Overview

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Recent scientific discoveries provide a better understanding of how the human brain, while relatively modest in size, is capable of providing each of us with awareness, personality, emotion, memory, and comprehension. In the history of neuroscience research, this enigma of how consciousness can be embedded in matter has proved to be extremely challenging since the brain, in order to carry out all of these functions, has miniaturized hundreds of trillions of connections among its numerous neurons. The question of how nervous system anatomy and electrical activity are related to psychological function is readily addressed in studies of sensory and motor functions. However, the high level of interconnectivity and integration of circuits makes it somewhat more difficult to identify the brain basis of cognitive functions. Observations in neurology patients have demonstrated localization of functions such as the speech modules and areas specific for recognition of distinct categories of visual objects. The development of experimental animal models permits complementary examinations of the neurophysiological bases of cognitive functions at a single cell level. Examples include studies in the monkey that demonstrate the presence of "mirror cells" (cells that respond when the animal views another animal making a given movement) and "face recognition cells" (cells that respond to the view of specific faces, in some cases oriented in certain directions).

Rodents such as rats and mice also serve as useful experimental models for studying the brain basis of specific cognitive functions. Perhaps because of the necessity for efficient memory and recall mechanisms, as well as resourceful capacities for spatial orientation, evolution has led to the conservation of brain areas with comparable anatomy and physiology among a variety of mammals, including man. In fact, both mnemonic and spatial cognitive functions are attributed to the same circuits in the limbic system, centered on a brain structure known as the hippocampus. This pairing of mnemonic and spatial functions is particularly valuable since it is often useful for memories to be associated with, and recalled at, particular places, and conversely, that the means for navigating toward important locations be well memorized.

Two important models for studying the neurophysiological basis for spatial cognition at the single cell level are the place responses of neurons of the hippocampus ("place cells") and the head direction cells (found in many structures of the brain's limbic system). Hippocampal place cells discharge action potentials when the animal occupies a small location within its environment. In open fields, these responses are often independent of the direction the animal is facing, although the responses can become directional when the animal performs stereotypic behaviors on a linear track. Complementing this, head direction cells discharge when the animal is facing a particular direction, independent of the position it occupies. In both cases the responses are independent of what the animal is viewing and they persist even in darkness or in the absence of prominent landmarks. Furthermore, different neurons are selective for different head orientations, or locations in the case of place cells, providing a fairly comprehensive representation by as few as a dozen or so neurons.

These properties suggest (but do not prove) that these neurons play an important role in signaling these types of information and could hence participate in fundamental mechanisms involved in determining orientation and in navigation. One clue that these properties are associated with high-level functions is that the activity of head direction cells is *stimulus-invariant*; that is, it does not depend upon any particular sensory stimulus, such as viewing a particular cue from a certain angle. Rather, the cell will fire, for example, whether the animal stands facing directly into a corner, or is scanning from the other end of (or even outside) the room, as long as it is oriented in the same direction. The responses depend only upon the topographic relation between the position of the head and the external environment. The neuronal discharges are not simply dependent on a single sensory modality like vision; rather, it is *supramodal* (i.e., drawing upon many modalities, but independent of each of them). Several chapters will elaborate on the essential roles of different sensory modalities, emphasizing the vestibular sense, which are utilized interchangeably in the elaboration of these responses. Furthermore, head direction cells depend upon movement-related signals. Another indication of the importance of the head direction signal is that it is *pervasive*. It has been reported that up to 10 different brain structures contain neurons selective for head direction. This finding is commensurate with the importance of orientation information for the planning and execution of many types of goal-oriented movements. The place and head direction signals are *stable*. Individual neurons maintain the same selectivity when the animal is placed in the same environment over the course of weeks or even months. Head direction cell firing shows little adaptation, and these neurons continue to discharge indefinitely as long as the animal maintains its head oriented in the same direction. This combination of properties indicates that these cells are viable candidates as reliable sources of highly processed, robust information concerning the head direction.

