



Review

Oscillatory correlates of memory in non-human primates

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ABSTRACT

The ability to navigate through our environment, explore with our senses, track the passage of time, and integrate these various components to form the experiences which make up our lives is shared among humans and animals. The use of animal models to study memory, coupled with electrophysiological techniques that permit the direct measurement of neural activity as memories are formed and retrieved, has provided a wealth of knowledge about these mechanisms. Here, we discuss current knowledge regarding the specific role of neural oscillations in memory, with particular emphasis on findings derived from non-human primates. Some of these findings provide evidence for the existence in the primate brain of mechanisms previously identified only in rodents and other lower mammals, while other findings suggest parallels between memory-related activity and processes observed in other cognitive modalities, including attention and sensory perception. Taken together, these results provide insight into how network activity may be organized to promote memory formation, and suggest that key aspects of this activity are similar across species, providing important information about the organization of human memory.

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Contents

Introduction	694
Neural correlates of declarative memory	695
The use of electrophysiology to study memory	695
Oscillations during cognition represent activity of neural networks	695
Conclusions	699
Acknowledgments	699
Conflict of interest	699
References	699

Introduction

The discovery, in 1957, that bilateral damage confined to the medial temporal lobes (MTL) of the human brain produced profound, selective impairment in the ability to form new declarative memories, i.e., the ability to remember facts and events (Scoville and Milner, 1957) ushered in a new era of memory research. Subsequently, a number of studies were able to replicate this memory loss in animal models, establishing that the neural correlates of at least some components of memory are likely conserved across species (Mishkin, 1982; Squire and Zola-Morgan, 1983). Through careful design of

behavioral tasks and use of specific lesions in non-human primates, it has been possible to test competing theories of the nature of memory and the role of specific brain areas in different aspects of memory formation and retrieval. In particular, the similarities between the brains of humans and non-human primates, combined with the common sensory modalities generally employed among primate species in exploration and sensory input, have made studies with non-human primates invaluable in probing the neural correlates of memory. While a great deal of knowledge about the physiology of the hippocampus and other MTL areas has been derived from studies of non-primate species, including rodents, non-human primates have provided a way to bridge the gap between rodent and human studies, which has led to greater understanding of the common mechanisms employed across species. In particular, research over the last few years has led to a greater understanding of the role of neural

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oscillations in memory formation through the use of electrophysiological recording methods in multiple species, including rodents, non-human primates, and humans. Studies across multiple species inform each other and provide a richer understanding of the complex mechanisms underlying memory. This review will focus on the role of neural oscillations in several aspects of memory, with an emphasis on findings from recent studies in non-human primates.

Neural correlates of declarative memory

Declarative memory involves several different processes: the initial storage, or encoding, of information; the subsequent reactivation, or retrieval, of this memory trace; and, over time, a process of consolidation, through which the initially transient memory trace is converted into a longer lasting form. The brain regions essential for declarative memory in mammals include the hippocampus (comprised of the CA fields, the dentate gyrus, and the subiculum) and the surrounding entorhinal, perirhinal, and parahippocampal cortices. Lesion studies in humans, monkeys, and rodents have revealed that damage to these areas produces deficits in declarative memory (Eichenbaum, 1997; Mishkin, 1982; Schacter and Tulving, 1994; Squire and Zola-Morgan, 1991; Squire et al., 2004), suggesting that this ability is reliant on neuronal operations occurring in these areas. However, while declarative memory is critically dependent on processing within these regions, this ability is also thought to involve the concurrent, coordinated activation of ensembles of neurons that are distributed throughout the brain, including the medial temporal and frontal areas, as well as association cortices across various sensory modalities (Damasio, 1989; Mishkin, 1982; Rolls and Treves, 1994). In addition to mediating the initial acquisition of stored memories, such coordinated activity across brain regions is also thought to facilitate the consolidation of memories over time. The standard model of consolidation, which states that memory is initially stored in the hippocampus but gradually shifts to a purely cortical representation, is derived from evidence that damage limited to the hippocampus produces some memory loss for information acquired before the damage occurred (retrograde amnesia), with more recent memories often showing greater vulnerability to damage than more remote memories (McClelland et al., 1995; Squire and Alvarez, 1995). Because information that has become consolidated in memory is largely resistant to MTL damage, this suggests that the neural structures mediating the reactivation of consolidated memories gradually become independent of the areas critical for the initial memory formation, as hippocampal-cortical reactivations strengthen connections in the cortical network. An alternative account proposes that, while the cortex can support memory traces that are purely semantic in nature, the hippocampus is critical for the spatial and temporal context inherent in detailed autobiographical and episodic memories, regardless of how remote those memories are (Nadel and Moscovitch, 1997). Both theories are in agreement that declarative memories are encoded in hippocampal-cortical networks and that these memory traces are reorganized over time, as memories are reactivated (Frankland and Bontempi, 2005). In addition, because the process of memory formation does not occur in isolation but in concert with multiple other modes of cognition, including sensory perception and attentional selection, it is likely that certain principles of neuronal communication are common to these different modes of cognition. For instance, episodic memory involves the binding of multiple elements (e.g., time, place, and multiple physical elements integral to the memory) in the formation of the complete memory trace, much the way perception involves integrating multiple components of sensory information to form a coherent representation. It is possible that similar neuronal mechanisms may underlie both processes.

