

Memory search and the neural representation of context

Sean M. Polyn and Michael J. Kahana

Department of Psychology, University of Pennsylvania, 3401 Walnut Street, Room 303C, Philadelphia, PA 19104, USA

A challenge for theories of episodic memory is to determine how we focus memory search on a set of recently learned items. Cognitive theories suggest that the recall of an item representation is driven by an internally maintained context representation that integrates incoming information with a long time-scale. Neural investigations have shown that recalling an item revives the pattern of brain activity present during its study. To link these neural and cognitive approaches, we propose a framework in which context is maintained and updated in prefrontal cortex, and is associated with item information through hippocampal projections. The proposed framework is broadly consistent with neurobiological studies of temporal integration and with studies of memory deficits in individuals with prefrontal damage.

Introduction

An attempt at reminiscence can comb recent moments or revive episodes long past, sometimes producing a flood of detail, and other times a mere impression of familiarity. Here, we review the behavioral investigations, computational modeling and neuroimaging studies of memory search for recently learned items, and the insights these investigations give us for cognitive processing in general. Most of the theoretical development in this area has arisen from laboratory-based investigations of human behavior during memory search and the use of these data to construct computational models of human memory. These models suggest that slowly changing representations in the cognitive system can be used to sweep the past for desired representations. These internal context representations enable the individual to probe memory in tasks such as free recall, in which a list of words (or other items) is studied and the individual is later asked to recall as many items as possible, in any order. In this view, context representations have the role of an internal stimulus associated with each of the items to be remembered, and the manipulation of the context representation enables us to flexibly search memory for behaviorally relevant information. Recently, neural investigations have started to characterize the patterns of brain activity associated with the retrieval of information during memory search. We suggest that the above-mentioned cognitive theories will have a crucial role in interpreting the significance of these neural signals, and might provide a framework enabling

detection of the neural correlates of these hypothesized context representations.

Episode and context – a cognitive perspective

The human memory system can do more than simply recognize that a particular item was encountered. Its flexibility arises from its ability to determine when, and in what context, a particular memory occurred. Thus, a primary responsibility of the memory system during learning is to bind together elements of a stimulus representation with co-active contextual features, such that during later memory search the individual can infer much about the circumstances of a prior observation of an item by inspecting the associated contextual features. However, these associations are latent in the system and require some sort of cue or search process to revive them [1]. A major challenge for researchers interested in memory search is characterizing this contextual retrieval cue. There is a consensus that if an individual wants to revive a particular stimulus representation, the cue should contain features of that stimulus [2]. However, there is also substantial evidence that the retrieval cue contains other information that does not directly correspond to stimulus features, most notably context information (Box 1).

Perhaps the most important behavioral observation in memory search is the finding that recent events are remembered better than distant events [3]. This finding, and its many nuances under experimental manipulation, led several researchers to propose the ‘temporal distinctiveness’ account of the recency effect [4–7]. Here, an analogy is made to driving down a long highway, with the events of an individual’s life being telephone poles along the road. Memory search is likened to scanning the road behind for a particular telephone pole. As one continues down the road, the fore-shortening effect of perspective causes the distant poles to crowd together, making any one pole less distinguishable from the others. Although this account provides a solid explanation of several behavioral phenomena, it treats context as a static entity during recall: at the time of test, context is in a particular state, which determines the relative availability of the items to be recalled.

Howard and Kahana [8] revisited these findings with a formal model of the context cue that drives memory search (Box 2). Their temporal context model (TCM) incorporates two major theoretical advances. First, the system can reinstate previous contextual states, providing a mechanistic interpretation of Tulving’s mental time travel [9]. Second, context drift is not random, but is driven by

Corresponding author: Polyn, S.M. (polyn@psych.upenn.edu).

Box 1. A historical perspective on temporal context

Early memory theorists [49] regarded decay as a minor factor in forgetting, giving more weight to competitive interference from other memories. By these classic accounts, a major factor giving rise to competitive interference between memories is association to similar contexts. Estes [50] was one of the first theorists to approach the issue of associations to context with mathematical rigor. His work treated stimuli and context as bundles of binary features, in which the set of active context features would slowly, and randomly, change over the time-course of memory encoding and retrieval processes.

