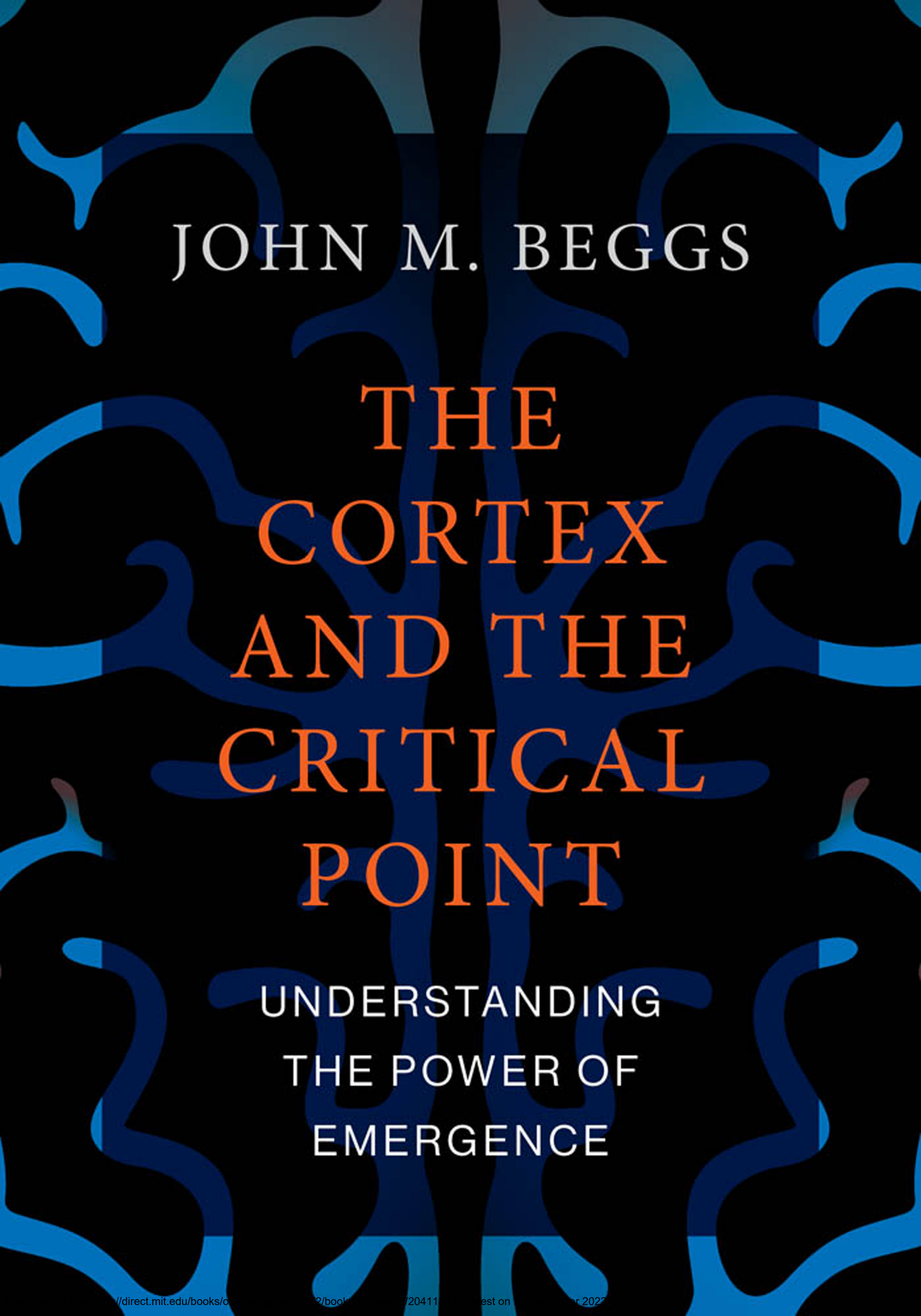

JOHN M. BEGGS

THE CORTEX AND THE CRITICAL POINT

UNDERSTANDING THE POWER OF EMERGENCE

The Cortex and the Critical Point

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Understanding the Power of Emergence

John M. Beggs

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This book is dedicated to my father, who gave me curiosity and an interest in science.

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Introduction

The Brain—is wider than the Sky—
For—put them side by side—
The one the other will contain
With ease—and you—beside—

The Brain is deeper than the sea—
For—hold them—Blue to Blue—
The one the other will absorb—
As sponges—Buckets—do—
—Emily Dickinson, c. 1862

Individual neurons have limited computational powers, but when they work together, they are astonishingly brilliant. Figuring out *how* they work together is the most important task in understanding how the brain works. And understanding how the brain works is, as Emily Dickinson might argue, the question that contains them all.