Non-human primates, including rhesus macaques and other related species, are important models for studying human memory for several reasons. Like humans, monkeys are predominantly visual, in that this is the primary modality utilized to gather information. The pathways

that transmit information from the primary visual cortex to the regions essential for memory are remarkably conserved between monkeys and humans. Furthermore, monkeys have demonstrated the ability to remember complex visual stimuli over periods of time comparable to that of humans. In fact, even the quantitative performance (including measures such as reaction time) of monkeys on attentional and working memory tasks is comparable to that of humans (Witte et al., 1996). While recent years have seen an increasing number of electrophysiological studies performed in human epilepsy patients (Abbott, 2009; Engel et al., 2005; Jacobs and Kahana, 2010; Mukamel and Fried, 2012), one advantage of utilizing monkeys as research subjects is the ability to record activity at both the single neuron level and at the field potential level in any target brain region, without the constraint of only recording in clinically relevant areas. There are some challenges: for instance, monkeys do not verbalize their experiences, necessitating alternative strategies to assess memory. These usually involve explicit training in reward-based paradigms, or, alternatively, using more covert measures of memory based on free-viewing paradigms. In addition, there is a lack of direct evidence that monkeys have the capacity for episodic memory, which stores representations of one's own personal past experience, giving rise to the need for tasks which measure specific components thought to be essential for episodic memory function (e.g., associative memory, and the ability to track memories in specific instances of time). However, there is evidence that monkeys can reflect and report on their own memory states (Hampton, 2001) as well as recall information from memory that is not present at the time of testing (Basile and Hampton, 2011), suggesting that monkeys may possess at least some of the memory abilities that were traditionally thought to be specific to humans. Despite the challenges revolving around the use of monkeys as a model of human memory, a comprehensive picture of the brain mechanisms underlying memory formation is beginning to emerge, in large part through research utilizing monkeys as a model to study human memory.

The use of electrophysiology to study memory

Of the many methods employed to study the neural correlates of memory in awake, behaving animals, the use of electrophysiology has provided significant information about the role of the precise activity of neuronal circuits in memory processes. These methods, which utilize measurements obtained from electrodes placed within (or in proximity to) the region of interest, rely on the ability to detect the extracellular voltage fluctuations that result from neural activity. The signals commonly recorded within the brain consist of extracellular spikes, the rapid voltage fluctuations that represent neuronal action potentials, and local field potentials (LFPs), the slower voltage fluctuations that reflect the aggregate activity occurring in an area of surrounding neural tissue. Spikes, which are assigned to the neurons that are in local proximity to the recording electrode, represent rapid, direct communication between neurons, either in the same brain area or in different brain areas. LFPs, on the other hand, reflect a combination of multiple neuronal processes occurring among neurons within several hundred microns to several millimeters of the recording electrode (Kajikawa and Schroeder, 2011), and are thought to be associated with synaptic input to a region (Buchwald et al., 1966; Mitzdorf, 1985, 1987).

Oscillations during cognition represent activity of neural networks

Along with evoked potentials (the averaged LFP response to a stimulus or behavioral event), oscillatory rhythms in the brain are currently a focus of intense investigation. While long recognized as a prominent component of neural signals (Berger, 1929), recent years have seen a growing interest in characterizing neural oscillations and their association with behavior and cognition. During this time, a number of principles related to this association have come to light, many from studies of

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