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.

Contents

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 discontiguous 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

timescales from seconds (Howard and Kahana, 1999) to tens of minutes (Howard et al., 2008), and suggest that storage and retrieval of item-to-context bindings are the fundamental associative processes at work in episodic memory (Howard and Kahana, 2002; Sederberg et al., 2010). A recent study by Manning et al. (2011) suggests that one can observe the neural signature of this contextual retrieval process in topographic patterns of intracranially recorded oscillatory activity.

The computational theory of mental time travel described here provides a set of properties we expect a neural contextual representation to exhibit (Polyn and Kahana, 2008). A neuroanatomical candidate contextual region should exhibit neural activity patterns that (1) are sensitive to the features and statistical properties of the perceptual environment, (2) exhibit autocorrelation over a long time-scale, and (3) return to a prior representational state when a past event is remembered. A number of challenges must be faced by researchers hoping to find evidence linking this model to neural signal. For example, (1) and (3) could be true of item-specific reactivation (Danker and Anderson, 2010), but if evidence for (2) is simultaneously observed, and the autocorrelated signal is itself reactivated (as observed by Manning et al., 2011), it becomes more difficult to support an item reactivation account of the findings.

The context representation is hypothesized to change slowly over time, but many physiological, as well as non-physiological, signals show autocorrelation over long timescales (Bullmore et al., 2001). However, if the autocorrelation in a candidate neural signal is found to be related to memory performance, this rules out many alternate interpretations (e.g., Jenkins and Ranganath, 2010; Manns et al., 2007; Morton et al., in press). A second challenge arises in distinguishing neural signatures of item-specific activity from neural signatures of contextual activity. As mentioned, retrieved context theory suggests that item-specific information is integrated into the contextual representation. Theoretical work suggests that this integrated item-specific signal could form the basis for our knowledge of the semantic relationships between words (Jones and Mewhort, 2007; Rao and Howard, 2008). As such, it can be difficult to distinguish between purely item-related signal, and contextual signal, as both may have item-specific components. Despite these challenges, recent work has used retrieved context theory to generate specific predictions regarding the autocorrelative structure of contextual activity, allowing one to disentangle the signatures of item and contextual representations (e.g., Manning et al., 2011; Morton et al., in press).

Oscillatory correlates of encoding and retrieval processes

The strength, coherence, and topography of oscillations observed when a particular stimulus is presented contains predictive power regarding whether that stimulus will be later remembered (Fell et al., 2001; Klimesch et al., 1997; Miltner et al., 1999; Sederberg et al., 2003; Weiss et al., 2000).These effects appear at widespread frequencies, though most work has focused on the theta and gamma bands, in part because of the theoretical work linking activity in these bands to low-level neural mechanisms involved in inter-regional communication and association formation (for a review, see Nyhus and Curran, 2010). Oscillatory shifts predictive of performance are also observed during memory retrieval, when an item is presented in a cued recall or recognition paradigm (Gruber et al., 2008; Klimesch et al., 1997, 2000, 2001; Summerfield and Mangels, 2005.

These studies provide important evidence linking particular oscillatory effects to encoding and retrieval processes, but can be challenging to interpret in terms of a cognitive theory of memory. As described above, retrieved context theory describes memory dynamics in terms of the structure, evolution, and reactivation of representations. In order to investigate these predictions, we require a neural approach capable of characterizing representational structure, such as multivariate pattern analysis (MVPA; Norman et al., 2006) or representational similarity analysis (RSA; Kriegeskorte et al., 2008). Sederberg et al. (2007)

took a step in this direction with an analysis of intracranially recorded oscillations in the gamma frequency band. They found that the topography of gamma oscillations identified at encoding with a contrast between subsequently remembered and subsequently forgotten items matched the topography of gamma oscillations identified at retrieval with a contrast between correctly recalled items and intrusions (i.e., items that were not on the list). Given that the same regions were identified under quite different task demands (study vs. memory search), it is possible that the overlapping topographies reflected the reactivation of neural representations present during the study period. However, it is also possible that the pattern of oscillatory activity in the gamma band reflected cognitive states conducive to forming and retrieving associations, such as a high-attention state. In order to rule out such accounts, more recent work has used MVPA and RSA to characterize the topographic patterns of oscillations associated with particular subclasses of studied items, and even individual study items, so as to draw more specific conclusions regarding the representational content of the neural activity.