I want to tell you something startling, almost magical, about how neurons work together. It is not easy to understand. In fact, it will take a whole book to fully explain. But if I were forced to try in just a paragraph, I would say this—it is like when water, at just the right pressure, changes into steam. For a moment it is both a flowing liquid and individual molecules zipping around through the air. Neurons can act that way too, firing synchronously and then breaking off to improvise by themselves. Just at this transition, they are paradoxically both independent and interdependent with all other neurons. Right here, near what we will call the critical point, information flows easily, computations are most facile, and the brain is exquisitely sensitive to inputs. Here, intricate patterns of waves, oscillations, and avalanches of activity arise most readily. Slip too far below this point, and neurons fall into the abyss of silence. Nudge above it, and they get swept up into the fatal storm of seizures. Right around the critical point there is a narrow passage that opens to an expanse of complexity and emergence that is wider than the sky and deeper than the sea.

What is this critical point, and why does it have these interesting properties? Perhaps the simplest way to understand the critical point is by considering the three ways activity could propagate in your brain. First, it could be damped, so that incoming signals quickly die out. You smell a rose, but it triggers no memory and no succeeding thoughts. Second, inputs could be amplified so that they rapidly grow. You smell a rose, and you think of your spouse and your first date, and then your wedding, and then what the kids were like when they were young, and you quickly wonder how you will pay for the kids' college tuition, and your thoughts accelerate until your saturated brain is overwhelmed with a seizure. The third way—the critical way—preserves the strength of inputs, neither weakening them nor strengthening them. Rather, when the network is near the critical point, it transforms incoming signals into different patterns that still preserve, as much as possible, their original information content. These signals can then bounce around within the brain a long time before dying out, colliding with other inputs, causing new patterns to form. You smell a rose, and you write a poem that connects your first date with your anniversary dinner.

It does not seem that we are born with brains right at the critical point. Research suggests that during development, sprouting connections compete with pruning to lead us to it (Tetzlaff et al. 2010; Stewart and Plenz 2008). Once near the critical point, there are homeostatic processes to keep us there. Lack of sleep seems to move us toward being overamplified, and seizures are known to occur more often in sleep-deprived people. But a good night's sleep reduces this amplification and brings the brain closer to the critical point (Meisel et al. 2013). Just like a thermostat keeping a room near a set temperature, the brain returns toward the critical point after being pushed away from it (Ma et al. 2019). The benefit of being near the critical point is that many information processing functions are thought to be optimized there (Shew and Plenz 2013).

But before we delve too deeply into the questions surrounding the critical point, let's first step back and take a broader view of current neuroscience research. This may help to put the idea of the critical point into its proper context.

The Critical Point in Context

This is, without doubt, a golden age for neuroscience. The last 30 years have seen an efflorescence of tools to manipulate the brain and collect data from it. It is now possible to record activity from every neuron in a zebrafish larva's brain while it is freely swimming and responding to stimuli (Kim et al. 2017). We have a nearly complete map of one hemisphere of the fly brain, with every neuron and most of its synapses accounted for (Pipkin 2020). The neurons responsible for a mouse's memory of an event can be recorded, tagged, and replayed by laser stimulation, causing the mouse to behave as if the event had happened again (Carrillo-Reid et al. 2019; Ramirez et al. 2013). Given this progress, it is reasonable to expect that in a decade or two we will record and stimulate most neurons in the mouse cortex (and maybe the monkey's) while it is interacting in a virtual reality environment, controlled by experimenters.

Once we reach these heights, will we then understand how the brain works? One might think so, but some of those working on the front lines don't share this optimism. In a recent article in *Nautilus* magazine (Guitchounts 2020), Harvard graduate student Grigori Guitchounts asks Professor Jeff Lichtman, who developed the brainbow technique for mapping the brain's connectome:

“I think the word ‘understanding’ has to undergo an evolution,” Lichtman said, as we sat around his desk. “Most of us know what we mean when we say “I understand something.” It makes sense to us. We can hold the idea in our heads. We can explain it with language. But if I asked, Do you understand New York City?” you would probably respond, “What do you mean?” There’s all this complexity. If you can’t understand New York City, it’s not because you can’t get access to the data. It’s just there’s so much going on at the same time. That’s what a human brain is. It’s millions of things happening simultaneously among different types of cells, neuromodulators, genetic components, things from the outside. There’s no point when you can suddenly say, “I now understand the brain,” just as you wouldn’t say, “I now get New York City.”

Yes, the details are immense and overwhelming, but must we give up on the project of understanding, or settle for some diminished version of it? Understanding necessarily means distilling general principles to the point where some details do not matter.