This stimulus sampling theory developed by Estes [51] was applied to recognition memory by Bower [52], who tied it to notions of internal context. Bower proposed that it was possible to determine approximately how long ago an item was seen by comparing the context state associated with the to-be-judged item to the current state of context. Because the context representation changes slowly over time, the similarity between the two representations can serve as an index of the recency of the judged item. Thus, a time-varying internal context, which in and of itself has no clock-like properties (only random drift), solves the problem (raised by Yntema and Trask [53]) of how people can make judgments of recency. In other words, an internal context representation can take the role of 'time-tag'.

The idea that context can have this drifting temporal component is supported by several investigations of proactive interference. Loess and Waugh [54] found that performance on a short-term memory task is enhanced by increasing the interval between successive trials. The amount of time passing between study of successive lists (and between the study periods and the recall test) also has a major role in the degree of interference observed in the A-B, A-C paired-associates paradigm [55,56]. These findings led Ceraso [57] to suggest that memories studied in close temporal proximity tend to 'crowd' each other more as time passes from the original learning episode. Theories of time-varying context broadly predict these phenomena: if an individual uses temporal context as a cue for targeting the most recent list, then interference from prior lists will be greater when those lists occurred more recently because the items on those lists are associated with a similar state of temporal context [58]. The notion of a time-varying internal context representation continues to resonate in modern investigations of memory search and has an important role in several formal models of the human memory system [8,59–63].

features associated with the stimuli studied. The primary behavioral finding motivating these proposals is the contiguity effect observed in free recall, whereby words studied nearby in time tend to be recalled successively during memory search. Using the telephone poles analogy, Howard and Kahana suggest that recalling an item is akin to jumping back to the location of a telephone pole from the road behind, and continuing to search memory in the vicinity of that pole. According to this theory, the temporal clustering underlying the contiguity effect is a consequence of nearby list items becoming associated with similar states of a slowly changing internal context representation.

Investigations of the contiguity effect suggest that it is remarkably durable, surviving the insertion of several seconds of distracting task performance between every list item [10]. Furthermore, in the paired-associates task, when participants incorrectly recall an item from a non-target pair, their recall errors are more likely to come from pairs studied in nearby list positions with a gradient extending several pairs in both the forward and backward directions [11]. Recently, Howard *et al.* [12] showed that when subjects are asked (at the end of a free-recall experiment) to recall all of the items they encountered in

the entire experiment, they tend to report items from neighboring lists nearby in the recall sequence. This suggests that the temporal integration underlying the contiguity effect might operate on a longer time-scale than was previously appreciated, on the order of at least several minutes. These long-range contiguity effects exhibit themselves in all of the major episodic memory paradigms [3], prompting the question of whether these effects have an observable neural basis.

The reactivation of neural representations during memory search

To recall an experienced item, some component of the pattern of cortical activity that accompanied its original presentation must be revived. Several neurorecording studies have shown reactivation of cortical patterns of activity during memory search [13–20]. The majority of these studies use recognition and cued-recall paradigms. In these paradigms, participants are shown a series of words, each of which is paired with a stimulus chosen from two distinct modalities (such as a sound or a picture). The studies found that cortical regions related to processing the associated modality reactivate during a later memory test, regardless of whether the test explicitly asked subjects to recall the associated modality, or simply asked them to recognize the word [13–20]. These studies have identified a network of brain regions involved in the encoding and retrieval of these stimuli, and have begun to characterize their differential contributions at different stages of processing.

In the paradigms described above, a studied item is a cue prompting recall of past events. However, one can engage in reverie without any such external cue; indeed, external stimuli can often disrupt or impede such a search. The question arises as to whether the unconstrained nature of the free-recall task causes distinct neural processes to be engaged, relative to the cued-recall and recognition paradigms. During the study period of all three types of memory paradigm (recognition, cued recall and free recall), certain brain regions show subsequent memory effects (increased activation for items that will be recalled later as opposed to those that will be forgotten [21]). Several studies have shown that distinct brain regions support subsequent memory in the free-recall paradigm, compared with recognition paradigms [22–24]. Recently, researchers have begun to investigate the patterns of brain activity observed during the search period itself. Here, we focus on two studies, each of which used a contrast based on study-period activity to help interpret the patterns observed during recall.

