x-X|/\sigma_e} \tag{29}$$

and

$$\begin{aligned} \rho(X,T) \;=\; & a_e \cdot [\alpha_e(\tilde{\rho}\psi_e(X,T) + p(X,T)) - \\ & -\tfrac{4}{3}\alpha_e^3(\tilde{\rho}\psi_e(X,T) + p(X,T))^3]. \end{aligned} \tag{30}$$

We perform the following Fourier transformations:

$$\psi_e(x,t) = \frac{1}{(2\pi)^2} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \mathrm{e}^{ikx - i\omega t} \psi_e(k,\omega)\,\mathrm{d}k\,\mathrm{d}\omega \tag{31}$$

$$\rho(x,t) = \frac{1}{(2\pi)^2}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \mathrm{e}^{ikx-i\omega t}\rho(k,\omega)\,\mathrm{d}k\,\mathrm{d}\omega \tag{32}$$

$$G(\xi,t_0) = \frac{1}{(2\pi)^2}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \mathrm{e}^{ik\xi-i\omega t_0}g(k,\omega)\,\mathrm{d}k\,\mathrm{d}\omega, \tag{33}$$

where

$$\xi = x - X \qquad t_0 = t - T, \tag{34}$$

and obtain the relation

$$\psi_e(k,\omega) = g(k,\omega)\cdot\rho(k,\omega). \tag{35}$$

The Fourier transform $g(k,\omega)$ of the Green's function $G(\xi,t_0)$ can be determined as

$$\begin{aligned} g(k,\omega) &= \int_{-\infty}^{\infty}\mathrm{d}\xi\int_{-\infty}^{\infty}\mathrm{d}t_0 G(\xi,t_0)\mathrm{e}^{-ik\xi+i\omega t_0} \\ &= \frac{\omega_0^2 - i\omega_0\omega}{(v^2k^2 + (\omega_0 - i\omega)^2)} \end{aligned} \tag{36}$$

with the parameter

$$\omega_0 = \frac{v}{\sigma_e}. \tag{37}$$

Rewriting (35) in the space and time domain, the following partial differential equation is obtained:

$$\ddot{\psi}_e + (\omega_0^2 - v^2\Delta)\psi_e + 2\omega_0\dot{\psi}_e = \left(\omega_0^2 + \omega_0\frac{\partial}{\partial t}\right)\cdot\rho(x,t) \tag{38}$$

with

$$\begin{aligned} \rho(x,t) &= a_e\cdot S_e\left[\tilde{\rho}\psi_e(x,t) + \sum_{i=1}^{m} p_i(x,t)\right] \\ &\approx a_e\cdot\left[\alpha_e(\tilde{\rho}\psi_e(x,t) + \sum_{i=1}^{m} p_i(x,t)) - \right. \\ &\quad \left. -\tfrac{4}{3}\alpha_e^3(\tilde{\rho}\psi_e(x,t) + \sum_{i=1}^{m} p_i(x,t))^3\right]. \end{aligned} \tag{39}$$

This fundamental field equation of the brain is our final result. It governs the spatio-temporal behavior of the electromagnetic brain activity. Our field equation

