



Review

Brain rhythms in mental time travel

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ABSTRACT

The memory theorist Endel Tulving referred to the ability to search through one's memories, and revisit events and episodes from one's past, as mental time travel. This process involves the reactivation of past mental states reflecting the perceptual and conceptual characteristics of the original experience. Widely distributed neural circuitry is engaged in the service of memory search, and the dynamics of these circuits are reflected in rhythmic oscillatory signals at widespread frequencies, recorded both in the local field around neurons and more globally at the scalp. Retrieved-context theory provides a theoretical bridge between the behavioral phenomena exhibited by participants in memory search tasks, and the neural signals reflecting the dynamics of the underlying circuitry. Computational models based on this theory make broad predictions regarding the representational structure of neural activity recorded during these tasks. In recent work, researchers have used multivariate analytic techniques on topographic patterns of oscillatory neural activity to confirm critical predictions of retrieved-context theory. We review the cognitive theory motivating this recent work, and the analytic techniques being developed to create integrated neural-behavioral models of human memory search.

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Introduction

We are just beginning to understand the neurophysiological processes of human memory, which give rise to abilities that are central to human experience, such as the ability to form associations between temporally discontinuous events (e.g., Wallenstein et al., 1998), and the ability to flexibly search through the details of one's own past (e.g., Tulving, 1983). These processes are widely distributed neuroanatomically, and involve, at the very least, communication

between neural circuitry in frontal, temporal, and parietal cortical regions, as well as subcortical structures including the hippocampus. The dynamics of these circuits are reflected in omnipresent oscillatory signals recorded from the local field around populations of neurons, as well as in more global electrical signals that can be detected at the scalp (Nunez and Srinivasan, 2006). At the lowest level, high-frequency oscillations have been hypothesized to control the timing of single-unit activity to solve the problem of sensory segmentation (von der Malsburg and Schneider, 1986; Tallon-Baudry and Bertrand, 1999), and to optimize neural plasticity processes (Axmacher et al., 2006). At a broader scale, lower-frequency oscillations have been posited to facilitate inter-regional communication, controlling whether signal from one region can effectively influence dynamics in another region (Buzsáki, 2006; Fries, 2005, 2009). Together, the topographic patterns of

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neural oscillations at different frequencies are sensitive to the neural processes engaged to carry out a given task (Canolty et al., 2006), and to the characteristics of perceptual stimuli (Jacobs and Kahana, 2009; Pasley et al., 2012). Here, we describe recent work relating these topographic patterns to a class of computational models designed to explain the dynamics of human memory.

In a laboratory setting, the free-recall task is used to observe memory search as it unfolds. A participant studies a set of items, usually presented one at a time. After some delay, the participant's task is to recall the studied items in whatever order they come to mind. During this recall period, the memory system is engaged in a covert search through one's past experience which yields a set of overt behavioral responses in the form of vocal report of the studied items. While much of memory search is behaviorally covert, reliable neural signals are produced which reflect the dynamics of the search and can reveal the influence of the associative structures formed during the study episode (Long et al., 2010; Morton et al., in press; Polyn et al., 2005, 2012; Savage et al., 2001; Shapira-Lichter et al., 2012). In order to interpret the functional properties of the cognitive processes giving rise to these neural signals, researchers have turned to computational models of the search process. While different models disagree in fundamental ways about the basic structure of memory, there has been theoretical convergence over the past decades, driven largely by the observed dynamics of memory retrieval, regarding the necessity of a temporally sensitive contextual representation that allows the system to target memories formed within a particular temporal interval (Davelaar et al., 2005; Howard and Kahana, 2002; Mensink and Raaijmakers, 1988; Sederberg et al., 2008). We focus on one class of memory models known as retrieved context models (Howard and Kahana, 2002; Howard et al., 2005; Polyn et al., 2009; Sederberg et al., 2008). These models provide a detailed description of the dynamics of this contextual representation, and have been used to provide a functional interpretation of the oscillatory signals recorded during study and memory search.