A study by Polyn *et al.* [25] placed participants in a functional magnetic resonance imaging (fMRI) scanner during the initial study period as well as a later free-recall period. For each subject, a pattern-classification algorithm [26] was developed to identify the neural patterns of activity associated with each of three classes of study items (celebrities, landmarks and objects). This classifier was then applied to the recall-period data from that subject, enabling the researchers to generate a second-by-second estimate of the relative presence of each of the three category patterns for the duration of the memory search

Box 2. The temporal context model (TCM)

The TCM (Figure 1) describes a simple mechanism for representing the passage of time over the course of a study list in the free-recall paradigm. In the text below, F and T refer to the item feature and the temporal context layers respectively. f and t refer to particular representations active in each of those layers. The participant studies a series of items (e.g. apple, cat, boat, dog) each of which can be thought of as a vector f_i , where i indexes list position.

As each item is presented to the participant, the item activates a pattern of related contextual features via associative connections between F and T (M^{FT} ; 'Update context' in Figure 1). This net input to the context layer (t^{IN}) is then incorporated into the context representation (t_i) by the following equation:

$$t_i = \rho_i t_{i-1} + \beta t_i^{IN} \quad (\text{Equation 1})$$

where β is a scaling parameter that determines how much new information (t_i^{IN}) is placed in context, and ρ_i weakens the current state of context (t_{i-1}) such that the overall level of contextual activation remains constant. So, when 'dog' is studied, dog-related information enters context, weakening the strength of boat, cat and apple. By this mechanism, the context representation changes slowly over time.

As each item is studied, new associations are formed between the item representation and the current context representation according to a simple Hebbian outer-product learning rule:

$$\Delta M^{FT} = t_{i-1} f_i^T \quad (\text{Equation 2})$$

$$\Delta M^{TF} = f_i t_{i-1}^T \quad (\text{Equation 3})$$

where T denotes the transpose operator. Here, the model is creating episodic associations that link each item representation to the context defined by the study list (M^{FT}), and that link the context elements back to the item representations (M^{TF}).

At the beginning of the recall period, the time-of-test context-state (t_{TOT}) is used as a retrieval cue ('Guide search' in Figure 1):

$$\tilde{f} = M^{TF} t_{TOT} \quad (\text{Equation 4})$$

Thus, \tilde{f} represents the different levels of support that the different item features receive, given the current state of context (by the example depicted in Figure 1, 'dog' will receive the most support). Finally, these activations must be transformed into recall choices, a decision process that can either be calculated within the probability choice framework of Luce [64], or using a dynamical choice rule that can arbitrate between

many alternatives [65]. Once the recall decision is made, an item is recalled. The newly reactivated item representation then triggers the retrieval of the contextual representation that was active when that item was studied, which in turn serves as a cue for the next recall. This enables TCM to mentally travel back to the time of the item's original occurrence, providing the contiguity effect. The competitive nature of the recall process means that the relative levels of support for the various to-be-recalled items are more important than their absolute levels of support; thus, contiguity and recency appear at short and long time-scales, as observed experimentally [3].

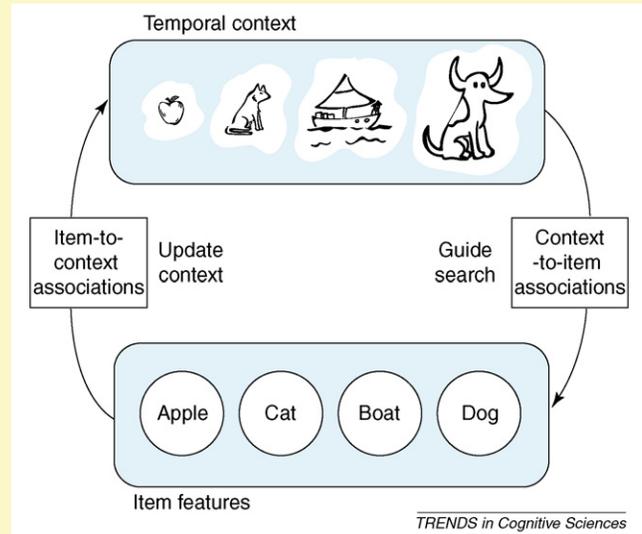


Figure 1. A schematic of the temporal context model (TCM) [8] at the end of a short study list: apple, cat, boat, dog. As each item is studied, the state of context is updated by incorporating features related to that item into the context representation; as new features are added the strength of the existing features is diminished. The currently studied item is then associated with the current state of context. The context representation can be used to guide memory search; by projecting back to the item feature layer it can provide support for recently seen items in a recall competition.

period. They found that the same category-specific pattern of activity observed during the study of an item was reinstated before the recall of that item (Figure 1), enabling them to predict the category of the recalled item based solely on the neural activity pattern. One interpretation of these findings is that these category-specific patterns of activity form a context for all of the specific exemplars of that category. By reactivating the general features of a given category, the system forms a cue that can be used to activate the representations of the exemplars. These category-specific features were found throughout the brain, including regions in the ventral temporal cortex, medial temporal cortex and prefrontal cortex (PFC).