Multivariate pattern analysis of neural oscillations in memory tasks

Studies using multivariate techniques (e.g., Duda et al., 2001) to characterize the informational content of neural signal are increasingly widespread, given the broad applicability of these techniques to multiple recording modalities (e.g., Haxby et al., 2001; Kriegeskorte et al., 2008; Manns et al., 2007; Miyawaki et al., 2008; Morton et al., in press; Norman et al., 2006; Pasley et al., 2012). These techniques have been developed to characterize neural oscillatory topographies (Mensh et al., 2004; Parra et al., 2005), leading to recent work examining how the structure of oscillatory representations corresponds to perceptual experience. Two recent successes of this approach involved intracranial recordings of oscillatory signals in the gamma frequency range. Jacobs and Kahana (2009), examining the encoding period of a memory-scanning paradigm, found that gamma oscillations contain information about the identity of particular letter stimuli. Similarly, Pasley et al. (2012), recording from higher order auditory cortex, were able to reconstruct speech stimuli heard by the participant based on gamma-band activity. However, as we will describe below, there is suggestive evidence that representational information is spread throughout the oscillatory spectrum and not restricted to the high-frequencies (Morton et al., in press).

Despite our incomplete understanding of the mapping from the oscillatory dynamics measured with scalp and intracranial EEG recordings to the dynamics of the underlying neural tissue (Nunez and Srinivasan, 2006), oscillatory signals are informationally rich. This is not surprising: given the tight relationship between oscillatory activity and single-unit activity (Fox et al., 1986; Jacobs et al., 2007; Wehr and Laurent, 1996), and the fact that the topography of single-unit activity contains a great deal of information regarding the higher-order perceptual properties of observed stimuli (e.g., Gross et al., 1969; Kreiman et al., 2006), one might expect that the topographic pattern of oscillatory activity also contains information about higher order stimulus properties (e.g., Freeman and Schneider, 1982).

These multivariate techniques allow us to bridge between model and neural data in a way not previously possible. Manning et al. (2012) identified neural representations whose dynamics are suggestively similar to the item representation described by retrieved context theory, in that they reflected the semantic characteristics of the stimuli, reactivated during memory search, and allowed one to predict the recall performance of individual participants. Principal component analysis was applied to intracranial oscillatory signals at widespread frequencies during a free-recall task, and the pattern of component amplitudes recorded while an item was studied (in this case, a visually presented word) contained information about the item's semantic identity. The fidelity of this semantic structure was quantified by comparing

the pairwise similarities of the neural patterns with pairwise similarities of representations derived from a computational model of semantic memory (LSA; Landauer and Dumais, 1997). Additionally, item-specific reactivation was observed prior to recall events, in frontal and temporal (including hippocampus) regions, where the correspondence between neural and model-based similarities predicted the degree to which an individual participant used semantic information to organize their recall sequences. Together, these results demonstrate that it is possible to decode the content of experience and memory from patterns of oscillatory activity, not just the phenomenological correlates of successful encoding and retrieval.

Oscillatory patterns related to categorical context

A study by Morton et al. (in press) examined neural oscillatory activity in a free-recall paradigm, and found oscillatory patterns consistent with both item and contextual representations. This work examined both intracranial and scalp EEG recordings (in separate participant groups) while participants studied lists composed of items drawn from three distinct taxonomic categories (celebrities, landmarks, and common objects). The intracranial recordings, while not showing clear evidence for integrative processes, showed strong category-specific oscillatory signals consistent with item-related neural activity. The topographic pattern of oscillations at study reflected the category identity of the stimulus, and these patterns were reactivated in frontal and temporal regions during an immediate recall test, as well as in parietal regions in a delayed recall test. In both the scalp and intracranial signal, category-specific oscillations were observed across the frequency spectrum, from delta frequencies through high gamma. Category-specific signals were strongest for the low frequencies in both scalp and intracranial recordings. However, there was a significant increase in category-specificity for intracranial high gamma signal that was not apparent in the scalp recordings.

