gravitational wave applications is limited to resonant bars, and even there almost exclusively to the properties of niobium. There is virtually no discussion of the history of the field, and, with the exception of the chapter on space experiments, no discussion of the scientific results (alas only upper limits on wave strengths) that have been obtained to date.

Readers from outside the field will have trouble obtaining a clear sense of the state of this field from the book. The overview chapters seem too sketchy for the purpose, and the book as a whole has the air of documenting a mature field rather than alerting newcomers to the potential of one that is dynamic and rapidly evolving. Perhaps the biggest lack is a coherent summary of all the factors that lead the scientists in the field to believe that successful detection of gravitational waves will come soon. (It would have been helpful to discuss the sensitivity of the best present-day detectors.) The case for LIGO and its cousins has to be pieced together from many chapters.

For those active in the field, the volume addresses an unmet need. Unlike the authors of the Rad Lab series, we cannot yet look back on how we successfully met the challenge of detecting the waves we are looking for. But with perseverence and luck, that day should come soon.

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A Slice of the Brain

Neuronal Networks of the Hippocampus. ROGER D. TRAUB and RICHARD MILES. Cambridge University Press, New York, 1991. xviii, 281 pp., illus. $39.50.

The experimental study of the neuronal networks underlying sensory perception, motor control, memory, and cognition has recently begun to advance beyond the data-driven phase in which phenomena are described and categorized ever more finely but without unifying and quantitative theories to a more mature, quantitative stage. The last few years have witnessed increasing use of methods from mathematical physics to study aspects of the nervous system as well as a dramatic growth in detailed computer modeling. These trends are embodied in *Neuronal Networks of the Hippocampus*.

The primary aim of the work reported is to understand from first principles one of the neuronal networks making up the mammalian hippocampus, part of the cortical system known to play a crucial role in the formation of episodic memory traces. This part of the brain, encompassing on the order of 10 million nerve cells in the human, is also particularly susceptible to epileptic seizures, with unfortunate consequences. In the celebrated case of H.M., intractable epilepsy led his doctors to remove the medial temporal lobe (which includes the hippocampus) on both sides, rendering him forever incapable of remembering for more than 1 or 2 minutes events that happened after the operation. His "procedural" or "habit" memory system is, however, not impaired (thus, he can learn how to solve the "Tower of Hanoi" without recalling ever having seen this puzzle before).

Though it has been popular to study epilepsy experimentally by recording in vitro from slices from a particular part of the hippocampus called CA3, Traub and Miles (and their collaborators, in particular Bob Wong) are unique in combining these investigations with large-scale realistic network simulations. The results of this exemplary interaction between experiment and computer model are described here.

The book is organized into three parts. The first three chapters introduce the hippocampus, the physiology of its two main types of neurons, and their synaptic connectivity. The authors focus on various collective population phenomena in which large assemblages of neurons fire simultaneously. Such synchronized activities include rhythmical EEG waves in the theta range (4 to 12 Hz), sharp waves and EEG spikes (short electrical events that reflect a limited degree of synchronized cell firing), and various types of epileptic seizures. The second part of the monograph describes in great detail the authors' computer model. They adopt the heroic position that understanding neuronal networks requires creating as close as possible a one-to-one copy of the system in the computer. Thus, they numerically simulate 9000 excitatory and 900 inhibitory cells (out of about 20,000 making up the CA3 slice preparation). The dendritic tree of each cell is approximated by a number of spatially discrete compartments containing voltage-dependent sodium, potassium, and calcium currents; individual cells can reproduce the various voltage trajectories observed experimentally, in particular isolated action potentials and bursts (a small group of tightly clustered spikes). The network topology mimics the known anatomy of the CA3 area: local random connections whose density decreases exponentially with distance. This section of the book also includes all the relevant equations and details of the computer program.

The crucial test of any model is its ability to make new predictions, and the heart of the book is in the third section, where the model reproduces the propagating waves and other synchronized events seen both in slice and in the intact animal when inhibition is reduced or blocked by various pharmacological agents. By the standard of the field, this model does quite well, having predicted that a burst in a single pyramidal cell can evoke a burst in another pyramidal cell and that stimulation of a single neuron can frequently evoke synchronous firing, lasting 50 to 100 milliseconds, in a large population of disinhibited CA3 cells. Both phenomena have subsequently been verified experimentally. The latter one is particularly intriguing, since it is a genuine collective phenomenon. In order for each neuron in a large network with random connectivity to fire—through the building up of a chain reaction among excitatory pyramidal cells—it is known both experimentally and theoretically that 1000 to 2000 hippocampal neurons are required. In other words, a "critical" number of neurons has to exist (as well as a minimal excitatory synaptic strength). If the network is spatially elongated, a wave of neurons bursting simultaneously moves slowly across the slice. The finite propagation velocity is due to the spatially decaying synaptic connectivity among neurons.

One chapter deals exclusively with field effects among neurons, mediated by extracellular potential gradients. Such effects are expected to be significant in the hippocampus, with its regular geometry and tight neuronal packing density. Experiments and computer modeling show that they can act as a weak but global synchronizing mechanism among neurons, compared to the sparse but powerful point-to-point interaction mediated by synapses. Finally, Traub and Miles discuss how various concepts from the theory of dynamical systems (chaos, embedding dimension, strange attractor) as well as Hopfield and connectionist neural networks and percolation theory (the study of transmission among randomly interconnected nodes in an evolving network) may be relevant for understanding the structure and function of the hippocampus.

