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**Neuronal oscillations as a critical
phenomenon and its implications for
information processing**

The Cover shows the human cortex overlaid with ocean waves and sand, to illustrate two forms of neuronal dynamics investigated in this thesis. Designed with help from Matthew Jarvis.

The research described in this thesis has been performed in the Neuronal Oscillations and Cognition group (NOC), Department of Integrative Neurophysiology (INF), Center for Neurogenomics and Cognitive Research (CNCR), Vrije Universiteit Amsterdam. It was made possible by a young talent grant (IAM-2009-F2-3) from Neuroscience Campus Amsterdam (NCA) and Netherlands Organization for Scientific Research (NWO) Physical Sciences Grant 612.001.123.



VRIJE UNIVERSITEIT

**Neuronal oscillations as a critical phenomenon and
its implications for information processing**

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Table of Contents

Introduction	1
Chapter 1: Detrended fluctuation analysis: A scale-free view on neuronal oscillations	5
Abstract	6
Introduction.....	6
Fundamental concepts required to understand DFA.....	7
The detrended fluctuation analysis (DFA).....	20
DFA applied to neuronal oscillations.....	23
Try it yourself using the Neurophysiological Biomarker Toolbox	25
Insights from the application of DFA to neuronal oscillations	27
DFA as a biomarker of neurophysiological disorder	31
Outlook	32
Acknowledgements	33
Chapter 2: Critical-state dynamics of avalanches and oscillations jointly emerge from balanced excitation/inhibition in neuronal networks	35
Abstract	36
Introduction.....	36
Materials and Methods	39
Results	42
Discussion	48
Acknowledgements	52
Chapter 3: Versatility of neuronal network function is maximized in the critical state	53
Abstract	54
Introduction.....	54

Results	56
Discussion	64
Methods	66
Acknowledgements	71
Chapter 4: Cortical excitation-inhibition ratio explains individual variation in perceptual processing	73
Abstract	74
Introduction.....	74
Results	77
Discussion	84
Methods	86
Acknowledgements	96
Discussion	97
Critical-state dynamics of neuronal oscillations.....	98
Integrating different measures of neuronal activity	99
Functions of critical-state dynamics	99
E/I and its future applications	101
Critical oscillations and learning	102
Conclusion	102
References	103
Summary	117
Samenvatting	119
Publications	123
Publications not included in thesis:.....	123
Curriculum Vitae	125
Acknowledgements	127

Introduction

“...a whole entity which at the same time oscillates, vibrates, flows within itself, pulsates and moves to-and-fro...” Hans Jenny, *Cymatics: a study of wave phenomena and vibration*

The brain consists of billions of neurons that coordinate their activity in a complex manner, but we still lack the necessary frameworks and tools to adequately characterize and understand the functions of this coordination. The importance of coordinated activity from groups of neurons is shown from its correlates with our mental states, perception and behaviors. Cell-assemblies defined by synchrony range in size from a few neurons to hundreds of thousands of neurons—providing temporal coupling at the micro- to centimeter scale. Limitations in recording techniques prevent us from tracing the neuronal activity *in vivo* at such a wide range of scales, which has left a number of fundamental questions unanswered, such as “How do synchronous cell-assemblies at different spatial and temporal scales form?” and “How do these correlations affect information processing in neuronal networks?”.

Whilst probing activity at different scales, several labs have begun to consider self-organized criticality (SOC) as an overriding neuronal organizing principle, where the neuronal network dynamics are attracted to the critical point of a phase transition poised between an ordered sub-critical phase and a disordered super-critical phase. At this critical point, the dynamics exhibit scale-free temporal and spatial activity. Evidence for this proposal has been found in two main forms: Neuronal avalanches—which are scale-free propagation of local field potential events—and critical oscillations—which are long-range temporal correlations (LRTC) in the amplitude modulation of band-limited oscillations. However, it is unknown how critical oscillations are generated in neuronal networks, and how the complex temporal dynamics present in the critical state effect the previously discovered functions of neuronal oscillations.

In this thesis, the aim is to understand the mechanism and functional role of critical oscillations in neuronal networks.

In **Chapter 1**, I give an introduction to scale-free dynamics and how it relates to neuronal oscillations. I then give an overview of experimental results that provide evidence for the non-triviality of this form of neuronal dynamics, and how alterations in the scale-free nature of oscillations have been found in epilepsy, schizophrenia and Alzheimer's disease.

In **Chapter 2**, I design a computational neuronal network model of CRITICAL OSCILLATIONS (CROS) that is capable of producing realistic amplitude modulation of oscillations that are similar to human magneto- and electroencephalography (M/EEG). The model shows that through the mechanism of balanced excitatory/inhibitory connectivity in a network, neuronal avalanches and critical oscillations can jointly emerge. This provides the first link between two previously separated fields investigating these two phenomena.

In **Chapter 3**, I investigate the role of critical oscillations in neuronal network responses to stimuli using the computational model developed in Chapter 2. I show that three important functions of a neuronal network are maximized in the critical state: Regulation of post-stimulus response by pre-stimulus amplitude and phase of ongoing oscillations, and the dynamic range of post-stimulus response. This shows that the versatility of network function is maximized in the critical state.

In **Chapter 4**, I use the CROS model to develop a novel method of estimating the excitation-inhibition ratio (E/I) from neuronal network signals. The model predicts a negative relationship between E/I and post-stimulus phase-locking response. I apply this method to human MEG recordings from a threshold stimulus detection task, and show that the model findings account for inter-subject variability in stimulus-evoked phase-locking response. I also provide the first evidence that the human cortex is capable of exhibiting sub-, critical and super-critical dynamics.

In **Discussion**, I explore the implications of the findings from the previous four chapters on how groups of neurons can give rise to versatile coordinated behavior, and how this behavior affects neuronal network function. I show that by revealing the mechanism of

critical oscillations—a balance of excitation and inhibition—we can understand why critical oscillations are affected in multiple disorders, and begin to understand how a reduction in critical oscillations can lead to a loss of functionality in neuronal networks that would impair mental states, perception and behaviors.