Although the extensive coverage of the brain afforded by fMRI makes it an excellent system for investigating brain function, it does not have the temporal resolution to tell us about the millisecond-level dynamics of neural activity during memory search. Sederberg *et al.* [27] examined intracranial electroencephalographic (EEG) activity in neurosurgical patients whose brain activity was being monitored in a clinical setting. These patients took part in a free-recall task and the researchers analyzed the pattern of brain oscillations during the study period and during free recall. They discovered that the same pattern of

high-frequency (gamma, 44–100 Hz) oscillatory activity that predicts (during study) that a given item will be recalled later also activates during the recall period for correctly recalled items, versus items erroneously recalled from previous lists (Figure 2). The areas showing this gamma activity matched well with those revealed by fMRI investigations of the subsequent memory effect (left hippocampal, left temporal and left prefrontal), and no other oscillatory band showed such an effect. Thus, both the Sederberg *et al.* [27] and the Polyn *et al.* [25] studies show the reactivation of study-related patterns of neural activity during memory search for the studied stimuli. Sederberg *et al.* [27] went a step further, observing that during recall the timing of the reactivation of this pattern across different brain regions suggests that the signal originates in the hippocampus and spreads out to the cortex. This second finding fits well with the observation in nonhuman primates that item-specific spiking activity propagates from mnemonic regions to more sensory regions during the delay period of a cued-recall paradigm [28].

In each of the studies highlighted here, researchers detected the reinstatement of study-related patterns of brain activity during memory search; however, it remains to be seen whether this reinstated activity

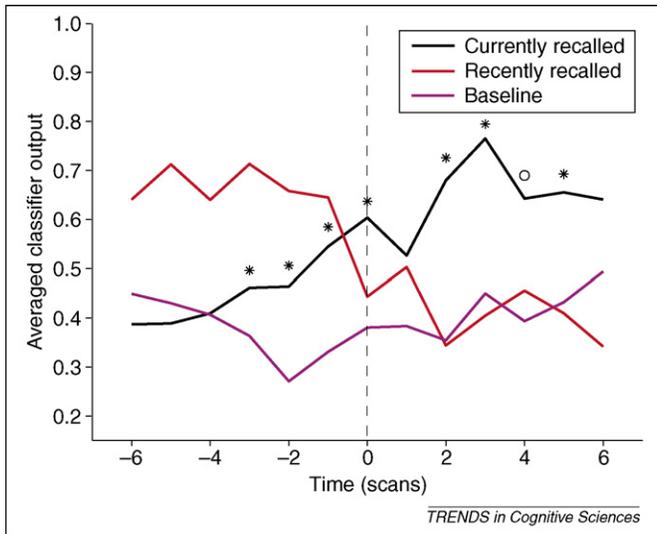


Figure 1. Patterns of category-related cortical activity gain strength before the recall of an item from that category during free recall [25] as shown by an event-related average of classifier estimates of category strength locked to the onset of recall verbalization. Time is indexed in terms of fMRI scans (each scan lasts 1.8 s and provides a full snapshot of brain activity). The black line corresponds to the average strength of the to-be-recalled category, centered on the set of recalled items for which there were no same-category recalls in the preceding 14 s. The red line corresponds to the average strength of any recently recalled categories, and the purple line corresponds to the average strength of any categories that had not been recently recalled; this serves as a baseline against which the emergence of the to-be-recalled category pattern can be assessed, which shows a significant increase 5.4 s before recall. Reproduced with permission from [25].

can be decomposed into item-related and contextual components. Cognitive theories of memory search, such as TCM, provide a framework with which to interpret neural activity patterns. Specifically, TCM predicts the existence of patterns of neural activity that (i) reflect the features and statistical properties of stimuli; (ii) integrate this information over a long time-scale; and (iii) return to a prior state, given the recall of an item. Furthermore, it seems reasonable to posit that a context representation will exhibit itself as a particular pattern

