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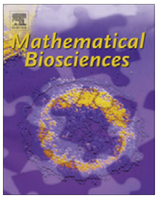

Neocortical dynamics at multiple scales: EEG standing waves, statistical mechanics, and physical analogs

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ABSTRACT

The dynamic behavior of scalp potentials (EEG) is apparently due to some combination of global and local processes with important top-down and bottom-up interactions across spatial scales. In treating global mechanisms, we stress the importance of myelinated axon propagation delays and periodic boundary conditions in the cortical-white matter system, which is topologically close to a spherical shell. By contrast, the proposed local mechanisms are multiscale interactions between cortical columns via short-ranged non-myelinated fibers. A mechanical model consisting of a stretched string with attached nonlinear springs demonstrates the general idea. The string produces standing waves analogous to large-scale coherent EEG observed in some brain states. The attached springs are analogous to the smaller (mesoscopic) scale columnar dynamics. Generally, we expect string displacement and EEG at all scales to result from both global and local phenomena. A statistical mechanics of neocortical interactions (SMNI) calculates oscillatory behavior consistent with typical EEG, within columns, between neighboring columns via short-ranged non-myelinated fibers, across cortical regions via myelinated fibers, and also derives a string equation consistent with the global EEG model.

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1. Introduction

What makes human brains so special? How do they differ from hearts, livers, and other organs? All organ systems are enormously complicated structures, able to repair themselves and make detailed responses to external control by chemical or electrical input. Yet, only brains yield the amazing phenomenon of consciousness [1]. Complex adaptive systems, for which human brains provide the most prominent examples, are composed of smaller parts interacting both within and across spatial scales. They typically exhibit emergent behavior not obviously predictable from knowledge of the individual parts and have the added capacity to learn from experience and change their global behaviors by means of feedback processes. Other examples include stock markets, ecosystems, and all living systems.

Several general features distinguish human brains from other organs, including the hallmark of richer hierarchical (or multiscale) interactions. In contrast to simple cognitive "theories", this paper explicitly acknowledges brains as highly complex adaptive systems, emphasizing the critical contribution of cross scale interactions to their dynamic behaviors. In order to minimize communication barriers due to the complicated mathematics, several analog systems from disparate fields are employed. Neuroscientists are typically skeptical of brain analogs, typically for good reason; however, we are *not* claiming that brains are actually just like stretched strings, social systems, quantum structures, resonant cavities, hot plasmas, disordered solids, chaotic fluids, or any other non-neural system. Rather, we suggest that each of these systems may exhibit behavior similar to brain dynamics observed under restricted experimental conditions, including the spatial scale of observation. The multiple analogs then facilitate development of complementary models of brain reality.

In many complex systems, as spatial–temporal scales of observation are increased, new phenomena become evident by virtue of synergistic interactions among smaller-scale entities, which serve to explain data, typically in a mathematically aesthetic fashion [2,3]. For example, in the classical thermodynamics of equilibrium systems, it is possible to transition from microscopic molecular scales to macroscopic scales and employ the macroscopic variable temperature to describe the average kinetic energy of microscopic molecular activity. Many complex systems, however, operate in non-equilibrium states, being driven by nonlinear and stochastic interactions. For such systems, classical thermodynamics typically does not apply [4]. For example, the description of weather and ocean patterns, which includes important features such as turbulence, rely on semi-phenomenological mesoscopic models,

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in agreement with molecular theories but not capable of being rigorously derived from them. Phase transitions in magnetic systems and many systems similarly modeled [5–9] require careful treatment of a continuum of scales near critical points. In general, rather than having a general theory of non-equilibrium nonlinear process, several overlapping approaches are employed, typically geared to classes of systems and often expanding on nonlinear treatments of stochastic systems.

Given this general outline of complex systems, it should not be surprising that human brains support many phenomena arising at different spatial–temporal scales. We can then study macroscopic neocortical phenomena such as electroencephalography (EEG) by appealing to a chain of arguments dealing with overlapping microscopic and mesoscopic scales. Such work is detailed in a series of papers presenting a theory of statistical mechanics of neocortical interactions [10–12]. This approach permits us to develop EEG and other models of dynamic processes whose variables and parameters are closely identified with ensembles of synaptic and neuronal interactions. The mathematical formalism supporting this approach has only recently been made possible by developments in mathematical physics since the late 1970s, in the field of nonlinear non-equilibrium statistical mechanics. The origins of this theory are in quantum and gravitational field theory.

