

Coherent Apertures in the Central Nervous System
A Model of the Internal Experience

**Coherent Apertures
in the
Central Nervous System
A Model of the Internal Experience**

Thomas D. Wason

• 2017 •

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Title: Coherent Apertures in the Central Nervous System: A Model of the Internal Experience

Summary: This monograph proposes a coherent apertures model of the generation of the internal experience. This is not a computer model; it is a model of biological processes acting on biological structures. Cortical areas—apertures—synchronously bind together, instantiating aspects of information, thereby creating the internal experience. A test of the model is proposed. 843 references.

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About the Author

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Dedication

To Marianne

This never would have happened without you.

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Preface

Alas, dear reader, this is a rather lengthy piece. If you wish, you can read Ch. 2, *A Framework*, to get an overview of the model (*what*) and Ch. 7, *Operations*, for its application to perception, memory, recognition, and recall (*so what?*). The intervening chapters describe the internal workings of the coherent apertures model (*how*) that is derived from the literature. These chapters are in a logical sequence, each building on the previous ones. Such a house of cards can be fragile. I have attempted to buttress this one with verifiable evidence and logic. Ch. 6, *Integration of Coherent Cortical Apertures*, describes the mechanisms of cortical integration, the main result. In the *Epilogue* I consider what this model has taught me. The *Epilogue* also explores issues raised, a test of the model, and possible future research. *Supplemental Materials*, which includes a Glossary, provides technical details not essential to the main flow.

This work in theoretical neurobiology draws from many domains beyond neurobiology. Concepts in radiant energy systems proved useful in many ways, the aperture being a fundamental concept. The model of Yoshiki Kuramoto on synchronization in complex networks, brought to my attention by Aleksandr Davydov, was invaluable in understanding the process of aperture cohering. Information entropy was useful for describing the nature of information instantiated in the CNS without actually specifying the detailed form of the instantiation, particularly important in dealing with what I came to recognize as undecipherable complexity. Since the coherent apertures model addresses biological structures and processes, it calls into question the idea of “encoding.” Information processing models, outside of this model, are abstractions, with no physical reality. The CNS performs biological processes within physical structures that are, therefore, processes that are physical. Information—whatever that is—is physically instantiated in the CNS, subject to biological processes.

This work proceeded from the bottom up. I started by working to understand how a cortical area could become coherent, leading to a model of cortical operation within a limited scope. I did not delve into neuronal circuit models since they do not capture concepts embodied in this model. For example, it appears that aperture cohering involves mechanisms beyond neuronal circuits, notably the local field potential and its source. The role of the glia, particularly the astrocyte, is now more fully appreciated. Phase also appears to be an important factor in instantiating information. I have approached the problem of the operation of the CNS by limiting the scope of this exploration to early stage sensory processing, specifically to declarative objects in perception and memory, and their access in recognition and recall. My intent was to reduce complexity such that, without loss of validity, I could understand meaningful aspects of the CNS processes. I have proposed principles that embody some of those aspects, perhaps contributing to future work. The potential for technological implementation, an attractive test of an abstraction of the model, can be addressed in the future.

Thomas D. Wason
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Raleigh, North Carolina, USA

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- Joseph Lappin, Professor Emeritus, Dept. of Psychology, Vanderbilt University
- Donald Mershon, Professor Emeritus, Dept. of Psychology, North Carolina State University
- William Troxell, retired, CIA, assigned to the U.S. National Reconnaissance Office as Director, Research and Technology, Imagery Systems Acquisition and Operations Directorate.

Jim Kalat and Don Mershon, my PhD and MS advisors, encouraged me to undertake this project, which is an extension of my graduate work. Jim provided significant guidance in expressing the concepts clearly. Will Troxell made invaluable technological comments and gave considerable encouragement, validating the soundness of some key technical ideas. I had many prolonged discussions with Jerry Katzin on the concepts proposed and terminology; in the process he taught me a great deal.

Marianne Wason, my wife, contributed much to this work with her substantial editorial and proofing skills. Most of all, I am deeply appreciative of her unflagging support and encouragement.

1. Introduction to the Coherent Apertures Model

1.1. Introduction

The coherent apertures model proposes an explanation of how biological structures and processes in the central nervous system (CNS) generate the internal experience. The internal experience includes awareness, consciousness, working memory, the global neural workspace, attention, and perception; I have not differentiated among them. How does the internal experience occur? Where does it occur? The internal experience occurs primarily in the cortex. I offer a model primarily focused on the operation of cortical areas and their dynamic binding into ensembles [1, 2, 3, 4, 5, 6] that contribute to the internal experience. The cortical areas and limited subcortical structures work together to instantiate, store, and subsequently access information, moving back and forth from working memory to the various forms of memory. The cortex is composed of many distinct areas, defined here as *apertures*. Apertures instantiate information; apertures communicate and store. Of central importance, apertures can synchronize, enabling information instantiations through coherence, hence becoming coherent apertures. Groups of coherent apertures can communicate, modulating each other, in the process generating the internal experience. The group's collective information instantiations can be stored as memories, and later retrieved as an internal experience by resurrecting the group. In this document I have considered processes related to structured dynamic sensory information in perception, memory, recognition, and recall as the sources of the internal experience.

Steven Rose [7] remarked that neuroscience is “data rich, but theory poor.” Churchland and Abbott [8] and Sejnowski et al. [9] similarly noted a need for theoretical work in the neurosciences to provide explanations derived from, and tested by, data. Models of brain operation have long reflected the technology of the time.¹ Descartes proposed a hydraulic model in the 1660s; in the 1920s Weiss proposed a radio model. Although the computer is the dominant technology today, I do not consider the CNS to operate like a computer. The CNS does not process information, which is an abstraction, but performs biological processes on biological structures: it's physics. The coherent apertures model incorporates biological and technological points of view, incorporating synchrony and coherence in both.

Scope of the Model

The coherent apertures model addresses three fundamental issues in the neurosciences:

- What is the internal experience?
- How does cortex work?
- How is information instantiated in the cortex?

The coherent apertures model of the CNS consolidates a broad range of topics into a theoretical framework, attempting to span from cellular to global scales. This model is a behavior of materials model—dynamic granular materials. The elements of the cortical material are minicolumns characterized by the behavior of their pyramidal cells. The cortex and subcortical structures operate on

¹ This historical perspective provided by James Kalat.

different principles.² The (neo)cortex of mammals fills multiple needs, effective over species and modalities, having developmental flexibility and malleability. This leads one to think that it has common principles with common underlying mechanisms.³

Considerable experimental and theoretical work has shown that the cortex is parceled into discrete areas—apertures—that can have synchronous local field potentials (LFPs). This raises the question, why might this be useful for the operations of the CNS? Of necessity the problem of the instantiation of information in the aperture is addressed. The framework hypothesizes a relationship between how and why a cortical area becomes synchronous. Synchronization provides a substrate for the instantiation of information through coherence. An argument is made here for the role of coherent cortical apertures in the CNS through discussions of the synchronization and cohering of apertures, the information contained in and exchanged among those apertures, aperture functionals, cortical integration, and in some operations performed within the CNS. I provide specific operations to illustrate the processes of the framework.

