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How cognitive theory guides neuroscience

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ABSTRACT

The field of cognitive science studies latent, unobservable cognitive processes that generate observable behaviors. Similarly, cognitive neuroscience attempts to link latent cognitive processes with the neural mechanisms that generate them. Although neural processes are partially observable (with imaging and electrophysiology), it would be a mistake to 'skip' the cognitive level and pursue a purely neuroscientific enterprise to studying behavior. In fact, virtually all of the major advances in understanding the neural basis of behavior over the last century have relied fundamentally on principles of cognition for guiding the appropriate measurements, manipulations, tasks, and interpretations. We provide several examples from the domains of episodic memory, working memory and cognitive control, and decision making in which cognitive theorizing and prior experimentation has been essential in guiding neuroscientific investigations and discoveries.

1. Introduction

Mental operations emerge from interactions among large populations of neurons and interconnected brain systems. Neuroscientists leverage the principles of physical reductionism and reconstructionism to explain not only the role of individual elements (neurons, ion channels, receptors, etc.) but also how these interact in a dynamical system with emergent properties that drive cognition and behavior. Causal manipulations of underlying circuits (with lesions, pharmacology, optogenetics, etc.) allow researchers to study the mechanisms required for cognition, by observing predictable and selective changes in relevant cognitive measures. This characterization might lead one to think that neuroscience experts can go along their merry way discovering the principles that explain the mind without the help from cognitive scientists or cognitive theory since one level encompasses or 'explains' the other. But *Cognition* readers can stop writhing in their seats; of course, this is not the case.

In this article we elaborate concrete examples articulating how principles of cognition – in particular, computational tradeoffs identified by studying functional requirements at the cognitive level – have, and will continue to be, instrumental in guiding neuroscientific discoveries. Neuroscience is rapidly accumulating a wealth of data at multiple levels ranging from molecules to cells to circuits to systems. However, in the absence of cognitive theory, this effort runs the risk of mere "stamp collecting", or the tendency to catalog the phenomena of the brain without gaining understanding or explanation. It follows, then, that many of the most influential findings in neuroscience have been understood within the functional context of cognitive theory. We focus on three examples: episodic memory, working memory and cognitive control, and decision making. In each case, we articulate how cognitive theory has set the stage to constrain measurements and manipulations which have advanced the neuroscientific enterprise. Thus, our primary focus in this review concerns how cognition has influenced neuroscience. The converse case, namely the influence that neuroscience can have on cognitive

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theory, is an important topic that we have each dealt with in detail elsewhere (see Chatham, Badre, & Badre, in press-a; Frank, in press, both of which emphasize the role of modeling endeavors that bridge across levels of analysis). However, for some examples, we also briefly note how reciprocally taking neuroscientific constraints into account has validated or refined cognitive models.

2. Hippocampus and functional tradeoffs in memory

The hippocampal formation has long been a focus of neuroscientists investigating its distinguishing anatomical and electrophysiological properties. Importantly, however, the progress of neuroscientific study of the hippocampus has been closely and continuously intertwined with cognitive theory regarding its widely celebrated role in episodic memory.

Henry Molaison, the famous patient H.M., had widespread hippocampal damage and exhibited profound episodic memory deficits, characterized by anterograde and retrograde amnesia (Scoville & Milner, 1957). But H.M.'s case was particularly compelling because of what he was still capable of learning. For example, he could acquire and retain complex motor skills, all while having no explicit memory of ever having performed these tasks. These results provided the strongest evidence to that time for the existence of multiple memory systems. However, these early investigations arose in a prevailing context of cognitive theory that already hinted at the existence of distinct forms of knowledge. Indeed, in her seminal paper on motor skill learning by H.M., Corkin (1968) motivated the investigation with "observations in normal man" that motor and other forms of memory were distinct, explicitly citing distinctions drawn in cognitive psychology between visual and kinesthetic codes (Posner, 1966, 1967) and verbal versus non-verbal forms of memory (e.g., McGeoch & Melton, 1929). This theoretical framing of H.M. grounded in cognitive theory led to a generation of investigations by neuropsychologists and cognitive neuroscientists studying multiple memory systems and their neural underpinnings (Cohen, Poldrack, & Eichenbaum, 1997; Squire, 1992), and influenced synaptic physiologists attempting to uncover the cellular basis of learning and memory in the hippocampus (Bliss & Lomo, 1973).