The book integrates experiments and computer modeling into a seamless fabric, something still rare in the neurosciences. The use of arguments from statistical physics and dynamical systems theory is compelling and to the point. The monograph should be required reading for any researcher seriously interested in networks of complicated and highly interconnected neurons, in particular for those of us reasoning about models of synchronized "40 Hz" oscillations observed in mammalian cortex. The novice should be warned, however; many important concepts (for example, depolarizing after-potentials, kindling, correlation dimension) are mentioned without proper introduction, and almost no overview and summarizing diagrams are provided.

Although I admire the Herculean attempt of the authors to understand the working of a small piece of nervous tissue in such detail, I also believe that the book starkly illuminates the limits of a purely bottom-up, physics-like research program in the brain sciences. Unlike a crystal or a galaxy, neuro-biological structures have a teleonomic aspect; that is, they evolved in such a way as to fulfill a particular function, in the case of the brain the processing and storing of information. Neglecting the computational role of the nervous system is like trying to understand the eye-like markings on the wings of a butterfly without taking into consideration that they evolved for reasons of mimicry. This is all the more so for the case of epileptic seizures, a highly degenerate brain state with no computational significance. Thus, though the research program presented in this monograph is a significant stepping-stone toward a "physics" of neural networks and the natural history of epileptic seizures, it tells us very little about the role of the hippocampus in computing and storing our memories.

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Pumping Ions

Electrogenic Ion Pumps. PETER LÄUGER. Sinauer, Sunderland, MA, 1991. x, 313 pp., illus. $44.95. Society of General Physiologists Distinguished Lecture Series, vol. 5.

All cellular life forms establish ionic concentration gradients across their cell membranes by active transport of ions. Apparently proteins that couple ion transport to a source of free energy have arisen several times in evolution. *Escherichia coli* uses an ATP-dependent ion pump that is homologous to the well-known Na^+-K^+, Ca^{2+}, and H^+-K^+ pumps of animals. Halobacteria evolved light-driven pumps for H^+ and Cl^-, and almost all bacteria and eukaryotes have cytochrome oxidase that pumps protons as part of electron transport and coupling proteins (F_0F_1 ATPase) that synthesize ATP at the expense of the proton gradient.

The Na^+-K^+ pump has been studied for half a century. The concept of energy-requiring vectorial transport was introduced more than 50 years ago, and by 30 years ago the energy source (ATP) had been identified, the concept of a strictly stoichiometric coupled transport cycle had been established, and an appropriate ATPase activity had been discovered in broken cell membranes. Subsequently the transport protein was solubilized, purified, and sequenced, and a large number of intermediate steps in the overall cycle were revealed. Perhaps the most interesting intermediates are several "occluded" states in which transported ions seem to be trapped as in an airlock in their transit across the membrane.

Despite a long history of sophisticated observation, we still do not understand the molecular details. How are ions picked up on one side of the membrane and deposited on the other? Peter Läuger's posthumous book provides an admirable distillation of a complex experimental literature and a clean theoretical structure for kinetic analysis. It is exciting to be guided by such a sure hand through what would otherwise be very difficult theoretical and experimental territory. Läuger's legacy will be a paradigm for thinking in this field for many years to come. This is a biophysical masterclass. It will reward repeated study.

The book begins with a short overview of classes of ion pumps and then settles into a serious introduction to physical principles and the theoretical background of each of the methods for studying pumps. We learn about the thermodynamics of state diagrams, energy levels and efficiency, steady-state and transient kinetics, the contribution of pumps to electrical properties of membranes, and the theory of membrane fragments coupled to planar bilayers. This part would make an excellent graduate reading seminar in biophysics, a skillful case study exercising a wide range of physical thinking in a biological context. It will be equally interesting to researchers studying bioenergetics and molecular motors who face the same problems of kinetics and energetics of cyclic state diagrams. The presentation here cuts deftly to the core and is a strong model of a self-consistent kinetic framework achieved through notational simplicity and deep physical insight.

The second half of the book reviews progress made on each of the pumps. This part will be especially useful to those who teach about primary active transport and bioenergetics in classes in cell physiology. The style is refreshingly direct. Sharp conclusions are drawn without waffling over fuzzy data. The greatest amount of space is devoted to the Na^+-K^+ ATPase. The classical Post-Albers cycle is reviewed in detail, together with newer extensions. Results of rapid mixing, filtration, current-voltage, voltage- and ATP-jump, and charge-transient experiments are brought in to establish microscopic rate constants and rate-limiting steps. All is summarized in a reaction diagram with 14 states and 20 reaction steps. Values for 29 rate constants are estimated. At this level tremendous progress has been made in the last 15 years.

As the title implies, active transport of ions moves electric charge as well as making a concentration gradient. In Läuger's earlier field of ion channels, the ability to measure charge movements and voltage sensitivity of elementary steps has been central to rapid progress in understanding. The same powerful approaches are now being applied to ion pumps, and the formalisms developed in this book show how electrical measurements can be used to dissect elementary steps of the transport cycle.

A valuable feature of this well-produced book is the combination into a neat and readable package of both the theoretical background and the observations of a large field of transport research. Experimentalists trained in the use of Ockham's razor may be surprised at the large number of steps, coefficients, and rate constants used to describe the action of one macromolecule. Indeed, the models go well beyond existing observation. However, the book teaches us how to prepare the framework for future analysis by meticulous representation of each anticipated process. Experiment then can determine which steps are rate-limiting or kinetically important. Structural biologists may also be surprised at the relative lack of structural correlates of any of the kinetic events in pumping. This book may be the first and last monographic summary of a great era that will surely stimulate molecular discovery through genetic engineering and possibly atomic-resolution crystallography. It is a great read and a must for all in the transport and bioenergetics fields.

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