Although some cortical circuits are discussed, this model is not a circuits model, but rather a framework of biological structures and processes. The coherent apertures model reveals a number of plausible common principles while still maintaining “irreconcilable differences” among individuals. The more difficult aspects of CNS function such as behavior and motivation must be addressed at a later time or, more appropriately, by others. My intent is to explore a system through which behaviors may operate. I have not given consideration to the limbic system, arousal, genetic expression, or signaling pathways—major components in the functioning of the CNS. They also affect the mechanisms of the CNS including profound impacts on the behavior of animals, all the way down to insects’ mating rituals. It is not my intent to provide a model that defines the specific activities of specific neurons when the cortex responds to specific inputs; such a model would be able to perform this action on any plausible input, producing a predictable result, a test proposed by Yamins and DiCarlo [10]. Given the variations among individuals and the continuous changes in the CNS, the success of such a model is unlikely.

Following a précis, I discuss the major themes within the coherent apertures model. This is followed by notes on the chapters, an enumeration of proposed principles, and a brief history of the model development. I have sketched some of the current research models. A Glossary is provided in Supplemental Materials. In the Epilogue I propose a test of the coherent apertures model and discuss some issues, speculations, and possible future research.

Précis

The coherent apertures model is a theoretical framework for the operation of cortical areas for the generation of the internal experience, principally from early stage sensory inputs. Synchrony provides binding within an aperture and among apertures. Coherence instantiates information within those synchronized contexts. In this model, synchrony refers to the gross behavior of a population, an aperture. Coherence describes the participation of a subpopulation of elements in that synchronization, and timing correlations among their behaviors, their phase differences. Thus coherence in an aperture occurs in the context of its synchronization, forming a coherent aperture. Instantiations are resolved to low energy, and hence entropy, forms in both the synchronous and coherent contexts, producing the internal experience, which can be stored as a memory, and recovered. I have adopted the term “instantiation” of information rather than “encoding” as the

² The subcortical structures provide much of the drive for cortical operations. Essentially the cortex is a consistent structure that can perform many functions; the different subcortical structures each have specific functions. In computational analogies, the subcortical functions could be modeled with a modest (1,000–2,000) set of rules; the cortex is a “programmable” structure able to perform many complex functions. The two systems interact. The cortex is evolution’s crown jewel.

³ “Mechanism” implies both a structure and associated processes.

latter implies that, with the appropriate tools, one might be able to decode something, extracting information, which I feel is unlikely, given the apparent undecipherable complexity of the processes and their results.

Modeling a set of elements—mini- and macro-columns—as comprising a single aperture supports the concept of projections among apertures. Information is instantiated in an aperture as a phase field, called a coherence map (CM) here to avoid confusion, and in coherent information structures (CISs), the active outputs of CMs, that are projected among apertures. Beyond the thalamus and thalamic reticular nucleus I have not included the subcortical structures in this paper, other than a reference to those structures as influencing the underlying natural frequencies of cortical apertures. The relationship of an aperture to its corresponding thalamic area and the intervening sector in the thalamic reticular nucleus (TRN) is reduced to a composite node (CN), an abstraction useful in describing how various cortical apertures could form a temporary synchronous network, an ensemble, bidirectionally exchanging these CISs. The bidirectional causation within the ensemble enables all its constituent apertures to contribute to its evolving resolution through information entropy minimization, differing from a flow-through, or waterfall, model.

The ensemble constitutes a working memory. An ensemble may form through perception or through access to a memory. Memory (I have reserved the term for the latent states) resides in associated latent CMs in multiple apertures. CMs are formed through various modulatory mechanisms such as synaptic remodeling and glial interactions. CMs may have both strength-of-coupling and phase-modulation mechanisms, the latter becoming more predominant during memory consolidation. An aperture may contain multiple CMs, each of which will be responsive to different input projections. When properly stimulated, a subset of CMs in multiple apertures can cause the re-establishment of the ensemble—resurrection—in recall or recognition. The associations for stabilized declarative memory are maintained in the medial temporal lobe (MTL, e.g., the hippocampus), but are maintained within the apertures themselves for consolidated memory. The MTL provides a stabilized memory bridge between the ensemble and the formation of a consolidated memory.

Themes

The coherent apertures model incorporates several themes that reveal underlying consistencies, which I presume are actually found in the CNS. These themes emerged as my understanding of the CNS evolved:

- Radiant energy concepts
- Networks
- Information and entropy.

A radiant energy system manipulates energetic waves such as light, microwaves, radio waves, and sounds. In the coherent apertures model, radiant energy concepts apply to many circumstances, with the property of coherence particularly significant. In this model, radiant energy is analogous to neural activity. Radiant energy will emanate from a source, potentially projecting through an aperture, a “hole,” within which the waves may be transformed or modulated in some manner, depending upon the characteristics of the aperture. The aperture may be a single “hole” or it may be formed from multiple elements that may or may not be adjacent or have some fixed pattern. Reflective and refractive concepts were particularly useful (e.g., thick mirror, phase conjugate mirror, dual phase conjugate mirror, hologram, Fourier optics, point spread function, and superposition), some of which were suited to the instantiation of information in the aperture. The

consolidated instantiation of information was modeled as analogous to a phase hologram, a phase-modulating latent coherence map. Phase quantization, applied in digital holography, enhanced the development and recovery of CMs. The pumped AFP model is analogous to a laser. An aperture-wide field potential (AFP) reflects the degree to which the LFPs are synchronous across the aperture. A coherence path length is the distance and/or time over which photons in a projection are coherent, here a measure of the distance across an aperture over which the LFP is coherent, and in the case of the LFP, synchronous. Coherence path length is useful in understanding the coupled array behavior of an aperture. The coherence of radiation projected from multiple points in one aperture to a point on another aperture can be described through application the van Cittert-Zernike theorem (VCZ), which allows a coherent aperture to be treated as a node in an ensemble.

A cortical aperture, in addition to being modeled as a radiant energy system, is often described as a flat lattice of coupled elements—minicolumns—to which the network dynamics concepts initiated by Kuramoto [11] have been applied, particularly with respect to the critical point for network synchronization. Applying the work of others, in Supplemental Materials I have extended Kuramoto's basic concepts of phase-modulated synchronization. An ensemble, although initiated from a limited source, recruits multiple areas, reflecting the network connections. Perception can be modeled as establishing an ensemble, the internal experience, incorporating both relatively stable and malleable apertures. Memory is instantiated among a network of distributed apertures with latent connections that can establish, reinforce, or re-establish an ensemble.