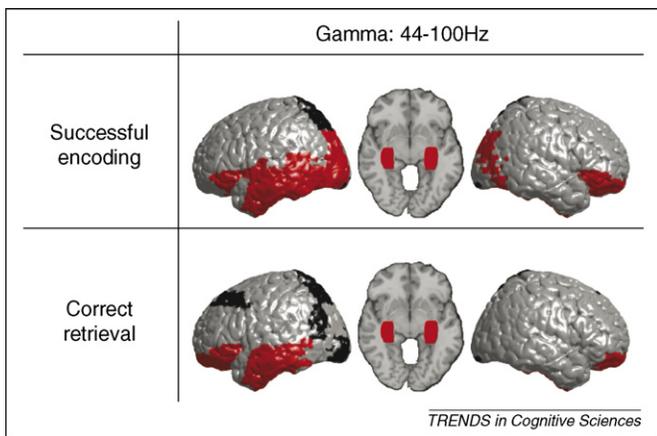


Figure 2. Brain oscillations associated with successful encoding are reinstated during correct retrieval [27]. The top row of brain maps contrasts gamma-band oscillatory activity during the two-second item presentation for items subsequently recalled and those that were forgotten. The bottom row contrasts gamma-band oscillations during the 500 ms preceding recall verbalization for correct items and for prior-list intrusions. In each map, red corresponds to regions where the contrast was significant, gray corresponds to non-significant contrasts and black indicates brain regions excluded from the analysis owing to insufficient electrode coverage. Adapted with permission from [27].

of neural spiking activity across a particular brain region (or a set of regions). If so, the full range of neural recording techniques will be valuable in characterizing this representation, with fMRI enabling us to examine system-wide patterns of brain activity and EEG revealing the finer temporal dynamics of these patterns. Perhaps the most constraining prediction made by TCM is the necessity that the context representation integrates information slowly over time; in the following section, we consider the recent literature on neural integration processes with particular attention to the role of PFC.

Neural integration, active maintenance and temporal context

As reviewed here, a neural representation of temporal context must integrate information across time. Recently, research teams have identified mechanisms of neural integration at several time-scales and in several neural systems, ranging from the goldfish oculomotor system to monkey parietal cortex [29–33]. However, many of these systems integrate in the millisecond-to-second range, whereas a system with a slower time-course is needed to give rise to the behavioral findings outlined above.

Neural activity patterns in PFC have been observed to persist over long time-periods [34] and this activity has been implicated in the cognitive control of behavior [35]. According to the prefrontal theory of cognitive control, patterns of activity in dorsolateral PFC have a role in the formation of context [36], in that they maintain information (such as task instructions or aspects of previous stimuli) that ensures that the system will respond appropriately to upcoming stimuli. Furthermore, it has been suggested that PFC might selectively maintain and update subsets of these activity patterns as dictated by task demands [37]. These mechanisms might imbue PFC with the properties necessary to serve as the neural seat of temporal context. Figure 3 presents a framework in which

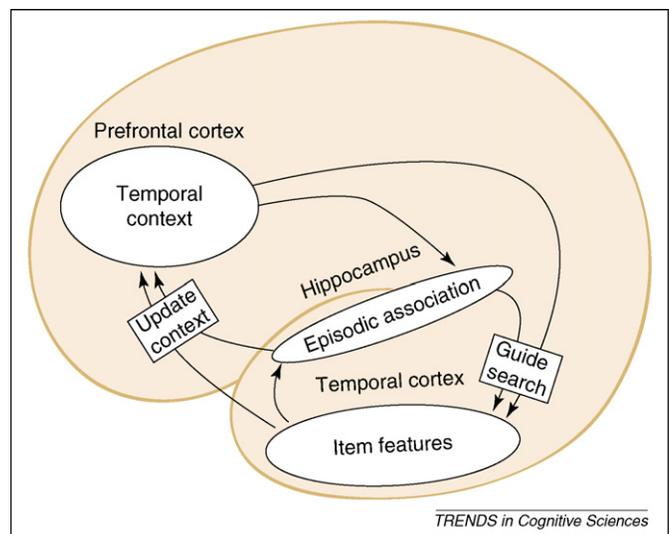


Figure 3. Prefrontal cortex (PFC) as the seat of temporal context. In this framework neural activity in temporal cortex represents the features of studied items; these update the state of a prefrontal representation of temporal context. Both item and context representations project to the hippocampus, where an episodic association is formed between the two. Direct connections between prefrontal and temporal cortices might also have a role in this process.