2. EEG and other experimental data

The ultimate test of any brain model is experiment, and different kinds of brain data are available at different spatial and temporal scales. Structural or static imaging is accomplished with computed tomography (CT) or magnetic resonance imaging (MRI). The label “static imaging” indicates changes on yearly time scales in healthy brains or perhaps weeks or months in the case of growing tumors. By contrast, intermediate time-scale methods like functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) track brain changes over seconds or minutes. Still more rapid dynamic measures are electroencephalography (EEG) and magnetoencephalography (MEG), which operate on millisecond time scales, providing dynamic images faster than the speed of thought. The “bad” news is that EEG spatial resolution is quite coarse; nevertheless, EEG provides most of the existing data on neocortical dynamic behavior and its relation to cognitive events in humans. Thus, we focus on EEG, a record of the oscillations of brain electric potential recorded from electrodes on the human scalp.

EEG allows for accurate identification of distinct sleep stages, depth of anesthesia, seizures and other neurological disorders. It also reveals robust correlations with cognitive processes occurring during mental calculations, working memory and selective attention. Scientists are now so accustomed to these EEG correlations with brain state that they may forget just how remarkable they are. The scalp EEG provides very large-scale and robust measures of neocortical dynamic function. A single electrode yields estimates of synaptic action averaged over tissue masses containing between roughly 100 million and 1 billion neurons. The space averaging of brain potentials resulting from extra-cranial recording is a fortuitous data reduction process forced by current spreading in the head volume conductor. Much more detailed local information may be obtained from intracranial recordings in animals and epileptic patients. However, intracranial electrodes implanted in living brains provide only very sparse spatial coverage, thereby failing to record the “big picture” of brain function. Furthermore, the dynamic behavior of intracranial recordings depends fundamentally on measurement scale, determined mostly by electrode size. Different electrode sizes and locations can result in substantial differences in recorded dynamic behavior, including frequency content and coherence. Thus, in practice, intracranial data provide different information, not more information, than is obtained from the scalp [13].

We expect brain electrical dynamics to vary substantially across spatial scales. Although cognitive scientists and clinicians have reason to be partly satisfied with the very low spatial resolution obtained from scalp EEG data, explorations of new EEG methods to provide somewhat higher spatial resolution continue. A reasonable goal is to record averages over “only” 10 million neurons at the 1-cm scale in order to extract more details of the spatial patterns correlated with cognition and behavior. This resolution is close to the theoretical limit of spatial resolution caused by the physical separation of sensor and brain current sources. MEG spatial resolution is also quite limited because its sensor coils are at least three times further from dominant brain sources than EEG electrodes [13]. Scalp data are largely independent of electrode size because scalp potentials are severely space-averaged by volume conduction between brain and scalp. Intracranial recordings provide much smaller scale measures of neocortical dynamics, with scale depending on the electrode size, which may vary over four or five orders of magnitude in various practices of electrophysiology. A mixture of coherent and incoherent sources generates the small and intermediate scale intracranial data. Generally, the smaller the scale of intracranial potentials, the lower the expected contribution from coherent sources and the larger the expected differences from scalp EEG. That is, scalp data are due mostly to sources coherent at the scale of at least several centimeters with special geometries that encourage the superposition of potentials generated by many local sources.

In practice, intracranial EEG may be uncorrelated or only weakly correlated with cognition and behavior. The information content in such recordings is limited by sparse spatial sampling and scale-dependent dynamics. Furthermore, most intracranial EEG data are recorded in lower mammals; extrapolation to humans involves additional issues. Thus, higher brain function in humans is more easily observed at large scales. Scientists interested in higher brain function are fortunate in this respect. The technical and ethical limitations of human intracranial recording force us to emphasize scalp recordings. These extra-cranial recordings provide estimates of synaptic action at the large scales closely related to cognition and behavior. Thus, EEG provides a window on the mind, albeit one that is often clouded by technical and other limitations.

3. Possible physiological bases for EEG

Since the first human recording in the early 1920s the physiological bases for the wide variety of rhythmic EEG activity, a proverbial “spectral zoo”, has been somewhat of a mystery. In particular, human alpha rhythms, which are quite robust in wide awake (but relaxed) subjects with closed eyes, may be recorded over nearly all of the upper scalp or cortex and have preferred frequencies near 10 Hz. Given any unknown physical or biological system that produces oscillations at some preferred (or resonant) frequency $f = \omega/2\pi$, one of the first questions a scientist might ask concerns the origin of the implied underlying time delay τ roughly estimated as:

$$\tau \approx \omega^{-1}. \tag{1}$$

The implied physiological time scales for the most robust human EEG rhythms (1–15 Hz) are τ = 10–160 ms. How does this delay range compare with mammalian physiology? Whereas early studies of membrane time constants in mammalian cortex were very short, typically less than 10 ms, more modern studies with improved recording methods report the wide range 20–100 ms [14]. But apparently in voltage-gated channels, the effective time constant becomes a “dynamical parameter” that depends on both

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