Information entropy provides a useful way of describing information in an instantiation, while still supporting a physical model. Information entropy and energy are associated, since higher degrees of freedom (more complex states) have higher entropies, requiring more energy. Information entropy, as determined by complexity, can be used as a relative measure of instantiation efficiency. The converse of complexity is orderliness, resulting from underlying biophysical processes. Increased efficiency is a reduction in the complexity of the instantiation that maintains the most important information. A decipherable neural code at all but the ends of the input and output subgraph apertures seems unlikely. Undecipherability does not mean that information is lost, only that it can't be directly recovered. I did not find undecipherable complexity a comforting idea. I could not find a reasonable alternative.

The Chapters

The coherent apertures model is theoretical, built on experimental evidence in the literature. I have attempted to provide plausible concepts as rationally constrained components of a useful operational framework. Each chapter has its role in the framework, introducing concepts that relate to coherent apertures and their collective and individual operations. Beyond the framework, the coherent aperture is the obvious starting point.

2. A Framework

The coherent apertures model has two frameworks: anatomical and conceptual. The system composed of the cortex, thalamus, and thalamic reticular nucleus provides a framework for integration of cortical areas—apertures—into synchronous subpopulations—ensembles—that are involved in a common task, creating the internal experience. Chapter 2 describes this system and its general operation.

3. The Coherent Cortical Aperture

Chapter 3 explores the evidence that a cortical area—an aperture—may become essentially synchronous over its extent. Why is the mechanism of aperture synchronization important? The mechanism(s) of synchronization can reflect information instantiation (Ch. 4). A synchronized

aperture may contain a coherent phase structure, which is composed of local phase differences relative to the overall synchronization. What good is coherence, anyway? The answers may help differentiate synchronization from coherence, as the relationship may be (and I would maintain, is) significant. The concept of an element in the aperture is less straightforward than expected. The pyramids provide the outputs from minicolumns, and the outputs from apertures; I have merged the terms for efficiency, as this is a model, not a strictly neuroanatomical discussion.

Gross aperture synchronization is a prerequisite of coherence. Measures of synchronization may differ: neural spikes or the LFP. They are not mutually exclusive, and may reflect a particular model under consideration, although an aperture-wide synchronized LFP will be considered the indicator in this model unless stated otherwise. I refer to an aperture-wide synchronized LFP as the Aperture Field Potential (AFP).⁴ Ising-like network arrays of minicolumn or pyramidal nodes underlie many aperture synchronization models, usually derived from the work originating with Yoshiki Kuramoto [11] describing phase modulation models, with a critical point in coupling strength leading to synchronization. In addition to modification of the Kuramoto model, I propose two additional synchronizing models. The pumped AFP model considers an aperture as a node connected to all of the elements. The laminar coherence model explores the possible effects of laminar differences in frequencies. I have attempted to unify this discussion of aperture cohering through expansion of the Kuramoto model, including the pumped AFP, in Supplemental Materials.

4. Information Instantiations in Apertures

The network, pumped AFP, and laminar aperture coherence models all contribute to information instantiation in the aperture through synchronization and subsequent coherence, described in Chapter 4. Cortical apertures synchronize. What is important about an aperture being synchronous, able to support coherence? How might this relate to information instantiation? The instantiation models are speculative, needing deeper modeling supported by experimental work and the analysis of large data sets arising from the simultaneous recording of many neurons within an aperture. I found no useful way to define particular information in an aperture. First, information was disseminated among the apertures of the ensemble. Secondly, as there were intermediate nodes that maintained relationships among CMs, such associations would be undecipherably complex, best characterized by information entropy. The relationships between memory types, their instantiations, and access are addressed in Ch. 7. Suffice it to say that a uniquely identified CM proves to be a useful, if abstract, concept.

5. The Aperture Operator

The model of an aperture operator is discussed in Ch. 5. The aperture in the coherent apertures model is a cortical area with a de facto operator that responds to inputs, producing outputs that are projected to other apertures. The operator of an aperture is composed of one or more functionals. Functionals are composed of functions, which respond to a particular facet or feature of input projections, e.g., edges. Functions are the local responses in the aperture, embodied in minicolumns and macrocolumns.

6. Integration of Coherent Cortical Apertures

It is well known that different sets of cortical areas synchronize depending on the task. In Ch. 6, I undertake modeling the binding of a set of specific synchronized cortical areas into an ensemble, with the exclusion of unsynchronized apertures. I elected to call such an active synchronous subgraph an “ensemble” for ease of reference. I favor the metaphor of the pieces playing together

⁴ I shall use the acronym LFP when used as such in the literature cited, although it may in fact be the AFP. It is presumed to be an aperture-wide synchronization unless noted otherwise.

harmoniously, as in an ensemble. The set of all apertures and their connections is a graph; an ensemble is a subgraph of apertures with synchronized LFPs, limited by its connections within the graph. The ensemble can be formed from perception, internal processes (e.g., recall), or a combination of them both. Three synchronizing models support the bidirectional causation between apertures, hence within the entire ensemble, resolving to a solution or consensus. I propose that an ensemble will resolve by minimizing its entropy, hence its energy expenditure. The ensemble, and its process of resolution, constitutes the internal experience.

7. Operations

Chapter 7 was fun, an exploration of the operations of perception, memory, and memory access of simple declarative sensory input. The coherent apertures model plausibly fits the situations and requirements. The formation of an ensemble and its resurrection reflected the coherence of apertures and their interchanges. A surprise was the emergence of potential outcomes as shaping the processes by which an ensemble operated: a face is recognized as being a face. We tend to see or do the expected. The resolution of an ensemble was biased by the most likely outputs and the early feature responses. The existence of three memory states—working, stabilized and consolidated—is well documented, their operation initially unclear. They all are, or were derived from, the ensemble, which is working memory.

1.2. Principles and Corollaries

Principles

Some principles for time-structured activity in the CNS, e.g., object perception, emerged while developing the coherent apertures model:

- The cortex is composed of functionally distinct areas—apertures (parcellation).
- A cortical area may synchronize.
- A synchronous aperture can produce a coherence map (CM), a phase field of a pattern of synchronized and disordered elements.
- The responses of the cohered functions within the CM produce one or more coherent information structures (CISs) that are embedded in the projections of activity from an aperture.
- Cortical apertures form a network graph.
- Communications in the cortical graph are bidirectional (with a few exceptions).
- A cohered aperture is a node in a subgraph.
- An aperture that is synchronized or about to synchronize will filter to accept CISs that are in the appropriate phase.
- Synchronized apertures seek a low net information entropy.
- An aperture may contain a pattern that, when active, is appropriate for activating one or more CMs, including those in other apertures.

