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★**Brain dynamics. (English. English summary)**
Synchronization and activity patterns in pulse-coupled neural nets with delays and noise.
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FEATURED REVIEW.

Mathematical studies of living neural networks must face three challenges. First, neural networks are pulse-coupled. This is because when neurons are physically separated, interactions between them are necessarily in the form of discrete synaptic potentials driven by neural spiking. Second, axonal conduction velocities are finite and hence the effects of time delays on network dynamics are unavoidable. Finally, noise is inevitable. This is the first text to address the dynamics of noisy and delayed pulse-coupled neural networks.

The text is divided into three main parts. Part I (Chapters 1–4) provides the background. The brevity of the neurobiological discussion in Chapters 1–3 will frustrate many neurobiologists. Nonetheless the author draws attention to two points seldom emphasized: (1) the use of the Naka-Rushton relation, a Hill-type function, to relate neural inputs to output spiking frequency (Section 2.5); and (2) that correlations between masses of neurons may be more accessible to the experimentalist than correlations between two spiking neurons, a subject favored by many mathematicians (Section 3.4). This latter point follows from the experimental observation that the probability of finding two neurons in the cortex that are significantly coupled is quite small.

Chapter 4 provides the mathematical toolbox. The key tools for the analysis of pulse-coupled neurons are the δ-function and the concept of phase. The properties of the δ-function are thoroughly discussed and extended to a general class of δ-functions that are a function of time given by the phase, φ. The most important tool for analytical work turns out to be the spike function $f(t)=\delta(\varphi(t))\dot{\varphi}(t)$, where the dot notation indicates the time derivative. Although at first sight the meaning of the spike function seems a bit obtuse, it is shown that in the presence of phase noise the spike function has practically the same properties as the δ-function (Section 4.2). The game of soccer is used to motivate the development of the Green function to derive Rall's α-function and to provide a framework to examine the effects of random kicks. This result is used in turn to define more precisely what is meant by phase noise (Section 4.10).

Part II presents the main result of this text, namely an analysis of spiking in neural nets. In general, the critical parameter for the dynamics of a pulse-coupled neural network is spike timing. However, in the case in which the neurons spike periodically it is natural to focus attention on considerations of the phase. Two approaches to pulse-coupled neural networks are described: the lighthouse model (Chapters 5 and 6) and models based on the concept of an integrate-and-fire neuron (Chapters 7 and 8). The lighthouse model for a spiking neuron is based on an analogy to a lighthouse with its rotating light beam: phase increases per unit time and when it equals 2π, or an integer model thereof, a neural spike is generated. Thus the neural spike train produced by a single neuron can be described by the phase angle. In Chapter 5 the author examines phase-locking between two neurons and then the effects of noise and delays. In Chapter 6 the results are extended to the case of many coupled neurons. The beauty of the lighthouse model is that many of the results can be readily obtained analytically.

Chapter 7 introduces integrate-and-fire (IF) models. IF networks are based on models for the action potentials of neurons whereas the lighthouse model uses phases and dendritic currents as variables. The introduction to IF models is very sketchy and for reasons unclear to this reviewer includes mention of Peskin's model for cardiac synchronization, a wonderful work itself, but somehow out of place in a text on neural networks. The meat appears in Chapter 8. It is shown that it is possible to connect the phase of axonal pulses with the action potential of the corresponding neuron. The response of the dendritic currents to the axonal pulses is modeled by a second-order differential equation. When the dendritic currents are eliminated from the models, it is possible to draw direct analogies between the lighthouse and IF models. Using suitable averages over the equations for a pulse-coupled neural network it is possible to obtain equations for the pulse rates and dendritic currents.

Part III is best described as a collage of interesting results. Chapter 9 considers models in which the coupling between two neurons can be described by a smooth periodic function of the phase difference between two neurons. Examples include coupling in a chain of neural oscillators, coupled finger movements, and quadruped motion. Chapter 10 shows that connections can be drawn between suitably averaged models of pulse-coupled neural networks (IF or lighthouse neurons) and previously proposed models for cortical dynamics and the electroencephalogram (EEG). In particular, the famous Wilson-Cowan equations for cortical dynamics arise when the dendritic currents are eliminated; the less well known, but equally important, Jirsa-Haken-Nunez (JHN) equations for the EEG arise when the axonal pulse rates are eliminated, leaving only the dendritic currents.

A number of unexpected vignettes are scattered throughout the text. For example there is a discussion of the use of the Hilbert transform to measure phase in experimental data (Section 4.9.3), the fractal derivative appears as an Appendix to Chapter 8, and the potential function is used to gain insights into the dynamics of the FitzHugh-Nagumo equation (11.2). Perhaps most interesting to computationally oriented neuroscientists is the comparison between neural synchronization and associative memory (Sections 6.4 and 6.5). In mathematical models, stable synchronized states arise only when the sensory inputs to all of the neurons are the same. This suggests that neural populations either are designed to work as a type of coincidence detector or are more concerned with transient behaviors than steady states. On the other hand, in order to incorporate associative memory into these mathematical models it is necessary to average over a number of spikes. Thus, in general, associative memory requires many different sensory inputs to work effectively. This is a potentially important distinction that has received little previous emphasis.

This textbook will likely be of most interest to specialists in the field of theoretical neurodynamics (advanced graduate students and researchers). Two other texts complement this one: [P. A. Tass, *Phase resetting in medicine and biology*, Springer, Berlin, 1999; MR 2000g:92002; H. R. Wilson, *Spikes, decisions, and actions*, Oxford Univ. Press, New York, 1999MR1972484]. I concur with the author's invitation to the reader to work through the derivations themselves with paper and pencil. In this way one gets a much better feeling for the importance of the material provided in the mathematical toolbox (Chapter 4). However, the presentation is at too advanced a level for the book to be of use to undergraduates or to those who do not share the author's passionate love of the subject. Throughout, the text is presented in the concise telegraphic style of a theoretician, with no concern for fueling the necessary intuition that would allow the reader to see what is going on without getting lost in the sea of equations. At times the style gets difficult, since the author has the unfortunate habit of using concepts before they are developed. For example, phase is used to develop the spike function before it is defined.

In summary I believe that this book is absolutely a must read for anyone seriously interested in developing realistic models for the dynamics of neural populations. Unanswered is the question of how the author was able to compact so many interesting results into a text of only 245 pages. And, as always, there is the issue of what to do with the vast majority of neurons that do not spike periodically.

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