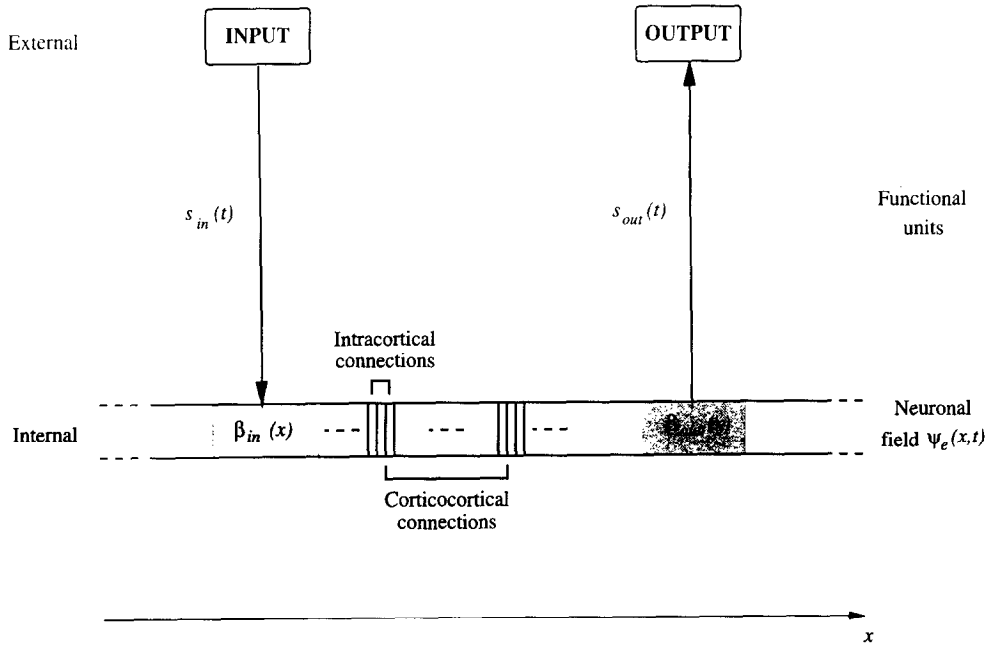

Figure 2. Functional input and output units are embedded as inhomogeneities in the neural sheet whose spatio-temporal dynamics is described by the field variable $\psi_e(x,t)$.

allows to make a connection to phenomenological macroscopic models which will be published elsewhere. Distinguishing functional input and output units we write an input unit which conveys diverse input to the neural sheet as $p_{in}(x,t) = \beta_{in}(x)s_{in}(t)$. The signal $s_{out}(t)$ of a functional output unit is defined by

$$s_{out}(t) = \int_{\Gamma} \mathrm{d}X \beta_{out}(X)\psi_e(X,t), \tag{40}$$

where $\beta_{out}(x)$ denotes the localization of the unit in the neural sheet. In Figure 2 we give a schematic presentation of the model we developed here.

4. Discussion, Summary and Conclusions

The present paper bridges the gap between a quasi-microscopic and a macroscopic description of the spatio-temporal dynamics of the brain. We introduced a mathematical description of the notion of conversion operations at the synapses and the somas of neurons in an ensemble which represents the quasi-microscopic level of description. Considering a time-scale hierarchy as well as a spatial-scale hierarchy we could derive equations governing the spatio-temporal behavior of synaptic activities and of action potential densities. The considered time scale of 100 msec is due to delays via propagation of action potentials along corticocortical fibers, the considered spatial scale of several cm is due to the spatial range of excitatory

corticocortical fibers and short-range inhibitory fibers. These scales are anatomically realistic. The macroscopic level of description is given by EEG and MEG measurements that mainly pick up the signals of dendritic potentials and currents which correspond to synaptic activities. We reduced the equations of the synaptic activities to a one-variable field equation given as a nonlinear partial differential equation. In this order of approximation around a fixed physiological state inhibition plays a minor role and could be eliminated. It contributes to the constant field parameters as inhibitory background effects. This approximation will not be valid any more, if higher order patterns, i.e. smaller spatial and/or temporal scales, in the EEG or MEG are considered. Our derivation substantiates the idea that the brain acts as a nonlinear medium with dispersive properties. Functional units like the motor cortex areas or the thalamus are assumed to interact as inhomogeneities with this medium. These inhomogeneities obviously have a strong impact onto the dispersive properties of the brain. One of the major tasks in the future will be the handling of the localization of these inhomogeneities.

Our proposed nonlinear field theory opens a vast variety of possible future theoretical and experimental investigations on the base of the ideas presented here. Particularly periodic phenomena like periodic driving or self-generated oscillations like in the case of α-waves, are interesting to view from this aspect.

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