Corollaries

Corollaries follow from the principles:

- Not all elements need to synchronize for the cortical area, or aperture, to synchronize.

- Synchronized elements may have local phase differences, i.e., they cohere.
- Aperture coherence may occur in response to coherent inputs.
- Aperture coherence may emerge.
- Concepts from radiant energy systems may be applicable.
- A CM may be characterized by its information entropy.
- A functional of an aperture is composed of elements performing some essentially common functions.
- The CIS instantiates some aspect of information in the synchronized portion of the aperture's projection.
- There is no coherent communication if both apertures in a pair are not cohered.
- A disordered aperture does not synchronize with other apertures.
- A subgraph of synchronized apertures will synchronize into an ensemble.
- Cohered apertures that are synchronized in an ensemble will comodulate through bidirectional causation.
- The internal experience is defined as the current ensemble.
- An active or latent CM may provide associations between or among other active or latent CMs.
- A CM may be latent, able to contribute to the self-assembly of an ensemble when receiving a critical level of appropriate excitation.
- Outcomes with higher probabilities of occurrence influence the resolution of the ensemble.
- Not all apertures in an ensemble may have instantiating CMs when the memory is latent.

1.3. History

Development of the Model

I did not begin by attempting to figure out how a resonant cortical network forms and works. I began with the cortical area. It was clear from the visual phenomena of (1) common fate [12, 13], in which a group of moving dots will perceptually separate from a stationary field of random dots, and (2) structure from motion [14, 15, 16], that the primary visual cortex would, and probably must, cohere. That led to the question of "how?" The cortical area does indeed cohere, and I found mechanisms supporting "how." Aleksandr Davydov pointed me to work initiated by Yoshiki Kuramoto [11, 17, 18] on the synchronization of coupled arrays and networks that was important. This expanded to include a more field-oriented model of a pumped local field potential, and a laminar differentiation of synchronization. This led to explorations of how information could be instantiated in such areas, how instantiations could be formed and modulated through local functions, how the instantiations could be communicated among cortical areas, how a group of areas could bind together around a common task, and how such a group could perform various operations, resolving to some conclusion. The overall model of synchronous groups of synchronous cortical areas emerged, almost of its own volition. It is a result of an exploration of coherent cortical apertures, not a starting point.

Background

This work has grown from many sources. Having received an undergraduate engineering degree (BSME, Massachusetts Institute of Technology) I worked in optoelectronics research and development for a large US corporation, including coherent optics and electronics. Following premedical studies (Duke University) I worked again in optoelectronics for industrial automation, leading to R&D in high accuracy electronic measuring systems involving electronic hardware, including custom digital and analog integrated circuit design, software, and statistical methods. During this period I undertook studies in perception, eventually leading to an MS and a PhD in experimental psychology (North Carolina State University), with theoretical and experimental work in hearing (thesis) and three-dimensional perception (dissertation). I have patents in auditory displays and a 3D display technology. I worked under grants and contracts from federal entities developing FAA audio displays, and 3D visual displays of molecular models and airspaces through software. Some of the work, and good collaboration on spatial perception, was done in the laboratory of Joseph Lappin at Vanderbilt University. I developed auditory displays in my company's laboratory (Allotech, Inc.), patenting one display method.

While working at Intelligent Automation, Inc. (Rockville, MD), Aleksandr Davydov introduced me to the work of Yoshiki Kuramoto [11] on the synchronization of large networks for consideration as a model of the behavior of the cortex. Kuramoto mentions this possibility himself. I had come to the conclusion that cortical areas could be considered as apertures and that they should self-cohere. I was not aware of Kuramoto's model, so his work was a joy to discover. I have incorporated it, and the considerable subsequent work, into my own in multiple scales and embodiments.

In addition to network modeling, I have been introduced to many ideas in radiant energy, from large array telescopes to lasers, that have had a significant input to this model. The concept of the coherent cortical aperture is a logical outgrowth, predating my dissertation (1993). Phase conjugate mirrors [19] and the thick mirror model together model both the cortical transform and memory. The pumped aperture field potential (AFP) model has some conceptual roots in the laser. Using the van Cittert-Zernike theorem to describe the projection of radiation from one coherent aperture to another [20] came to me while I was exercising (I guess it is good for you). Research by others on the coherence and synchronization of multiple lasers in various configurations led to the realization that a transient (ad hoc) network of such nodes could form a synchronous network during working memory that could decompose into a latent memory, and re-form from it. The use of Shannon and Weaver's [21, 22] work in information entropy reflects my exposure to statistics in work and academia, allowing consideration of information instantiated in various forms to be described by its entropy.

A rather remarkable result from modeling an active bidirectionally coupled subgraph was the realization that all nodes in such an ensemble would influence the behavior of the ensemble; thus, past the initiation stages, the potential outcomes would influence the trajectory of the entire ensemble: you tend to see faces in clouds. My future work is undetermined. There are many paths to follow, many questions left unanswered, concepts in need of testing. An abstract model and potential technological implementations are topics for a separate document.

1.4. Research Models

Computational Neuroscience

Computational neuroscience is theoretical research, employing models as representations of a system, intended to further the understanding of brain function. The CNS is considered to be composed of structures that collectively provide information processing capabilities. Computa-

tional neuroscience reaches beyond models of symbolic processing [23] into modeling of neural activity, attempting to describe the operating principles of the central nervous system and its components. Models differ in their relationships to neurophysiology, from computerized large scale neuron-based architectures (e.g., Eliasmith et al. [24], Merolla et al. [25]) to more abstract systems (e.g., Grossberg [26]). Attempts to model the brain with tools such as NEST [27] computationally stress the limits of computers [28]; in 2013 a supercomputer required 3 minutes to calculate the operations of a model of about 1 mm² of cortex over one second [29]. Computational power is increasing but the finite limits of computers probably limit the success of such modeling. Different paradigms have attempted to model CNS function from operational standpoints rather than neurological modeling. De Garis et al. [30] have reviewed such work.

Technology [30, 31] has supported the growth of computational neuroscience, creating both a great opportunity for more complete knowledge of the activities in the CNS and frustration over what to do with this wealth of data. Neural circuit models [32, 33, 34] have been overwhelmed despite of massive computational capabilities, as more data compounds the problem [35]. Computational neuroscience is in a state of flux—nothing new in the neurosciences—as new hypotheses emerge. The very concept of computing is changing. Computation beyond Turing machines is being explored [36]. Goldin et al. [37] propose that beyond the Church-Turing model of computation, communication and computation occur together as one might expect in the mammalian central nervous system (CNS). In a review Hepp [38] describes approaches to a global workspace (GW) [39] of coherently linked neurons. Liquid state [40], analog computer [41], and quantum mechanical [42] models of the CNS have been proposed. Ideas abound.

