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Editorial overview: Theoretical and computational neuroscience

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Introduction

One of the distinctive features of contemporary neuroscience research is the growing prominence of computational neuroscience, the study of the computational properties of the nervous system. Implicit in the focus on neuronal computations is the view that neuronal dynamics implement algorithms that execute well-defined functions. Theoretical neuroscientists study these computations by developing mathematically articulated theories and models and studying them by analytical and simulation methods.

Over the past two decades theoretical and computational research has advanced on several fronts. Research on the neural code has established quantitative measures to characterize neural sensory representations and uncovered underlying design principles. More recently, optimality theories have been used to characterize cognitive functions such as inference, expectations, decisions, and behavior, motivating the search for the underlying neuronal correlates. Theory of brain dynamics has transformed our perspective of brain function, by mapping the collective dynamical properties of neuronal circuits and elucidating their role as mechanisms of distributed neuronal computations as well as of brain dysfunctions.

The rapid development of high-throughput experimental techniques to collect anatomical and physiological data, even from animals behaving in complex environments, brings the role of theory to the forefront. New ideas are needed to develop methods to reduce this data to meaningful models and, more fundamentally, to provide testable hypotheses for the algorithms that these signals and anatomical structures reflect.

The reviews compiled in this issue discuss both the progress in computational neuroscience as well as the challenges the field faces. These challenges are the topic of two companion commentaries. Focusing on neural representations, Fairhall [1] notes that new theoretical and methodological approaches have led to major advances in our understanding of the features that are represented by sensory systems, how they are extracted by neural circuitry and why they take the form they do. However, richer stimulus and behavioral paradigms expose the problems with even the best coding characterizations: they do not yet accommodate many of the complexities of adaptation, nonlinear interactions, feedback from self-motion and behavioral state dependence. Resolving these issues, and perhaps rethinking current concepts of brain representation, is an important direction for the future, and one which may benefit from a dialogue with practitioners of machine learning and robotics.

Sompolinsky [2] notes that most computational research has focused on local relatively homogeneous circuits that implement single functions. Further, it is commonly assumed that circuits can be abstracted by networks of simplified units interacting with connections that resemble synaptic connectivity patterns in the brain (the 'Network Paradigm'). Sompolinsky [2] suggests that future research needs to (1) develop multi-scaling methods for a systematic determination of the appropriate level of abstraction for a given system and functionality; (2) develop models and analysis techniques to study large brain structures engaged in a variety of tasks and to uncover the underlying hierarchical/modular structural and functional architecture; and (3) address the dynamic reciprocal interaction between the neuronal networks to chemical and environmental variables.

The reviews compiled in this issue reflect the diverse range of topics and approaches characterizing this fast growing field. They range from global frameworks and methods, the study of computational modules, to the status of our understanding of sensory and motor computations, concluding with advances in analysis of large-scale brain dynamics and its relation to brain dysfunction.

Brain functions are often characterized as computations or as information processing. Piccinini and Shagrir [3] ask what we actually mean by applying these terms to nervous systems and whether these terms can be objectively distinguished from other levels of analysis of the same systems. The computational perspective of brain theory was first articulated in David Marr's three level framework: Computation, Algorithm, and Implementation. Valiant [4] updates this perspective, arguing that for a global theory of cortex to succeed, it has to meet quantitative challenges imposed by theoretical bounds on computation, communication and learning, as well as by architectural constraints of cortical circuitry. Perhaps the most mysterious aspect of cognition is consciousness, which nevertheless, has gained entrance into mainstream neuroscience. Dehaene *et al.* [5] review our current understanding of the contribution of consciousness to neural information processing and the potential mechanisms associated with nonlinear amplification, integration, and routing of neuronal signals. Stephan and Mathys [6] survey recent developments of computational approaches to psychiatric diseases, suggesting that in the future, Bayesian-based generative models may serve as diagnostic tools in the clinic. Several authors address the role of the Bayesian framework in computational neuroscience. Kording [7] argues that adopting the Bayesian approach provides new insight into neural codes, particularly revealing the ways in which prior knowledge and uncertainties are coded in neuronal representations. Lee [8] discusses how the brain might perform *dynamic* update of current beliefs about the environment, drawing upon Bayesian Filter methods in robotics and automatic navigation systems. Multisensory cue combination is a compelling example of Bayesian behavior; Seilheimer *et al.* [9] report on neural mechanisms that might underlie this integration. Wander and Rao [10] make the case that the combination of brain and machine in brain–computer interfaces may be a powerful tool to validate and further probe theories of coding and computation.

Computational neuroscience has entered the era of large-scale data acquisition and computation, raising high expectations about the prospects of data-rich neuroscience research, but also debates about their scientific merit and the justification of the resources that are committed to such programs. Eliasmith and Trujillo [11] review recent initiatives in creating large-scale computer models of the brain. While echoing Feynman's famous 'That which I cannot create, I do not understand', they caution that such simulations should (1) be explicitly oriented to explain concrete behaviors, rather than hoping that they will emerge bottom-up, and (2) adopt a level of detail that is matched to the questions at hand. Efforts to reconstruct large-scale connectomes are described by Plaza *et al.* [12] who stress the importance of incremental approaches to circuit reconstructions that make partial data available for researchers while at the same time track accurately the associated uncertainties.

The next group of articles describes studies of the dynamics and information processing of neuronal modules. The fundamental computation of a single neuron and its synapses is to map input spike trains of its presynaptic sources into appropriate output spike trains. Brunel *et al.* [13] explore the electrophysiological properties of neurons, dendrites, and synapses, that shape this input–output transfer function and the recent advances in capturing these properties using phenomenological statistical models, followed by Gütig's [14] survey of algorithms and models of spike-time based learning and computation at the level of a single neuron and its afferent synapses. Bhalla [15] argues that the often-neglected aspect of molecular computation adds considerable power and complexity to neural processing.

Dynamic principles governing the function of local cortical circuits are discussed by Wolf *et al.* [16], emphasizing the prominent role of feedback inhibition in stabilizing and balancing the cortical circuit's operating point. An alternative view, expressed by Sussillo [17], considers the cortical circuit as a generator of complex dynamics that, when coupled with appropriate learning rules, can be used to realize complex dynamical tasks. One of the generic tasks of cortex is working memory, a topic which has attracted great interest because of its prominent role in cognition and because its dynamic origin is still not understood. Barak and Tsodyks [18] explore a host of circuit-based mechanisms of working memory, from the tuning of excitation and inhibition to short-term synaptic facilitation, and suggest that the brain recruits a host of mechanisms to implement this function. While attractor dynamics is a classical model for long-term memory, Burak [19] examines networks exhibiting moving

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