The category-related signal recorded at the scalp showed dynamics consistent with a contextual representation during both study and recall. Retrieved context theory makes a specific prediction regarding the structure of the contextual representation when multiple items from the same category are studied successively. Specifically, the integration process creates a recency-weighted average of the individual items; this causes idiosyncratic item-specific features to be deemphasized, and category-general features to become more prominent. This prediction was borne out in the neural signal: The oscillatory signals recorded at the scalp became more category-specific as multiple items from the same category were studied in a row (Fig. 1A; the intracranial experiment had shorter lists and fewer category repeats, precluding this specific analysis). Furthermore, the rate at which the category specificity increased with successive same-category items predicted the degree to which a participant would cluster items by category during the recall period. The scalp signal during memory search also showed evidence of an integrative process. Participants tended to successively remember multiple items from the same category, and as they did, the oscillatory topography became progressively more category-specific (Fig. 1B).

Oscillatory patterns related to retrieved temporal context

Manning et al. (2012) and Morton et al. (in press) each showed reactivation of neural patterns related to the meaning of the remembered item. However, retrieved context theory makes a specific prediction regarding the structure of the neural patterns reactivated during memory search. In order to test retrieved context theory, Manning et al. (2011) contrasted intracranial oscillatory activity to synthetic neural data constructed by applying three computational models to the actual recall sequences produced by a set of participants. The first model generated autocorrelated noise unrelated to the cognitive processes, the second model reactivated item-related information when a given item was recalled, and the third model
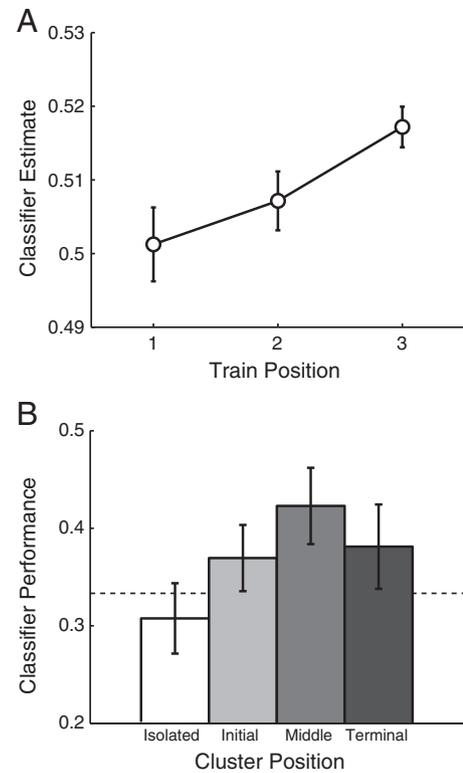

Fig. 1. A. Classifier estimate corresponding to the category of the presented item rises as items from the same category are studied successively. B. Classifier performance is sensitive to recall organization in immediate free recall. Cluster position label indicates the position of the item in the recall sequence. Isolated: surrounded by other-category items. Initial, Middle, and Terminal correspond to position in a sequence of same-category items. Dashed line indicates chance performance.
Figures from Morton et al. (in press).

reactivated the contextual state present when that item was studied. As described above, context-related neural activity is proposed to exhibit autocorrelation on long timescales. During memory search, this autocorrelated contextual signal is reactivated, giving rise to a specific prediction. When a particular item is remembered, the pattern of reactivated neural activity should match the neural pattern observed while that item was studied, and moreover, the reactivated pattern should show a graded similarity with the patterns corresponding to the neighboring items in the study list, with similarity falling as the lag to the recalled item increases. In contrast, the item-reactivation model showed this graded similarity only in the forward direction (corresponding to a lingering representation of the item during study), and the noise-based model showed no reliable relationship between study patterns and recall patterns. As in Manning et al. (2012), principal components analysis was used to reduce the dimensionality of the signal. Here, however, only components showing a strong autocorrelation profile were selected for the analysis. The neural pattern recorded prior to each recall event was compared to the neural patterns from the corresponding study-period, and the gradual fall-off of similarity in both directions confirmed the prediction of the retrieved context model (Fig. 2A). Furthermore, the slope of this fall-off was estimated for each participant, and the reliability of the neural effect showed a positive correlation with the size of the contiguity effect for that participant.