For comparison, let us look at what happened in celestial mechanics. At first there was the massive data collection with scientists squinting at night to track planets; some took decades to orbit the sun, so the work took generations. Early models hardly provided understanding and were little more than fitting the data. Tycho Brahe thought each planet moved on a circle around the sun. Any backward, or retrograde, motion could be accounted for by having a smaller circle, rotating the other way, on top of the main circle. If need be, stacking three or four such epicycles could fit any planet’s motion. Later, Kepler thought ellipses worked better and this led him to discern three laws that described planetary motion. This set the stage for Newton’s grand synthesis of universal gravitation, where all was governed by a single equation. It worked for the planets, no matter their distance or size. After only a few observations, Gauss relied on it to declare where the planetoid Ceres would reappear nine months later (Teets and Whitehead 1999). This type of understanding made us think the universe was predictable like a clockwork and gave us ambitions to master it. It was this confidence that drove technology, transforming the next centuries. Understanding our brains would be no less momentous.

A nice story, but could anything like this happen in neuroscience? Biology is messy and not like physics in that way. Perhaps there isn’t yet a set of equations that could fit on a T-shirt to describe the brain, or even part of it, with any precision. But it does seem like we should at least try to move toward this. History says we must go there eventually. Indeed, there are several overarching theories of how the brain works already in the literature (Friston 2010; Carandini and Heeger 2012; Poggio 1990; Kelso, Dumas, and Tognoli 2013). Some of these are speculative and not widely embraced. Neuroscientists are cautious and want to see testable predictions with details.

It is into this milieu that I am offering the idea that the cortex operates in the vicinity of a critical point—*the criticality hypothesis* (Beggs 2008). It is not my idea alone; many people have contributed to it before me (Kauffman 1969; Wilson and Cowan 1972; Kelso 1984; Freeman 1987; Dunkelmann and Radons 1994; Bienenstock 1995; Herz and Hopfield 1995; Bak 1996; Chialvo and Bak 1999; De Carvalho and Prado 2000; Linkenkaer-Hansen et al. 2001; Greenfield and Lecar 2001; Worrell et al. 2002; Eurich, Herrmann, and Ernst 2002). You can judge for yourself whether it accounts for the data, generates specific testable predictions, and has general principles that transcend details. You can also decide if it is a step toward understanding.

Let us now discuss some of the background behind this idea. Over the last twenty years, there has been a growing body of research investigating this hypothesis. While this interest began with behavioral work and modeling studies decades ago, it grew most rapidly in the early 2000s, when experimental support for a critical point in the cortex first appeared. The criticality hypothesis is provocative because it claims to be a unifying framework at a time when neuroscience is dominated by data-driven work. It imports theory, not methods, from physics to understand the brain. If correct, the concept of a critical point could explain how information transmission, storage, computation, and controllability are simultaneously optimized in cortical networks. It also offers testable predictions about how failures to attain optimality could lead to neuropathologies like epilepsy.

The growth of this field is evidenced by steadily increasing citations, conferences focused on criticality, a breadth of new research approaches and consistent media attention. While some of the earliest work began with cortical slices in rats, investigations of the critical point now include diverse species like worms, zebrafish, turtles, mice, monkeys and humans. The techniques employed have spanned from electrode recordings to calcium imaging, electroencephalography (EEG), magnetoencephalography (MEG), and functional magnetic resonance imaging (fMRI). More recent work has shown the critical point is behaviorally relevant to sensory processing, is predictive of health outcomes, and that deviations from the critical point can be restored by sleep. Citing this research as inspiration, electrical engineers have found networks of memristors can self-organize to operate near the critical point to perform computations and learn (Stieg et al. 2012; Pike et al. 2020; Hochstetter et al. 2021). *New Scientist* magazine identified the hypothesis that the brain operates near the critical point as one of the top five mathematical ideas driving brain research (Barras 2013).

Despite the potential promise of this idea, there is still a lack of consensus among neuroscientists as to its validity. What could be causing this hesitation? One reason may be rooted in the evidence that was originally offered in support of the critical point. Early work relied heavily on the existence of power laws. Skeptics rightly pointed out that while power laws are necessary to establish the existence of a critical point, they are not sufficient to do so. Other mechanisms can also produce power laws, yet do not necessarily indicate a critical point. This led to several years of confusion. While the field ultimately responded with better methods for quantifying proximity to the critical point, time had gone by. In addition, these new methods are highly technical and clear descriptions of why they work have been rare. There is now a great need to clearly explain how these early objections have been resolved and how solid evidence supporting operation near the critical point has accumulated.

