

The Complexity of the Brain: Structural, Functional and Dynamic Modules

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1 Introduction

Structural modular architectonics is an important concept of neural organization. Neuronal connectivity in a typical neural center is sufficiently specific to permit disassembly of the whole network into neuronal modules of characteristic internal connectivity; and the larger structure can be reconstituted by repetition of these modules.

Functional modules or schemas are behavioral units. Arbib (1989) provided a neural theory of functional modules (schemas). It is typically a top-down theory, but it is time to talk about a partially new topic, what I call structure-based modeling of schemas (Érdi 1998).

Can we talk also about dynamic modules? Networks of neurons organized by excitatory and inhibitory synapses are structural units subject to time-dependent inputs and they also emit output signals. From a dynamical point of view, a single neural network may be considered sometimes as a pattern generating and/or pattern recognizing device. More often it is not a single network but a set of cooperating neural networks that forms the structural basis of pattern generation and recognition. (Pattern generating devices are functional elements of schemas.)

2 Complexity of the brain: the need of integrative approach

It is often said in colloquial sense that the brain is a prototype of complex systems. A few different notions of complexity may have more formally related to neural systems. First, structural complexity appears in the arborization of the nerve terminals at single neuron level, and in the complexity of the graph structure at network level. Second, functional complexity is associated to the set of tasks performing by the neural system. Third, dynamic complexity can be identified with the different attractors of dynamic processes, such as point attractors, closed curves related to periodic orbits, and strange attractors expressing the presence of chaotic behaviour.

The understanding of neural organization requires the integration of structural, functional and dynamic approaches (Arbib et al, 1997, Arbib and Érdi 2000). Structural studies investigate both the precise details of axonal and dendritic branching patterns of single neurons, and also global neural circuits of large brain regions. Functional approaches start from behavioural data and provide a (functional) decomposition of the system. Neurodynamic system theory (Érdi 1993) offers a conceptual and mathematical framework for formulating both structure-driven bottom-up and function-driven top-down models.

3 Structural modules

Experimental facts from anatomy, physiology, embryology, and psychophysics give evidence of highly ordered structure composed of 'building blocks' of repetitive structures in the vertebrate nervous system. The building block according to the modular architectonic principle is rather common in the nervous system. Modular architecture is a basic feature of the spinal cord, the brain stem reticular formation, the hypothalamus, the subcortical relay nuclei, the cerebellar and especially the cerebral cortex. After the anatomical demonstration of the so-called cortico-cortical columns it was suggested by Szentágothai (1978) that the cerebral cortex might be considered on a large scale as a mosaic of vertical columns interconnected according to a pattern strictly specific to the species.

Szentágothai applied the modular architectonics principle to the cerebral cortex, linking observations of anatomical regularities to the observations of Mountcastle on physiological "columns" in somatosensory cortex and of Hubel and Wiesel on visual cortex. Other important anatomical regularities are the quasi-crystalline structure of the cerebellar cortex and the basic lamellar structure of the hippocampus.

Vernon Mountcastle, one of the pioneers of the columnar organization of the neocortex, states (Mountcastle, 1997) that modules may vary in cell type and number, in internal and external connectivity, and in mode of neuronal processing between different large entities, but within any single large entity they have a basic similarity of internal design and operation. A cortical area defined by the rules of classical cytoarchitectonics may belong to different systems. Therefore distributed structures may serve as the anatomical bases of distributed function.

4 Functional modules

Michael Arbib's schema theory is a framework for the rigorous analysis of behavior which requires no prior commitment to hypotheses on the localization of each schema (unit of functional analysis), but which can be linked to a structural analysis as and when this becomes appropriate.

Complex functions such as the control of eye movements, reaching and grasping, the use of a cognitive map for navigation, and the roles of vision in these behaviors, by the use of schemas in the sense of units which provide a functional decomposition of the overall skill or behavior.