One puzzling aspect of these findings concerns the relationship between the neural similarity structure (falling off symmetrically in both directions) and the behavioral contiguity effect, which shows a strong and reliable forward-going asymmetry (Fig. 2B; Kahana, 1996; Kahana et al., 2008). The retrieved context theory suggests that two associative components contribute to the shape of the contiguity effect:

long-standing pre-experimental associations, and rapidly formed episodic associations. The long-standing associations are what drive the integration process; these associations allow each studied item to project item-specific information into context. If only this item-specific information was detected, the reactivated neural signal would be expected to exhibit similarity only to items following the remembered item. The rapidly formed episodic associations, on the other hand, are formed as the list progresses, binding the currently studied item to the prevailing state of context. If only this episodic information was detected, the reactivated neural signal would be expected to exhibit symmetric similarity to items preceding and succeeding the studied item. According to the model, the blend of these two components (one forward-going, one symmetric), gives rise to the characteristic forward asymmetry of the contiguity effect (Howard and Kahana, 2002). Thus, one interpretation of these results is that Manning et al. (2011) only detected the episodic contribution to the contextual reactivation process, perhaps due to the exclusive selection of neural components showing strong autocorrelation.

Convergent findings and future directions

Computational models of cognitive processes provide a framework for generating and testing hypotheses about the functional properties of neural circuitry (Davis et al., 2012; Polyn et al., 2012; Purcell et al., 2010; Ratcliff et al., 2009). Developing a computational model to understand a particular cognitive process forces a theorist to be explicit about the mechanisms giving rise to observed behavior,

which often leads to broad predictions that can be investigated with multiple recording modalities, each one providing a unique perspective on the neural dynamics.

The two mechanisms focused on in this review are contextual integration and contextual reactivation. Contextual integration processes should exhibit themselves as autocorrelated neural signals, and the structure and rate of change of these signals should relate to behavior in context-sensitive tasks. Suggestive evidence along these lines has been reported in both human and rodent work, using a number of neural recording modalities. In addition to the human studies described above, Jenkins and Ranganath (2010) reported that the rate of change of neural representations in rostrolateral prefrontal cortex (measured with fMRI) predicted performance on a temporal estimation task. Manns et al. (2007) found that the rate of change of neural representations in rodent hippocampus (measured in terms of single-unit spiking activity) predicted performance on a judgment of temporal order. Cognitively relevant drift in representational structure may be a property of anatomically widespread neural circuitry. As such, it will be important to characterize the different factors contributing to this drift, in order to contrast the contribution of different regions. Recent work by Hyman et al. (2012) takes a step in this direction, reporting systematic shifts in the representational structure of spiking activity in rodent medial prefrontal cortex that are sensitive to the animal's environment, movement patterns, task-related actions, and the passage of time. The drift in medial prefrontal patterns was contrasted with drift in hippocampal spiking patterns, which showed a less prominent temporal component.

The idea that the reactivation of past experience will be reflected in neural activity patterns has a great deal of support from studies of humans as well as non-human primates (Chadwick et al., 2010; Danker and Anderson, 2010; Hasegawa et al., 1998; Hassabis et al., 2009; Wheeler et al., 2000). Retrieved context models explain the importance of neural reactivation during memory search, in that retrieved information is integrated into a contextual retrieval cue that guides the search process. Many studies in humans have found evidence for reactivation in self-guided memory search tasks like free recall, implicating widespread neural circuitry, including medial temporal structures like hippocampus, and prefrontal, temporal, and parietal cortical regions. Along with the studies described above, researchers have found evidence for reactivation of category-specific fMRI activity (Polyn et al., 2005), single-unit activity related to individual items (Gelbard-Sagiv et al., 2008), and encoding task specific fMRI activity (Polyn et al., 2012).

While mental time travel is critical for carrying out memory search, the neural correlates of this process should be exhibited whenever a person must recover the details of past experience. The evidence for reactivation of temporal context during memory search, as reported by Manning et al. (2011) is supported and complemented by a study of spiking patterns in human hippocampus during a continuous recognition task (Howard et al., 2012). In this study, participants viewed a stream of stimuli, and had to report when a particular stimulus was repeated. Upon the repeated presentation of a stimulus, the distributed pattern of spiking activity shifted to resemble the state that was present just prior to the original presentation of the stimulus, as would be expected if that prior contextual state was retrieved, as opposed to the reactivation of the item representation itself.