Networks: ANNs

Network models, a class of computational neuroscience, are currently of considerable interest, although complex [43]. Synaptic timing, strength, and plasticity provide the bases for many artificial neural network (ANN) models [33, 34, 44, 45, 46, 47, 48, 49]. Such neural network models are incorporated into higher level models [26, 50, 51] either directly or by implication, acknowledging the division of the cortex into many interacting areas [52]. The network models of the CNS are long standing. Hebbian models [53] of changes in synaptic strengths through long-term potentiation (LTP) and long-term depression (LTP), particularly under conditions of critical timing, have been applied to ANNs operating in fixed and flexible architectures. Spike timing dependent synaptic plasticity (STDP) is often incorporated in ANNs [49]. Such ANNs have had widespread applications, but have little direct relationship with current models of the CNS. Cortical ANNs (CANNs) [54] attempt more cortically oriented models to explore hypotheses of cortical function. Consistent with empirical evidence, such models presume a similarity across all areas within the cortex, against which differences are interpreted. Neural network models may employ the columnar structure of the cortex to provide the nodes. The generation of such columns may itself represent self-organization in the cortex [55, 56]. The outputs of these cortical models are the activity patterns of the elements as a corpus [57]. Hierarchical convolutional neural networks (HCNNs) [10] attempt to maintain significant neurophysiological validity by modeling cortical areas as layers performing increasingly abstract functions. Feedback loops create goal-driven aspects of such modeling.

In most models the architecture (connectivity) is predetermined (e.g., Edelman 1982 [45]), although Risi and Stanley [58] propose an evolved connectivity. The CNS is composed of a well organized set of neural elements with connectivity described at multiple scales. That is not to say that the connections between the elements are obvious—great effort has gone into elucidating these patterns [59, 60, 61]; more is yet to be done [62]. In principle the CNS can be mapped, although there are always individual differences. Potentially the CNS is a deterministic system [63, 64] with sensitive locally definable functions, making it difficult to predict results from inputs, as such systems are often chaotic [65, 66]. Models that attempt to use operational regularity face the

challenges of deterministic systems that have simple behaviors that are exercised in a large number of instances—in the CNS in the form of a great many neurons or minicolumns. Given the increases in computing power and multiprocessor architectures, very large scale models incorporating synaptic plasticity within hierarchical network architectures are being developed [24, 25, 30, 67, 68, 69]. Consistently, these models are based on synaptic actions, although Steck et al. [70] propose an ANN model with an optical field in a bulk non-linear continuum.

Neurophysiological Models

The coherent apertures model is basically a neurophysiological model with a network emphasis. The Hodgkin–Huxley model [71, 72, 73, 74, 75] of neural action potential generation underlies higher level models and is reflected in the pumped LFP model of synchronization in the coherent apertures model. Neurophysiological models of the CNS describe functions and operations in terms of biological structures and actions. They are based on anatomy, physiology, and activity flows. Peripheral inputs to thalamic nuclei are modulated and subsequently relayed to primary perceptual cortical areas. Higher order cortical areas have corresponding thalamic nuclei that have no peripheral inputs. The majority of inputs to the thalamus are not of peripheral sensory origin. Destexhe [76] proposes that the majority of activity is the modulation of internal dynamics of the cerebral cortex, consistent with the models of vision of Jehee et al. [77] and Lamme et al. [78] in which layers or levels of visual areas reciprocally interact to refine function. Synchrony in dynamically networked cortical areas is considered a hallmark of consciousness [79, 80, 81, 82]. Boustani and Destexhe [3] and Muller and Destexhe [83] propose that such synchrony is large-scale, while local cortical activity incorporating complex information has more overtly chaotic behavior [84]. Dehaene et al. [85] and Dehaene and Changeux [86] support the concept that consciousness arises from the long-range synchronization of cortical areas into a Global Neuronal Workspace (GNW) with a subsequent taxonomy of consciousness. Along that line, Henke [87] proposes that CNS modes for memory formation and consciousness differ.

The thalamic reticular nucleus (TRN) is a component of some models. The TRN is a sheet-like structure of inhibitory neurons receiving collaterals from both thalamocortical and corticothalamic projections. Relevant to the framework suggested in the coherent apertures model, Min [80] and Drover et al. [88] proposed an operation of CNS function focused on the TRN as providing the underlying synchronization among cortical regions and their corresponding nuclei in the thalamus through loopbacks. Destexhe et al. [89] propose the TRN as capable of generating oscillations within its population. The TRN is an important structure, but perhaps not of such singular importance as Min proposes. It has an inherent natural frequency, being an active component of a more complex system.

There are many model types employed in theoretical descriptions of the operation of the CNS. The large number, type variety, and complexity of structures make any model a simplification. What is gained by the simplification may be lost through excessive reductions. The end result of any modeling must be amenable to some tests that can be performed with real, living creatures. Otherwise it is self-referential; perhaps a useful exercise in thinking about how the CNS works, but still a speculation. Some tests are post hoc—how well does the model fit actual data? Are there data that refute it? What tests can be proposed? Can they tease apart to true and false aspects of the model? I have addressed some of these issues through extensive references and a proposed test of the model.