PFC might have this role. Here, the context-related representations resident in PFC and stimulus-related representations of temporal cortex both project into hippocampus, where they are associated with one another [38,39]. Once associated, the maintenance and manipulation of these prefrontal representations can alter the relative accessibility of recently experienced posterior representations, as described by TCM.

Taking this view, damage to the hippocampus makes it difficult to recall that an item was recently experienced in a given context (e.g. the most recent list, although patients with such damage often perform well when forced to guess about the prior occurrence of such an item) because the item representation has not been associated with temporal context. Unlike hippocampal damage, which would be expected to damage binding of context to items, damage to PFC should impair the ability to maintain and update context in a flexible manner. Indeed, several theorists have characterized the frontal deficit in episodic memory as an impaired ability to focus on, or target, particular memories [40–43], and the empirical literature lends support to this view. For example, patients with frontal damage show increased susceptibility to proactive interference in the A–B, A–C paired-associates paradigm [44], suggesting an inability to stop the previously learned (and now irrelevant) A–B associations from intruding upon the now-relevant A–C associations. Furthermore, patients with frontal damage tend to show general impairment in the free-recall paradigm, showing reduced overall recall, reduced category clustering and reduced tendency to organize their recalls given multiple trials using the same set of words [45–47]. This framework predicts that frontally damaged patients will also show a greatly diminished contiguity effect in free recall because the mechanisms supporting the maintenance and updating of temporal context are disrupted.

These speculations regarding the role of PFC in memory search are also in accordance with the neuroimaging literature – lateral prefrontal activation is nearly universally observed in studies of subsequent memory [48]. Blumenfeld and Ranganath [48] point out that although activity in the ventrolateral PFC is observed in nearly all studies of subsequent memory, dorsolateral PFC activity during study is selectively correlated with subsequent memory in paired-associates learning as well as during free recall [24]. This pattern of results would be expected of any region involved in the maintenance of a temporal context representation, and makes the further prediction that dorsolateral PFC activity during study will be related to the magnitude of the contiguity effect observed during memory search.

Concluding remarks

Recent developments in computational models of episodic memory and the cognitive neuroscience of human memory retrieval suggest that a unification of cognitive and neural memory theory is on the horizon (Box 3). Neuroimaging researchers are developing ever more sensitive techniques for probing the state of the neural system, while computational models of episodic memory are converging on the importance of context in guiding self-initiated retrieval of

Box 3. Questions for future research

- Do the same mechanisms that support working memory processes in PFC [34] also support context representations that guide memory search? The study of individual differences suggests that this unification might be possible [66].
- Recent studies of rodent entorhinal cortex have characterized neural circuitry that integrates information over time [67,68]; what is the evidence that regions other than PFC could have the role of providing temporal context? In particular, slowly changing activity states observed in rodent hippocampus during a behavioral task [69] might provide an intriguing alternative.
- Memory deficits associated with healthy aging have been linked to disrupted context updating and association formation [70]. Might these deficits share underlying mechanisms with those observed in task performance in healthy older people [36]?
- Do the principles of temporal context that arise in laboratory studies of episodic memory also come into play at a longer time-scale, such as during autobiographical memory search [71]?
- Single-unit studies [72,73] give us unprecedented ability for identifying the neural representations of individual stimuli. Can we use this to determine the relationship between the neural representations of the specific study items and the broader context representation?

episodic memory. As highlighted in this article, recent evidence suggests that neural integration underlies context representation in the brain, and PFC might have a crucial role in the representation and use of this temporal context in memory search. The pattern of deficits observed in patients with damage to the frontal lobes is consistent with this interpretation. Multivariate approaches to neuroimaging analysis [26] might foster the unification of cognitive and neural memory theory, enabling us to link the representations characterized by computational investigations to system-wide changes in neural responses as an individual attempts to recall the past.

Acknowledgements

This work was supported by the National Institutes of Health grants MH055687, MH062196, MH078513, and National Science Foundation grant SBE0354378. We thank M. Howard, P. Sederberg and C. Weidemann for helpful comments on the manuscript.