Perhaps the most promising domain for translational work into the oscillatory signatures of mental time travel comes from studies of rodent spatial cognition. This literature describes how hippocampal circuitry reactivates neural assemblies corresponding to previously experienced spatial locations and spatial trajectories (Foster and Wilson, 2006; Gupta et al., 2010; Pastalkova et al., 2008). These sequentially activated assemblies may play a critical role in the hippocampal-dependent ability to associate temporally discontiguous events (Bunsey and Eichenbaum, 1996; Eichenbaum, 2013; Levy, 1996; MacDonald et al., 2011; Wallenstein et al., 1998). Furthermore, this work points to a
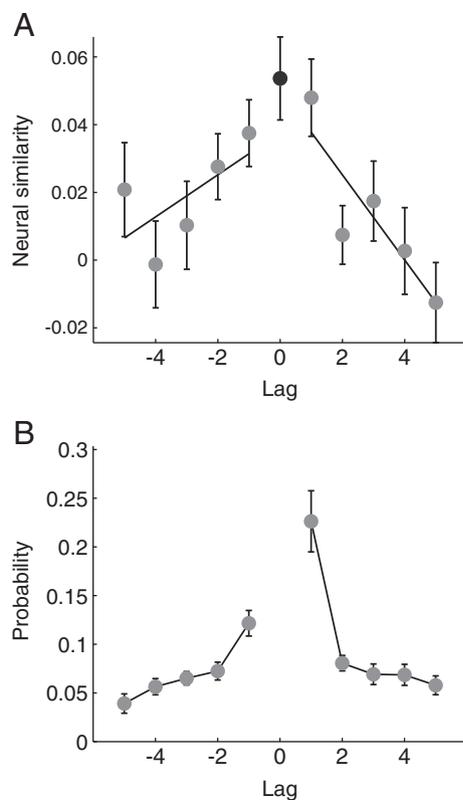

Fig. 2. A. The neural pattern recorded just before a particular item is recalled is most similar to the neural pattern recorded when that same item was studied (lag 0), and this neural similarity falls off smoothly when the recall pattern is compared to study patterns with increasing lag to the recalled item, suggesting the reactivation of an autocorrelated neural signal. Black lines indicate lines of best fit to the neural similarity scores. B. The contiguity effect of free recall, calculated from the same recall sequences used to create panel A. When a particular item is recalled, the next response tends to be from a nearby serial position, with the conditional probability of this response falling as lag to the just-recalled item increases, and with a general forward asymmetry. Figures from Manning et al. (2011).

critical role for oscillatory dynamics in organizing the replay of these spatial representations (Buzsáki, 2006; Dragoi and Buzsáki, 2006; Mehta et al., 2002). Computational models of rodent spatial navigation propose a central role for oscillatory activity in the formation of the spatial representations supporting navigational behavior (Burgess et al., 2007; Hasselmo et al., 2007).

Preliminary steps have been taken to integrate rodent-based theories of spatial navigation with human-based retrieved context theories (Howard et al., 2005), but a great deal of work remains to be done to create a species-spanning, unified theory of spatial and episodic memory. Progress along this path will require an interplay between neuroscientific investigation and computational development. Computational models provide mechanistic interpretation for neural signal and inspiration for novel analytic approaches, while neural signals and behavioral data provide constraint for the form of the computational model. Many of the studies reported here use a computational model to bridge between neural signal and behavioral observation, but often do so indirectly, relying on confirmation of qualitative model predictions, or observation of correlations between model estimates and neural signals. While these are important first steps for proving the validity of the approach, a goal for future work is to create hybrid neural–behavioral models, which describe both the neural dynamics of the system and the behavioral consequences of those dynamics. A challenge that often arises with purely behavioral models is determining whether a given hypothesized process arises during study or during retrieval, since all one can observe is the behavioral response of the participant. By directly incorporating neural signal into the model, which can be recorded during all phases of the experiment, one may be able to disentangle these study and retrieval processes. Such a hybrid approach would come with its own challenges, such as the multiplicity of potential neural signals to examine, and the many potential forms of the computational model. However, these challenges are being met with recent work in the domain of Bayesian modeling. This work promises to provide joint modeling frameworks that span the behavioral and neural domains, providing the ability to map neural activity and behavior onto specific computational mechanisms and model parameters simultaneously (e.g., Turner et al., 2013).

Conflict of interest statement

The authors state that there is no conflict of interest arising from the publication of this work.

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