Cognitive theory of mental time travel

The notion of context has many meanings in the memory literature. It can refer to the spatial environment in which an event occurs (Bjork and Richardson-Klavehn, 1989; Smith, 1988), the spatial environment during a particular temporal interval (Schacter, 1987; Tulving, 2002), the task performed while studying an item (Cohen et al., 1990), or something more inclusive, such as the array of thoughts, feelings, and emotions present in the mind at a given moment (Bower, 1972), or just the general circumstances surrounding a particular event (Norman and Schacter, 1996). The idea of a context is central to the theory of mental time travel; in order to revisit a past experience, some detailed characteristics of that past experience must be reactivated in the cognitive system. Retrieved context theory focuses on the mechanistic properties of the contextual system, and different researchers have explored the consequences of these mechanisms operating on item-specific information (Howard and Kahana, 2002; Sederberg et al., 2008), source information (Polyn et al., 2009), and spatial information (Howard et al., 2005; Miller et al., 2013; Sederberg et al., 2011).

Generally speaking, retrieved context theory describes memory formation in terms of an interaction between executive processes that sculpt a neural context representation, and associative processes that link this contextual representation to the perceptual representations of experience, in other words, an item representation (Howard and Kahana, 2002; Polyn and Kahana, 2008). During memory search, the particular state of the contextual representation, along with the associative structures created during past experience, determine which memories are likely to be recalled. The reactivation of past contextual states allows the model to access the memory of the experiences that took place in that context. The theory describes

two representations: An item representation containing information about the characteristics and features of the perceptual environment, and a slowly changing contextual representation reflecting a summary version of recent experience. These representations interact via the associative circuitry of the brain, which is assumed to consist of both long-standing associations as well as associations based on recent experience.

Stimulus-related neural activity projected along these associative pathways forms the major source of input to the contextual representation. As such, every experience involves an act of memory, in that the associative connections one forms throughout one's lifetime determine the structure of the activation patterns that influence context. A given perceptual state, projected along these associative pathways, retrieves a blend of the contextual states that it, or similar perceptual states, have been associated with in the past. In other words, ongoing experiences continually retrieve prior contextual states that modify the current contextual representation. When an item is studied, the item representation retrieves contextual information that is unique to that item, which is then incorporated into the contextual representation.

The neural circuitry supporting the contextual representation has integrative properties which allow it to maintain its representational state in the absence of supportive bottom-up inputs from perceptual regions. At the same time, when new information is projected to the contextual region, these maintenance processes cause the contextual representation to have a long time-constant. In other words, it retains some trace of its past states, even as new information is incorporated into it. The theory doesn't specify the specific neural substrate of this integration process, though there are a number of plausible neurophysiological mechanisms that could give rise to these dynamics (e.g., Aksay et al., 2001; Gold and Shadlen, 2007; Miller and Cohen, 2001).

The integrative machinery causes the contextual representation to change slowly over time, yet there is a tension between allowing incoming activity to be prominently represented and allowing the system to continue to maintain prior states (Cohen et al., 1996). The model has a parameter which controls the balance between these two sources; if the parameter is low, the contextual representation is dominated by prior states (i.e., it changes very slowly), and if the parameter is high, the contextual representation is dominated by incoming activity (i.e., it changes very quickly). This parameter, in a sense, controls the drift rate of this ever-changing contextual representation. A recent study by Morton et al. (in press), examining a potential neural signal of contextual integration in scalp EEG oscillatory activity, suggests that individual differences in this integration rate can be characterized neurally.

When an item is studied, new associations are formed between the current perceptual representation and the current contextual representation. These episodic associations cause the contextual representation to become an effective retrieval cue for that perceptual state, and similarly, cause that perceptual state to become a good retrieval cue for that state of context. The associations themselves are latent in the system, but their presence can be inferred through interpretation of either behavioral performance or neural signal.

During the recall period, the contextual representation is used to probe the associative structures of memory in order to remember the studied items. With each successful recall, the reactivated representation of the studied item is used to retrieve past states of context. When, for example, an item from the middle of the list is recalled, the retrieved context will match the contextual pattern observed at that mid-list position. Since the context changed slowly over the course of the list, this retrieved context is a good cue for items studied in neighboring list positions, leading to a sequential dependency in the set of responses made by the participant. Specifically, recall of a particular item is likely to be followed by neighboring study items, a behavioral phenomenon known as the contiguity effect. Contiguity effects are ubiquitous in episodic memory studies at a range of

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