This book aims to help better understand how this type of signal arises, its properties, and how it may be used for elaborating orienting and navigation behaviors. The book is divided into five parts, whose subjects are, respectively: (1) representations of directional orientation: head direction cell properties and anatomy, (2) the influence of vestibular and motor cues on head direction cells and place cells, (3) relations between the head direction system, spatial orientation, and behavior, (4) neural mechanisms of spatial orientation in nonhuman primates and humans, and (5) theoretical studies and computational approaches to modeling head direction cell firing and navigation. The book may be read in order, or individual chapters may be selected for more rapid responses to burning questions. Although the chapters have been written so that they can also be read separately, themes introduced in the first three chapters are returned to many times.

The first chapter by Sharp provides an overview of the basic properties of head direction cells and introduces some fundamental concepts. The chapter is based on the anatomical framework discussed in further detail in the next chapter, and it provides a comparison of the properties of the head direction neurons in the respective structures. The second chapter by Hopkins presents the anatomical infrastructure of the head direction system. These brain structures are the basis of the functional circuitry that gives rise to the properties of these neurons, and they are taken into account in most discussions of head direction cells. This chapter also provides information that will be indispensable for computational neuroscientists to understand the circuit dynamics as the basis for internal representations of direction in models of the head direction system. For those not yet familiar with the anatomical substrates of the head direction system, this chapter is an excellent place to start, and the reader's attention here will be amply rewarded. Toward this end, the chapter is didactically presented in the framework of establishing general organizing principles. Many details have necessarily been left out, but interested readers will appreciate the extensive bibliography that serves as a springboard to the technical and specialized literature.

The next two chapters explore the influence of visual cues on head direction cell activity. Taube begins by providing a two-part discussion. The first part is concerned with how landmarks exert control over the directional tuning of head direction cells. We can immediately discard the idea that head direction cells encode direction in "absolute space," since rotation of stable distal visual cues in the absence of the animal (and often in its presence) leads to similar shifts in the cells' preferred direction of firing. The second part is concerned with how head direction cells respond when the animal locomotes in planes other than earth horizontal—specifically, in the vertical plane and upside down on the ceiling. The findings from these studies lead to important constraints on how the brain evolved to process spatial information efficiently. In fact, the insensitivity of the head direction system to linear translations and distances relative to cues demonstrates an anatomical division of function every bit as revealing as the separation of color, motion, and form processing in the primate visual system. Similarly, head direction cells are principally selective for the orientation of the head in the horizontal plane (in other words, about the yaw axis, or the azimuthal direction). If the head is pointed upward or downward (i.e., along the pitch axis) the directional firing concerns the projection of the head orientation onto the horizontal plane. Similarly, there is no evidence for modulation by rotations along the roll axis (leaning over to the left or right). Two mysteries that will not be resolved in this and following chapters are why head direction cells are selective only for the head direction in the horizontal plane, and where in the brain one finds representations of head direction in roll or pitch planes (although some clues are provided in the chapters by Duffy et al., and Taube). After Taube's explanation of visual cue control over head direction cells, Zugaro and Wiener delve into the issue of characterizing the nature of, and mechanisms by which, visual cues control head direction cells (and most likely place cells as well).

To understand the head direction system, it is necessary to consider how the signals originate and are updated through analysis of information processing in various nuclei. The first section, therefore, concludes with a chapter by Bassett and Taube that discusses how the head direction signal is generated, most likely by areas within the brainstem that are associated with the vestibular system. The authors describe an ascending flow of information that propagates rostrally and culminates in the projection of the head direction signal into the entorhinal cortex, the major gateway into the hippocampus. The authors also discuss a descending stream of information that contains information about visual landmarks and how the two information streams are integrated to form a stable representation of one's perceived directional heading.

