**Computational Theories and their Implementation in the Brain:**

**The Legacy of David Marr**

**Edited by LM Vaina and RE Passingham**

**Contents**

**Foreword** Lucia M. Vaina

**Theme**: This will use correspondence between David Marr and colleagues about the papers on the cerebellum, archicortex and neocortex around the time that they were published. It will also use unpublished materials from his talks some years later and extract his comments about the papers. The foreword will also discuss how this book came about and the intention of the editors in putting it together.

**Introduction** Richard E. Passingham

**Theme:** This will use the abstract of David Marr's first cerebellar paper to show that a satisfactory theory concerning implementation must satisfy four criteria. 1) It must have the correct idea about the function of the structure (computational level). 2) It must specify the input/output transformations of the structure (algorithmic level). 3) It must give a detailed account of how the cell types, cell properties and connections between cells carry out that function and those transformations (implementational level). 4) It must make clear predictions that can be tested, and preferably predictions that are not made by other theories.

### *Section 1: A Theory of Cerebellar Cortex*

**Authors:** Takeru Honda and Masao Ito

**Title***: From the Marr-Albus-Ito hypothesis to liquid state machine theory*

**Chapter theme:** The chapter will start by recalling the great impact of David Marr's cerebellum paper. When it appeared in 1969 in Journal Physiology, it was a revelation, which one might only rarely experience in one’s life. The chapter will continue by reviewing the effect that Marr’s model had in experimental neuroscience in the field of synaptic plasticity and memory processes. Finally, the chapter will present the liquid state machine as an advanced model of cerebellar circuits.

**Author:** Egidio D’Angelo

**Title:** *Challenging the Marr theory of cerebellum*

**Chapter theme:** The focus of the chapter will be on how the Marr’s theory has been challenged by recent experimental findings. Recent experimental studies have raised several challenging issues. (1) The cerebellar granular layer does not simply perform a simple combinatorial decorrelation of the inputs: there is evidence both that it performs complex nonlinear spatio-temporal transformations and that it is endowed with synaptic plasticity. (2) Transmission from granule cell to Purkinje cells does not simply lead to beam formation but also to vertical columns of activation. (3) The olivo-cerebellar loop may perform complex timing operations rather than just error detection and teaching. (4) The dynamics of the Purkinje cell firing cannot be accounted for a simple linear integrator: they include pacemaking, burst–pause discharges, and bistable states in response to inputs from the mossy and climbing fiber synaptic. (5) In additional to parallel fiber LTD, long-term synaptic plasticity involves multiple mechanisms at several cerebellar synapses. (6) Oscillation and resonance could set up coherent cycles of activity, so designing a functional geometry that goes beyond pre-wired anatomical circuits.

**Authors:** Paul Dean & John Porrill

**Title:** *The Importance of Marr's Three Levels of Analysis for Understanding Cerebellar Function*

**Chapter theme**: The main theme of the chapter will be to show that Marr’s very general three-level framework for understanding complex information-processing systems (computation, algorithm, implementation) is extremely useful for research on cerebellar function. It is not clear why so few people use it.

The chapter will discuss how the original model differs from the Albus model, and why it has never been implemented to solve an actual motor-control problem. One of these points concerns the learning rule, and how it differs from the Least Mean Squares rule typically used nowadays.

***Section 2:*** [***Simple Memory: A Theory for Archicortex***](http://rstb.royalsocietypublishing.org/content/262/841/23.short?rss=1&ssource=mfc)

**Author:** Alessandro Treves

**Title:** *The Dentate Gyrus, defining anew memory of David Marr*

**Chapter theme**: The focus will be on the dentate gyrus. The dentate is one subdivision of the hippocampus that demonstrates, almost by absurdum, the degree to which Marr’s intuition was more advanced than current knowledge at the time. He attempted a hypothesis, in the knowledge that later work might lead to a revision

**Author:** Mike Hasselmo

**Title:** *Marr's influence on the standard model of hippocampus, and the need for more theoretical advances.*

**Chapter theme**: David Marr's seminal paper on archicortex in 1971 laid the foundation for what can be currently considered as the standard model of hippocampus. This involves a pattern separation stage in dentate gyrus, followed by a pattern completion stage in region CA3.  These ideas have only reached their peak influence over the past decade, as both rat unit recording studies and human fMRI studies explicitly test predictions about pattern separation and completion - using techniques that David Marr could not have foreseen.  There have been many additions, modifications and controversies addressing the standard model, as well as exciting findings about the representations formed in the major input structure, the entorhinal cortex.  However, the field needs another influential paper at the level of Marr's paper that integrates the available data into a more sophisticated theory that mathematically integrates the dynamics and function of the archicortex.

**Author:** Sue Becker

**Title:** *Marr's Simple Memory theory of Archicortex, then and now: Four decades later, things are not quite as simple*

**Chapter theme**: Marr's computational simple memory theory of archicortex set the stage for the past four decades of research on the medial temporal lobe memory system. His ideas about sparse coding, pattern separation and pattern completion in the hippocampus have had a profound influence on subsequent computational theories of memory. While Marr's model has garnered considerable empirical support, more recent neuroscientific discoveries including neurogenesis in the adult hippocampus, biological rhythms and sequence replay have led to more refined computational theories of how episodic memories are encoded.

***Section 3: A theory of Neocortex***

**Authors:** Kevan Martin and Rodney Douglas:

**Title:** *A Vision of Neocortex*

**Chapter theme:** In 'A theory for cerebral neocortex'  David Marr concluded that “finally, it is unprofitable to attempt a comprehensive survey of cortical cells at this stage, neither the theory, nor the available facts permit more than the merest sketch.” The field has made some progress here in understanding the computational significance of cortical circuits built of several different structural and functional types of neurons, but his contribution impels us to take a harder, and likely revisionist, look at current ideas. The chapter will paint a picture that draws together neuron motifs, local circuits, computational operations such as winner-take-all, for which there are now well-worked theories. It will embed these in the concept of the cortical sheet for behaviour.

**Authors:** Terry Sejnowski&(David Mumford??)

**Title:** *Theories of Cortical Function*

**Chapter theme**: The chapter will review computational theories of the cortex. It will then consider to what extent our knowledge of the physiological properties of cortical cells is consistent with those theories. **This can be modified**

**Authors:** ***Invited, response expected in a week***

**Title:**

**Chapter theme:**

**Authors:** Invited 08.23.2014; response requested in a week

**Title:**

**Chapter theme:**

***Overview***

**Author:** Randall O’Reilly

**Title:** Going beyond the pieces

**Chapter theme**: The chapter will consider how Marr’s ideas captured the principal component functionality of the cerebellum, archicortex and neocortex. Models are now being developed that bring all of these components together. These enable us to see how these areas interact so as to produce higher-level functionality.