References

- 1 Buzsáki, G., & Schomburg, E. W. (2015). What does gamma coherence tell us about inter-regional neural communication? *Nat. Neurosci.*, *18*(4), 484-489.
- 2 Crick, F., & Koch, C. (2003). A framework for consciousness. *Nat. Neurosci.*, *6*(2), 119-126.
- 3 El Boustani, S., & Destexhe, A. (2010). Brain dynamics at multiple scales: can one reconcile the apparent low-dimensional chaos of macroscopic variables with the seemingly stochastic behavior of single neurons? *Int. J. Bifurcat. Chaos*, *20*(06), 1687-1702.
- 4 Gray, C. M. (1999). The temporal correlation hypothesis review of visual feature integration: Still alive and well. *Neuron*, *24*(1), 31-47.
- 5 Uhlhaas, P., Pipa, G., Lima, B., Melloni, L., Neuenschwander, S., Nikolic, D., & Singer, W. (2009). Neural synchrony in cortical networks: history, concept and current status. *Front. Integrative Neurosci.*, *3*(Article 17), 1-19.
- 6 Wolfe, J. M. & Cave, K. R. (1999). The psychophysical evidence review for a binding problem in human vision. *Neuron*, *24*(1), 11-17.
- 7 Rose, S. (2004). Part I. Introduction: The new brain sciences. In Rees, D., & Rose, S. (Eds.). *The new brain sciences: Perils and prospects*, (pp. 1-14). NY: Cambridge Univ. Press.
- 8 Churchland, A. K., & Abbott, L. F. (2016). Conceptual and technical advances define a key moment for theoretical neuroscience. *Nat. Neurosci.*, *19*(3), 348-349.
- 9 Sejnowski, T. J., Churchland, P. S., & Movshon, J. A. (2014). Putting big data to good use in neuroscience. *Nat. Neurosci.*, *17*(11), 1440-1441.
- 10 Yamins, D. L. K., & DiCarlo, J. J. (2016). Using goal-driven deep learning models to understand sensory cortex. *Nat. Neurosci.*, *19*(3), 356-365.
- 11 Kuramoto, Y. (1975). Self-entrainment of a population of coupled non-linear oscillators. In *International Symposium on Mathematical Problems in Theoretical Physics* (pp. 420-422). Berlin Heidelberg: Springer.
- 12 Ehrenstein, W. H., Spillmann, L., & Sarris, V. (2003). Gestalt issues in modern neuroscience. *Axiomathes*, *13*(3-4), 433-458.
- 13 Lappin, J. S., Wason, T. D., & Akutsu, H. (1987). Visual detection of common motion of spatially separate points. *Bull. Psychonomic Soc.*, *25*(5), 343-343).
- 14 Lappin, J. & Wason, T. (1991). Chapter 28. The perception of geometrical structure from congruence. In Ellis, S. (Ed.). *Pictorial communications in virtual and real environments*. London: Taylor & Francis. (Previously published in Ellis, S. R., Kaiser, M. K., & Grunwald, A. (Eds.). *Spatial Displays and Spatial Instruments; NASA Conference Publication 10032* (pp. 18-1 - 18-15).
- 15 Wason, T. (1993). Construction and Evaluation of a Three-Dimensional Display from a Two-Dimensional Projection Surface Based On Theoretical Considerations of Metrification and Affine Space (Doctoral dissertation). North Carolina State University. (UMI No. 9409172)
- 16 Wason, T., (1998). *U.S. Patent No. 5,751,927*. (Method and apparatus for producing three dimensional displays on a two dimensional surface). Washington,DC: U.S. Patent and Trademark Office.
- 17 Arenas, A., D'iaz-Guilera, A., Kurthsl, J., Moreno, Y., & Zhou, C. (2008). Synchronization in complex networks. *Phys. Rep.*, *469*(3), 93-153.
- 18 Kuramoto, Y. (1984). Cooperative dynamics of oscillator community a study based on lattice of rings. *Prog. Theor. Phys. Supp.*, *79*, 223-240.
- 19 Weiss, S., Sternklar, S., & Fischer, B. (1987). Double phase-conjugate mirror: analysis, demonstration, and applications. *Opt. Lett.*, *12*(2), 114-116.
- 20 Baltes, H., & Peeweeda, H. (1980). Partially coherent sources with phase profile and the Van Cittert-Zernike theorem. *Lettere Al Nuovo Cimento (1971 - 1985)*, *27*(16), 541-543.
- 21 Shannon, C. E. (1948). A mathematical theory of communication. *Bell Syst. Tech. J.*, *27*, 379-423, 623-656 July, October 1948.
- 22 Shannon, C. E., & Weaver, W. (1963). *The Mathematical Theory of Communication*. (pp. 45-61). University of Illinois Press. (Original work published in 1949)
- 23 Wittrock, M. C. (1992). Generative learning processes of the brain. *Educ. Psychol.*, *27*(4), 531-541.
- 24 Eliasmith, C., Stewart, T. C., Choo, X., Bekolay, T., DeWolf, T., Tang, C., & Rasmussen, D. (2012). A large-scale model of the functioning brain. *Science*, *338*(6111), 1202-1205.

- 25 Merolla, P. A., Arthur, J. V., Alvarez-Icaza, R., Cassidy, A. S., Sawada, J., Akopyan, F., Jackson, B. L., Imam, N., Guo, C., Nakamura, Y., Brezzo, B., Vo, I., Esser, S. K., Appuswamy, R., Taba, B., Amir, A., Flickner, M. D., Risk, W. P., Manohar, R., & Modha, D. S. (2016). A million spiking-neuron integrated circuit with a scalable communication network and interface. *Science*, 345(6197), 668-673.
- 26 Grossberg, S. (2013). Adaptive resonance theory: How a brain learns to consciously attend, learn, and recognize a changing world. *Neural Networks*, 37, 1-47.
- 27 Gewaltig, M.-O., & Diesmann, M. (2007) NEST (Neural Simulation Tool), *Scholarpedia*, 2(4), 1430. http://www.nest-initiative.org/Software>About_NEST
- 28 Kunkel, S., Potjans, T. C., Eppler, J. M., Plesser, H. E., Morrison, A., & Diesmann, M. (2011). Meeting the memory challenges of brain-scale network simulation. *Front. Neuroinformatics*, 5, 35.
- 29 Kunkel, S., Schmidt, M., Eppler, J. M., Plesser, H. E., Igarashi, J., Masumoto, G., Fukai, T., Ishii, S., Morrison, A., Diesmann, M., & Helias, M. (2013). From laptops to supercomputers: a single highly scalable code base for spiking neuronal network simulations. *BMC Neurosci.*, 14(Suppl 1), 163.
- 30 De Garis, H., Shuo, C., Goertzel, B., & Ruiting, L. (2010). A world survey of artificial brain projects, Part I: Large-scale brain simulations. *Neurocomputing*, 74(1), 3-29.
- 31 Nature Neuroscience (2011). Focus on computational and systems neuroscience. *Nat. Neurosci.*, 14(2), 121.
- 32 Dehaene, S., Kerszberg, M., & Changeux, J-P (1998). A neuronal model of a global workspace in effortful cognitive tasks. *P. Natl. Acad. Sci.*, 95(24), 14529-14534.
- 33 Hebb, D. O., (1976). Physiological learning theory. *J. Abnorm. Child Psych.*, 4(4), 309-314.
- 34 Hopfield, J. J. & Tank, D. W., (1986). Computing with neural circuits: a model. *Science*, 233(4764), 625-633.
- 35 Hodges, A. (2012). Beyond Turing's machines. *Science*, 336(6078), 163-164.
- 36 Wegner, P., & Goldin, D. (2003). Computation beyond Turing machines. *Commun. ACM*, 46(4) 100-102.
- 37 Goldin, D., Wegner, P., Cooper, S., & Löwe, B. (2005). The Church-Turing thesis: Breaking the myth. *Lect. Notes Comput. Sci.*, 3526, 31-64.
- 38 Hepp, K. (2012). Coherence and decoherence in the brain. *J. Math. Phys.*, 53(095222), 5 pages.
- 39 Baars, B. J., Franklin, S., & Ramsay, T. Z. (2013). Global workspace dynamics: cortical "binding and propagation" enables conscious contents. *Frontiers in Psychol.*, 4, 200.
- 40 Maass, W. (2011). Liquid state machines: Motivation, theory, and applications. In Cooper, S. B., & Sorbi, A. (Eds.), *Computability in context: Computation and logic in the real world* (pp. 275-296). Singapore: World Scientific.
- 41 Shagrir, O. (2010). Brains as analog-model computers. *Stud. Hist. Philos. Sci., Part A*, 41(3), 271-279.
- 42 Penrose, R. (1989). *The emperor's new mind*. Oxford, New York, Melbourne: Oxford University Press.
- 43 Sporns, O. (2014). Contributions and challenges for network models in cognitive neuroscience. *Nat. Neurosci.*, 17(5), 652-660.
- 44 Basheer, I. A., & Hajmeer, M. (2000). Artificial neural networks: fundamentals, computing, design, and application. *J. Microbiol. Meth.*, 43(1), 3-31.
- 45 Edelman, G. M., & Reeke, G. N. (1982). Selective networks capable of representative transformations, limited generalizations, and associative memory. *P. Natl. Acad. Sci.*, 79(6), 2091-2095.
- 46 Hinton, G. E. (1992). How neural networks learn from experience. *Sci. Am.*, 267(3), 145-151.
- 47 Hinton, G. E. (2011). Machine learning for neuroscience. *Neural Systems & Circuits*, 1(1), 1-2.
- 48 Hoppensteadt, F. C., & Izhikevich, E. M. (1997). *Weakly connected neural networks*. New York: Springer-Verlag.
- 49 Song, S., Miller, K. D. & Abbott, L. F. (2000). Competitive Hebbian learning through spike-timing-dependent synaptic plasticity. *Nat. Neuro.*, 3(9), 919 - 926.
- 50 Faugeras, O., Touboul, J. & Cessac, B. (2009). A constructive mean-field analysis of multi-population neural networks with random synaptic weights and stochastic inputs. *Front. Comput. Neurosci.*, 3(1), 1-28.
- 51 Grossberg, S. (2007). Consciousness CLEARs the mind: Brain and consciousness. *Neural Networks*, 20(9), 1040-1053.
- 52 Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex*, 1(1), 1-47.
- 53 Hebb, D. O. (1949). *The Organization of Behavior*. New York: Wiley & Sons.
- 54 Fung, C. C. A., Wong, K. Y. M., & Wu, S. (2009). A moving bump in a continuous manifold: A comprehensive study of the tracking dynamics of continuous attractor neural networks. *Neural Comp.*, 22(3), 752-792.