The next section characterizes the types of sensory and motor information that control head direction cell firing. The stimulus invariance referred to above derives from the particularly intriguing capacity of head direction cells to integrate signals concerning the environment, in particular, visual cues with other information generated by self-movements (referred to as *idiothetic*; Mittelstaedt and Mittelstaedt, 1980; cited in chapter 7). These often ignored sensory modalities, including vestibular, proprioceptive, and optic field flow inputs, will prove to be crucial. This convergence and integration raises several theoretical issues. For example, how are these diverse types of information calibrated so that the motor signals concerning a particular rotation are coherent with the resulting shift in angular heading of a visual cue in the environment? First, Glasauer describes the brain's infrastructure for processing vestibular input signals that enter into the head direction system. Stackman and Zugaro then discuss the impact of this information on head direction cells, emphasizing the studies that show their critical role in generating the head direction signal, since vestibular lesions suppress them. They also review the many studies that examine how head direction cells respond under conditions of cue conflict, where the spatial information from one sensory or motor source differs from that of a second source.

The next chapter extends these themes in discussions of areas associated with the principal circuit that carries head direction signals between brainstem, thalamus, and cortex. Knierim describes studies comparing head direction cell and hippocampal place responses. The coherence of these two representations after cue manipulations is shown to be related to the familiarity of the animal with the environment, and a conceptual model is proposed to account for the findings. Continuing with the theme of hippocampal place responses, Muller and Brunel discuss the issue of the extent to which place cells contain secondary firing correlates that are related to the directional heading of the animal. They review and provide a theoretical basis for understanding studies that show that place cell activity is directionally modulated when behavior is stereotypically oriented, such as when an animal shuttles back and forth on a linear track.

The next section concerns the relationship between head direction cell activity and an animal's spatial behavior. Mizumori and colleagues show how sensory control of directional responses varies in structures outside the core limbic system pathways, with some exciting new data on a cortical zone that may be involved in the expression of directional navigation behaviors. The next chapter by Wiener and Schenk reviews the directional discrimination capacities in rodents, as well as studies of their ontogenesis. Dudchenko and colleagues then review the current state of knowledge on the relation between head direction cell responses and orientation behaviors. While the former data are derived primarily from rats, behavioral and physiological observations in monkeys and the presence of homologous underlying neuroanatomical pathways among mammalian species studied leads us to suppose that similar functions are present in humans. The final chapter in this section by Aggleton reviews the literature concerning behavior and learning deficits associated with lesions to various structures of the head direction cell system, and compares results from studies in man and rodent.

The next section is concerned with spatial and directional orientation in non-human primates as well as humans. The chapter by Rolls reviews the various types of directional and view responses found in monkeys, and proposes several computational frameworks by which this activity could participate in spatial learning. Duffy et al. then review brain systems in the monkey that process other types of orienting information, in particular the heading-related activity in the posterior parietal cortical area MSTd with special emphasis on the importance of optic flow signals. The next two chapters focus on psychophysical studies of directional orientation in man. First, Israël and Warren study how perception of static and dynamic orientation is informed by visual and self-movement signals in humans. Then, Hicheur and colleagues deal with anticipatory processes in the control of head orientation during locomotion in man and provide evidence for distinct processing of angular and linear displacements.

Computational studies are an effective way to consolidate the existing knowledge about head direction cells and to test the feasibility of theories concerning the functional organization of these millions of neurons, as well as their applicability for navigation problem solving. In the last section of the book, Touretzky first presents a tutorial demonstrating how to implement a popular model of head direction cells, the continuous attractor network. Arleo and Gerstner then apply this approach for guiding the navigational system for mobile robots.

The fact that as many as ten different brain structures show head direction responses reinforces the notion that this signal has proved useful over the course of evolution. Thus, nature has provided us with a robust message that this signal is important and hence can serve as a vital key for understanding brain function. The prominence, strength, and clarity of this signal is the rationale for assembling our knowledge on these fascinating cells and how they may underlie mechanisms of spatial orientation and our sense of direction. Unfortunately, because of space limitations, related issues such as angular direction processing for gaze orientation or pointing are not dealt with. Nonetheless, head direction processing is carried on in parallel (and sometimes overlapping) circuits with these other functions, and important general concepts will undoubtedly be arrived at by comparative studies. We hope the present volume will facilitate this endeavor.