5 Dynamic modules

Neural systems can be studied at different levels, such as the molecular, membrane, cellular, synaptic, network, and system levels. Two classes of the main neurodynamical problems exist: (i) study of the dynamics of activity spreading through a network with fixed wiring; (ii) the study of the dynamics of the connectivity of networks with modifiable synapses - both in normal ontogenetic development, and in learning as a network is tuned by experience. The key dynamical concept is the attractor, a pattern of activity which "captures" nearby states of an autonomous system. An attractor may be an equilibrium point, a limit cycle (oscillation), or a strange attractor (chaotic behavior). We have the structure-function problem: for what overall patterns of connectivity will a network exhibit a particular temporal pattern of dynamic behavior?

5.1 Neural networks and dynamics

Depending on its structure, an autonomous NN may or may not exhibit different qualitative dynamic behavior (convergence to equilibrium, oscillation, chaos). Some architectures shows unconditional behavior, which means that the qualitative dynamics does not depend on the numerical values of synaptic strengths. The behavior of other networks can be switched from one dynamic regime to another by tuning the parameters of the network. One mechanism of tuning is synaptic plasticity, which may help to switch the dynamics between the regimes (e.g. between different oscillatory modes, or oscillation and chaos, etc. ...)

5.2 Computation with attractors: scope and limits

"Computation with attractors" became a paradigm which suggests that dynamic system theory is a proper conceptual

framework for understanding computational mechanisms in self-organizing systems such as certain complex physical structures, computing devices, and neural networks. Its standard form is characterized by a few properties. Some of them are listed here: (i) the attractors are fixed points; (ii) a separate learning stage precedes the recall process whereby the former is described by a static 'one-shot' rule; (iii) the time-dependent inputs are neglected; (iv) the mathematical objects to be classified are the static initial values: those of them which are allocated in the same basin evolve towards the same attractor, and can recall the memory trace stored there. In its extended form, not only fixed points, but also limit cycles and strange attractors can be involved; a continuous learning rule may be adopted but, in this case, the basins of the attractors can be distorted which may even lead to qualitative changes in the nature

of the attractors. Realistic models, which take explicitly into account the continuous interaction with the environment, however, are nonautonomous in mathematical sense (Érdi et al. 1992, Aradi et al. 1995). Such systems do not have attractors in the general case. Consequently, attractor neural network models cannot be considered as general frameworks of cortical models.

5.3 Rhythmicity and synchronization

The existence of single cell level oscillation does not imply the generation of global oscillatory behaviour. To avoid "averaging out" due to irregular phase shifts, some synchronization mechanism should appear. Synchronization phenomena in different neural centers have been the subject of many recent investigations. The appearance of single cell oscillation is, however, not a necessary condition for global oscillations, since the latter may arise as an emergent network property. This was suggested based on combined physiological - pharmacological experiments in the thalamus (3), and also on theoretical studies discovering the connection between network structure and qualitative dynamic behaviour.

Specifically, following the work of Wang and Buzsáki (1996) we studied the emergence of different types of synchronized oscillations in the model of networks of hippocampal inhibitory interneurons (Kiss et al, in preparation.)

6 Population models

As we have seen, 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 activity patterns of single cells, small and moderately large networks based on data on detailed morphology and kinetics of voltage- and calcium-dependent ion channels. The second offers a computationally

efficient method for simulating large network of neurons where the details of single cell properties are neglected.

To make large-scale and long-term realistic neural simulations there is a need to find a compromise between the biophysically detailed

multicompartmental modeling technique, and the sometimes oversimplified network models. Statistical population theories offer a good compromise. Ventriglia (1974, 1994) introduced a kinetic theory for describing the interaction between a population of spatially fixed neurons and a population of spikes traveling between the neurons. In our group (Érdi et al, 1997, Gröbner et al 1998, Barna et al. 1998) a scale-invariant theory (and software tool) was developed, which gives the possibility to simulate the statistical behavior of large neural populations, and synchronously to monitor the behavior of an "average" single cell. There is a hope that activity propagation among neural centers may be realistically simulated, and schemas can be built from structure-based modeling.

7 Acknowledgements

This work was supported by the National Scientific Research Foundation (OTKA) No T 025500.

8 References

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