Cognitive theory has not only framed and motivated new neuroscience investigations, it also provides a functional level of analysis that motivates a deeper investigation as to why the brain evolved to support distinct systems. For example, computational cognitive modeling has indicated that multiple memory systems may be required to confront the functional tradeoffs between memory processes required to remember "where did I park my car today?" versus "what has been on average the best place to park my car?" (O'Reilly and Norman, 2002). The former question requires keeping overlapping memories separate, so as to not mistake yesterday's parking spot for today's, whereas the latter question requires an integration of many previous parking experiences into a coherent representation linked to its average value (McClelland, McNaughton & O'Reilly, 1995; Norman & O'Reilly, 2003; O'Reilly and Rudy, 2001). A single system would have difficulty handling both of these functions, leading neuroscientists to conduct studies providing evidence that the hippocampus supports distinct memories for overlapping events, whereas the cortex and basal ganglia are well suited to represent similarities among these memories and to integrate their reward values across time. This complementary learning systems (CLS) perspective accounts for existing lesion studies (Myers et al., 2003; Squire & Knowlton, 1995) and motivated experiments involving pharmacological manipulations differentially affecting these systems, and imaging to identify their neural signatures, combined with the requisite cognitive manipulations for uncovering their dissociable effects (Curran, DeBuse, Woroch, & Hishman, 2006; Frank, O'Reilly, & Curran, 2006; Huffman & Stark, 2014). Finally, the seminal work of Tolman, who suggested that rats use cognitive representations to map space and plan behavioral actions, and Hull, who argued for habit-like stimulus–response learning are both encompassed within the CLS framework and have directly informed modern neuroscientific investigations showing that these strategies coexist and tradeoff against each other between distinct hippocampal and striatal networks in rodents (Johnson & Redish, 2007; Packard & McGaugh, 1996; van der Meer, Johnson, Schmitzer-Torbert, & Redish, 2010) and humans (Daw, Gershman, Seymour, Dayan, & Dolan, 2011; Poldrack & Packard, 2003). Nevertheless, whether these systems truly compete or collaborate seems to depend on task demands (Sadeh, Shohamy, Levy, Reggev, & Maril, 2011) and further cognitive theory may be useful to resolve this controversy.

The 2014 Nobel prize in physiology and medicine was awarded to three neuroscientists (John O'Keefe, May-Britt Moser and Edvard Moser) for their work on the hippocampus. The prize was awarded for the discoveries of hippocampal "place cells" that fire when an animal visits a particular location, and "grid cells" that fire in a grid-like fashion across multiple locations in an environment with a particular spatial frequency. Importantly, the impact of these discoveries, and what elevated their influence to the highest levels in science, was their straightforward relationship to cognitive theory regarding cognitive maps. This relationship was first proposed in the seminal book by O'Keefe and Nadel (1978). Notably, this book takes as its starting point two detailed chapters focusing on cognitive theory regarding the nature of space, physical and psychological, and its ubiquitous role in memory, followed by a review of the principles and studies of navigation. Only after more than 100 pages do the authors begin to discuss the anatomy and physiology of the hippocampus in the context of this literature. To the present day, theorizing regarding the hippocampus and the role of place and grid cells has focused on spatial codes and their ability to bind separate elements, provide linking contexts, and naturally encode relationships among distinct features. Indeed, this general property of binding to location (spatial or virtual) is fundamental to many functions, and has led to a broadened view of the function of the hippocampus beyond declarative memory, as highlighted in a recent special issue of *Journal of Experimental Psychology: General (Vol. 142, No. 4)* devoted to the topic.