Preface

I remember the episode when I first started to do research on memory function. By episode, I mean an experience covering a specific time interval in a specific location. I was working on a term paper one afternoon in the fall of 1981. I was searching the Psychology Department library on the 6th floor of William James Hall at 33 Kirkland Street in Cambridge, Massachusetts. This was about 10 years before I first had access to literature searches on the web, so I remember my path walking back and forth between a wooden card catalog and the shelves of books and journals. Based on my experience taking physics that same term, I expected to find a textbook on memory analogous to the treatment of mechanics in a physics textbook. I expected to find a book describing the brain mechanisms for encoding and remembering the times and locations of my path through the library, analogous to the description of the spatiotemporal trajectory of a falling object in physics. I did not.

Even now, almost 30 years later, there is not a standard, quantitative description of the brain mechanisms of memory analogous to the theory available in most areas of physics and engineering. However, exciting recent physiological data and modeling have laid out a framework for modeling the memory of episodes as spatiotemporal trajectories. These recent developments include the discovery of grid cells and their relationship to oscillatory dynamics in the entorhinal cortex. This recent work builds on an extensive body of older work on memory function.

In this book, I try to present what I was searching for in 1981, a quantitative model of the brain mechanisms for encoding and remembering an episode as a spatiotemporal trajectory. In the main text, I will present the model in a more narrative form. In the appendix, I will present the material in the quantitative style of a textbook. Because of limits on space and time, there are unfortunately many areas of research that I have not been able to include.

When describing episodic memory, researchers often give the example of remembering where you parked the car or remembering where you left your reading glasses or keys. Here, I will directly address real-world examples of episodic memory, describing how your brain might encode and retrieve the location where you parked your

car. A familiar solution to problems such as finding your glasses or keys is to "retrace your steps," that is, to retrace your trajectory through space and time. Related to this, mnemonic strategies for enhancing encoding include the method of loci in which one imagines placing items in a sequence of familiar locations.

Though other models will be discussed, the book will focus on one specific model of episodic memory as the encoding and retrieval of spatiotemporal trajectories. We build models to evaluate our theories and to generate predictions that can then be tested. Testing the models provides us with information about where the models need to be revised, and this information can then be used to improve the models. The current models can address a range of physiological and behavioral data but do not accurately address the full range of data. However, despite the incomplete nature of current models, it is useful to describe how existing models address components of the data and to compare the strengths and weaknesses of different models. This process may be helpful to others interested in these questions and has certainly been helpful to me. A primary focus of this work will be data on the activity of neurons during memory-guided behavior. Some of this data has been shown in humans and primates but most data is available from research on rodents.

This book is intended to be accessible to the general educated reader. Based on my teaching experience, I find that neuroscience is so broad a field that experienced researchers in one area commonly do not know the basic principles in another area. For this reason, I present the data on a basic level that I feel will be useful to faculty and graduate students in many fields as well as advanced undergraduates. The Appendix provides mathematical descriptions appropriate for coursework or independent study by advanced undergraduates and graduate students in neuroscience.

Presenting the model of episodic memory requires some background. In the first chapter, I will present some of the behavioral data on episodic memory and give a general overview of the model. In the second chapter, I will provide an overview of the anatomical data on structures involved in episodic memory and an overview of the physiological data obtained from these structures. In the third chapter, I will present an overview of the mechanisms in the entorhinal cortex and hippocampus for encoding space and time in episodic memories, including models of grid cells. In the fourth chapter, I will present the full model of the mechanisms of episodic memory. In the fifth chapter, I will address the role of the hippocampus in forming associations between spatiotemporal trajectories and individual items or events. In the sixth chapter, I will address the role of neuromodulators such as acetylcholine in episodic memory function, and in the seventh chapter I will address models of the use of episodic memory function for memory-guided behavior.

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