- 55 Chawanya, T., Aoyagi, T., Nishikawa, I., Okuda, K. & Kuramoto, Y. (1993). A model for feature linking via collective oscillations in the primary visual cortex. *Biol. Cybern.*, 68(6), 483-490.
- 56 Bressloff, P. C. (2005). Spontaneous symmetry breaking in self-organizing neural fields. *Biol. Cybern.*, 93(4), 256-274.
- 57 Tommerdahl, M., Favorov, O. V., & Whitsel, B. L. (2010). Dynamic representations of the somatosensory cortex. *Neuroscience & Biobehavioral Reviews*, 34(2), 160-170.
- 58 Risi, S., & Stanley, K. O. (2012). An enhanced hypercube-based encoding for evolving the placement, density, and connectivity of neurons. *Artif. Life*, 18(4), 331-363.
- 59 Modha, D. S., & Singh, R. (2010). Network architecture of the long-distance pathways in the macaque brain. *P. Natl. Acad. Sci.*, 107 (30), 13485-13490.
- 60 Shepherd, GM (ed.) (2004). *The synaptic organization of the brain* (5th ed.). NY: Oxford.
- 61 Wakana, Setsu, Jiang, Hangyi, Nagae-Poetscher, Lidia M., van Zijl, Peter C. M., & Mori, Susumu (2004). Fiber tract-based atlas of human white matter anatomy. *Radiology*, 230(1), 77-87.
- 62 Alivisatos, A. P., Chun, M., Church, G. M., Deisseroth, K., Donoghue, J. P., Greenspan, R. J., McEuen, P. L., Roukes, M. L., Sejnowski, T. J., Weiss, P. S., & Yuste, R. (2013). The brain activity map. *Science*, 339(6125), 1284-1285.
- 63 Bressloff, P. C. (2009). Stochastic neural field theory and the system-size expansion. *SIAM J. Appl. Math.*, 70(5), 1488-1521.
- 64 Giacomini, G., Luçon, E. & Poquet, C. (2014). Coherence stability and effect of random natural frequencies in populations of coupled oscillators. *J. Dyn. Differ. Equ.*, 1040(7294), 333-367.
- 65 Kellert, S. H. (1993). *In the Wake of Chaos: Unpredictable Order in Dynamical Systems* (p. 62). University of Chicago Press.
- 66 Wagner, T., Fell, J. & Lehnertz, K. (2010). The detection of transient directional couplings based on phase synchronization. *New J. Phys.*, 12, 053031.
- 67 Bhuiyan, M. A., Pallipuram, V. K., Smith, M. C., Taha, T., & Jalasutram, R. (2010). Acceleration of spiking neural networks in emerging multi-core and GPU architectures. In *2010 IEEE International Symposium on Parallel & Distributed Processing, Workshops and Phd Forum (IPDPSW)* (pp. 1-8). IEEE.
- 68 Djurfeldt, M., Lundqvist, M., Johansson, C., Rehn, M., Ekeberg, O., & Lansner, A. (2008). Brain-scale simulation of the neocortex on the IBM Blue Gene/L supercomputer. *IBM J. Res. Dev.*, 52(1-2), 31-41.
- 69 Preissl, R., Wong, T. M., Appuswamy, R., Datta, P., Flickner, M., Singh, R., Esser, S. K., McQuinn, E., Risk, W. P., Simon, H. D., & Modha, D. S. (2012). Compass: A scalable simulator for an architecture for cognitive computing. In *Proceedings of the International Conference for High Performance Computing, Networking, Storage, and Analysis* (p. 54). IEEE Computer Society Press.
- 70 Steck, J. E., Skinner, S. R., Cruz-Cabrera, A. A., Yang, M., & Behrman, E. C. (2007). *Field Computation for Artificial Neural Network Hardware: Nonlinear optical materials*. <http://www.scientificcommons.org/42986830>.
- 71 Hodgkin, A. L., Huxley, A. F. & Katz, B. (1952). Measurement of current-voltage relations in the membrane of the giant squid axon of *Loligo*. *J. Physiol.*, 116(4), 424-448.
- 72 Hodgkin, A. L., & Huxley, A. F. (1952). Currents carried by sodium and potassium ions through the membrane of the giant squid axon of *Loligo*. *J. Physiol.*, 116(4), 449-472.
- 73 Hodgkin, A. L., & Huxley, A. F. (1952). The components of membrane conductance in the giant squid axon of *Loligo*. *J. Physiol.*, 116(4), 473-496.
- 74 Hodgkin, A. L., & Huxley, A. F. (1952). The dual effect of membrane potential on sodium conductance in the giant squid axon of *Loligo*. *J. Physiol.*, 116(4), 497-506.
- 75 Hodgkin, A. L., & Huxley, A. F. (1952). A quantitative description of membrane current and its application to conduction and excitation in nerve. *J. Physiol.*, 117(4):500-44.
- 76 Destexhe, A. (2011). Intracellular and computational evidence for a dominant role of internal network activity in cortical computations. *Curr. Opin. Neurobiol.*, 21(5), 717-725.
- 77 Jehee, J. F. M., Roelfsema, P. R., Deco, G., Murre, J. M. J., & Lamme, V. A. F. (2007). Interactions between higher and lower visual areas improve shape selectivity of higher level neurons—Explaining crowding phenomena. *Brain Res.*, 1157(0), 167-176.
- 78 Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.*, 23(11), 571-579.