The Goals and Structure of This Book

For that reason, the main goal of this book is to explain the critical point and its relevance to the brain as clearly as possible. I describe the central concepts from an intuitive perspective first, with more detailed descriptions later, leaving most technical aspects for the appendix. I also use figures abundantly so readers will have the chance to grasp what is going on both verbally and visually. Many of these figures were generated by computer models that can be freely accessed through links in the appendix. I hope that curious readers will find them useful for their own explorations, and that tired professors may find them helpful in creating homework assignments. At the end of many chapters, there are suggested exercises. In addition, we have collected several example datasets so that students can perform analyses and test these ideas for themselves. I think that interacting with the material is crucial for understanding it.

Because this book is positioned as an introduction to the field, it is not a comprehensive review of criticality research. For that, there are already excellent books (Plenz and Niebur 2014; Tomen, Herrmann, and Ernst 2019) covering most aspects of current work with technical details. These can be read with great profit by those already in this area. Instead, this book is organized around using a few examples of models and data to convey some key principles. With respect to models, I have chosen to rely on the simple branching model, even though there are hundreds of different models in this area. With respect to data, I have emphasized spike recordings, even though the field routinely deals with all data types. In making these decisions I aimed to keep the presentation as clear and consistent as possible. It was simply not feasible in an introductory work to give each of the contributions in this area the detailed attention it deserves. I hope that by drawing attention to this field I will encourage readers to later learn for themselves about the research of the many excellent scientists I was not able to include here.

My own research for the past 20 years has been deeply involved with criticality. I coauthored a paper with Dietmar Plenz that contributed to spurring the growth of this field (Beggs and Plenz, 2003). In other work, my colleagues and I developed the critical branching model that has become a workhorse in studies of critical neural networks. This model illustrates how information transmission and information storage would be optimized simultaneously at the critical point (Haldeman and Beggs 2005). We also introduced the exponent relation as an authentic signature of proximity to the critical point in neuronal data (Friedman et al. 2012), an approach that is increasingly adopted. Most recently, we advanced a new theory, *quasicriticality*, about how cortical networks hover around the critical point (Williams-Garcia et al. 2014; Fosque et al. 2021), and this has received popular coverage (Ouellette 2018; Helias 2021). These experiences give me a perspective from which to describe the overall trajectory of this field, the challenges it has faced, and the potential promise it holds.

A key theme of this book is that neurons are far more powerful when they work together than when they operate independently. While this seems obvious, the focus on emergent properties in current neuroscience is still relatively underdeveloped. There has been excellent work on rhythms, synchrony, and waves, but more complex emergent phenomena are rarely discussed. With the current abundance of multichannel neuronal data, now is an ideal time to demonstrate that the framework of emergence has the potential to reveal still higher-level phenomena in the brain. The avalanches of neuronal activity that appear near the critical point are an emergent phenomenon that is more complex than those previously studied yet are still approachable when clearly explained. I hope to use the concept of the critical point and the cortex to illustrate the power of the emergent perspective, making it more accessible to a broad range of investigators.

Very broadly, the book has three parts. Part I is introductory and gives background to the main ideas behind the criticality hypothesis and emergent phenomena. Part II addresses the critical point and its main consequences. Part III explores issues that are likely to drive future research in this field. Here is a slightly more detailed overview of the book's structure:

Chapter 1 attempts to show readers, as briefly and clearly as possible, the central ideas underlying criticality research in neuroscience. Chapter 2 is a general discussion of emergent phenomena and how they can be understood. Here I employ some simple computer models for illustrations. This is meant to pave the way for a detailed discussion of the properties that emerge in networks near the critical point.

Part II is the heart of the book, dealing with the most central issues. In chapter 3, we go over the specific signatures of the critical point that can be seen in neural network models, and then we turn to the data to see if these exist. Once we have considered the evidence that the cortex operates near the critical point, we turn to the two main consequences of being there. The first consequence is scale-free properties that confer optimum information processing; this is covered in chapter 4. The second consequence is universality, covered in chapter 5. Universality is the idea that complex emergent behavior, like that seen near the critical point, can be explained by relatively simple models that are applicable across species and scales. If true, universality would show us that there is hope for understanding the brain without having to first know all the details. This concludes part II of the book.

In part III, we consider the future of this field. Chapter 6 covers how operation near the critical point is homeostatically regulated, like blood pressure and body temperature in healthy individuals. A consequence of this is that departures from the critical point are associated with neurological disorders. In chapter 7 we address quasicriticality, the idea that the brain can never fully reach the critical point because it is always being driven by inputs and noise. Very recent work supports this idea; we discuss this and competing theories as an issue not yet resolved. Chapter 8 focuses on how operating near the critical point allowed the cortex to amplify our intelligence. Chapter 9 is an epilogue, to briefly cover what we know, what we do not know, and remaining open questions.

The appendix contains technical descriptions that would have interrupted the flow of the text in the main chapters.

I have not yet explained in much detail what the criticality hypothesis is, or why operating near the critical point would profoundly affect a network. To begin that, let us move on to chapter 1, next.

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