- 79 Contreras, D., Destexhe, A., Sejnowski, T. J., & Steriade, M. (1996). Control of spatiotemporal coherence of a thalamic oscillation by corticothalamic feedback. *Science*, 274(5288), 771–774.
- 80 Min, B-K. (2010). A thalamic reticular networking model of consciousness. *Theor. Biol. Med. Model.*, 7(10), 1-18.
- 81 Nunez, P. L. (2000). Toward a quantitative description of large-scale neocortical dynamic function and EEG. *Behav. Brain Sci.*, 23(3), 371-398.
- 82 Wendling, F., Ansari-Asl, K., Bartolomei, F., & Senhadji, L. (2009). From EEG signals to brain connectivity: A model-based evaluation of interdependence measures. *J. Neurosci. Meth.*, 183(1), 9-18.
- 83 Muller, L. E., & Destexhe, A. (2012). Propagating waves in thalamus, cortex and the thalamocortical system: experiments and models. *J. Physiol. (Paris)*, 106(5), 222-238.
- 84 Destexhe, A. (2009). Self-sustained asynchronous irregular states and Up/Down states in thalamic, cortical and thalamocortical networks of nonlinear integrate-and-fire neurons. *J. Comput. Neurosci.*, 27(3), 493-506,
- 85 Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn. Sci.*, 10(5), 204-211.
- 86 Dehaene, S., & Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, 70(2), 200-227.
- 87 Henke, K. (2010). A model for memory systems based on processing modes rather than consciousness. *Nat. Rev. Neurosci.*, 11(7), 523-532.
- 88 Drover, J. D., Schiff, N. D., & Victor, J. D. (2010). Dynamics of coupled thalamocortical modules. *J. Comput. Neurosci.*, 28(3), 605-616.
- 89 Destexhe, A., Contreras, D., Sejnowski, T. J., & Steriade, M. (1994). A model of spindle rhythmicity in the isolated thalamic reticular nucleus. *J. Neurophysiol.*, 72(2), 803-818.
- 90 Edelman, G. M., & Gally, J. A. (2001). Degeneracy and complexity in biological systems. *P. Natl. Acad. Sci.*, 98(24), 13763-13768.
- 91 Marder, E., & Taylor, A. L. (2011). Multiple models to capture the variability in biological neurons and networks. *Nat. Neurosci.*, 14(2), 133-138.
- 92 Toro, R., Perron, M., Pike, B., Richer, L., Veillette, S., Pausova, Z., & Paus, T. (2008). Brain size and folding of the human cerebral cortex. *Cereb. Cortex*, 18(10), 2352-2357
- 93 Henery, C. C., & Mayhew, T. M. (1989). The cerebrum and cerebellum of the fixed human brain: efficient and unbiased estimates of volumes and cortical surface areas. *J. Anat.*, 167, 167–180.
- 94 Pallas, S. L., Roe, A. W. & Sur, M. (1990). Visual projections induced into the auditory pathway of ferrets. I. Novel inputs to primary auditory cortex (AI) from the LP/pulvinar complex and the topography of the MGN-AI projection. *J. Comp. Neurol.*, 298(1), 50–68.
- 95 Sharma J., Angelucci A., Sur M. (2000). Induction of visual orientation modules in auditory cortex. *Nature*, 404(6780), 841-847.
- 96 Glasser, M. F., Coalson, T. S., Robinson, E. C., Hacker, C. D., Harwell, J., Yacoub, E., Ugurbil, K., Andersson, J., Beckmann, C. F., Jenkinson, M., Smith, S. M., & Van Essen, D. C. (2016). A multi-modal parcellation of human cerebral cortex. *Nature*, 536(7615), 171-178.
- 97 Power, J. D., Cohen, A. L., Nelson, S. M., Wig, G. S., Barnes, K. A., Church, J. A., Vogel, A. C., Laumann, T. O., Miezin, F. M., Schlaggar, B. L., & Petersen, S. E. (2011). Functional network organization of the human brain. *Neuron*, 72(4), 665-678.
- 98 Behrens, T. E. J., & Sporns, O. (2012). Human connectomics. *Curr. Opin. Neurobiol.*, 22(1), 144-153.
- 99 Hagmann, P., Cammoun, L., Gigandet, X., Gerhard, S., Grant, P. E., Wedeen, V., Meuli, R., Thiran, J-P, Honey, C. J., & Sporns, O. (2010). MR connectomics: Principles and challenges. *J. Neurosci. Meth.*, 194(1), 34-45.
- 100 Sporns, O., Tononi, G., & Kötter, R. (2005). The Human Connectome: A structural description of the human brain. *PLoS Comput. Biol.*, 1(4), e42.
- 101 Yap, P-T, Wu, G., & Shen, D. (2010). Human Brain Connectomics: Networks, techniques, and applications [Life Sciences]. *IEEE Signal Proc. Mag.*, 27(4), 131 - 134.
- 102 Amunts, K., Malikovic, A., Mohlberg, H., Schormann, T., & Zilles, K. (2000). Brodmann's areas 17 and 18 brought into stereotaxic space—where and how variable? *Neuroimage*, 11(1), 66-84.
- 103 Stanley, G. B (2013). Reading and writing the neural code. *Nat. Neurosci.*, 16(3), 259-263.
- 104 Anderson, R. C., Pichert, J. W., Goetz, E. T., Schallert, D. L., Stevens, K. V., & Trollip, S. R. (1976). Instantiation of general terms. *J. Verb. Learn. Verb. Be.*, 15(6), 667-679.