References

- 1 Tulving, E. (1983) *Elements of Episodic Memory*, Oxford University Press
- 2 Tulving, E. and Thompson, D.M. (1973) Encoding specificity and retrieval processes in episodic memory. *Psychol. Rev.* 80, 352–373
- 3 Kahana, M.J. et al. Associative processes in episodic memory. In *Learning and Memory: A Comprehensive Reference* (Vol. 2), (Byrne, J. ed.), Elsevier (in press)
- 4 Crowder, R.G. (1976) *Principles of Learning and Memory*, Lawrence Erlbaum and Associates
- 5 Glenberg, A.M. et al. (1980) A two-process account of long-term serial position effects. *J. Exp. Psychol.* 6, 355–369
- 6 Glenberg, A.M. and Swanson, N.G. (1986) A temporal distinctiveness theory of recency and modality effects. *J. Exp. Psychol. Learn. Mem. Cogn.* 12, 3–15
- 7 Nairne, J.S. et al. (1997) Positional distinctiveness and the ratio rule in free recall. *J. Mem. Lang.* 37, 155–166
- 8 Howard, M.W. and Kahana, M.J. (2002) A distributed representation of temporal context. *J. Math. Psychol.* 46, 269–299
- 9 Tulving, E. (2002) Episodic memory: from mind to brain. *Annu. Rev. Psychol.* 53, 1–25
- 10 Howard, M.W. and Kahana, M.J. (1999) Contextual variability and serial position effects in free recall. *J. Exp. Psychol. Learn. Mem. Cogn.* 25, 923–941
- 11 Davis, O.C. et al. Temporal associative processes revealed by intrusions in paired-associate recall. *Psychon. Bull. Rev.* (in press)

- 12 Howard, M.W. *et al.* The persistence of memory: Contiguity effects across several minutes. *Psychon. Bull. Rev.* (in press)
- 13 Wheeler, M.E. *et al.* (2000) Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proc. Natl. Acad. Sci. U. S. A.* 97, 11125–11129
- 14 Vaidya, C.J. *et al.* (2002) Evidence for cortical encoding specificity in episodic memory: memory-induced re-activation of picture processing areas. *Neuropsychologia* 40, 2136–2143
- 15 Kahn, I. *et al.* (2004) Functional-neuroanatomic correlates of recollection: implications for models of recognition memory. *J. Neurosci.* 24, 4172–4180
- 16 Slotnick, S.D. and Schacter, D.L. (2004) A sensory signature that distinguishes true from false memories. *Nat. Neurosci.* 7, 664–672
- 17 Prince, S.E. *et al.* (2005) Neural correlates of relational memory: successful encoding and retrieval of semantic and perceptual associations. *J. Neurosci.* 25, 1203–1210
- 18 Wheeler, M.E. *et al.* (2006) Evidence for separate perceptual reactivation and search processes during remembering. *Cereb. Cortex* 16, 949–959
- 19 Dobbins, I.G. and Han, S. (2006) Cue- versus probe-dependent prefrontal cortex activity during contextual remembering. *J. Cogn. Neurosci.* 18, 1439–1452
- 20 Johnson, J.D. and Rugg, M.D. (2007) Recollection and the reinstatement of encoding-related cortical activity. *Cereb. Cortex* 17, 2507–2515
- 21 Paller, K.A. and Wagner, A.D. (2002) Observing the transformation of experience into memory. *Trends Cogn. Sci.* 6, 93–102
- 22 Alkire, M.T. *et al.* (1998) Hippocampal, but not amygdala, activity at encoding correlates with long-term, free recall of nonemotional information. *Proc. Natl. Acad. Sci. U. S. A.* 95, 14506–14510
- 23 Strange, B.A. *et al.* (2002) Dissociable human perirhinal, hippocampal, and parahippocampal roles during verbal encoding. *J. Neurosci.* 22, 523–528
- 24 Staresina, B.P. and Davachi, L. (2006) Differential encoding mechanisms for subsequent associative recognition and free recall. *J. Neurosci.* 26, 9162–9172
- 25 Polyn, S.M. *et al.* (2005) Category-specific cortical activity precedes retrieval during memory search. *Science* 310, 1963–1966
- 26 Norman, K.A. *et al.* (2006) Beyond mind reading: multi-voxel pattern analysis of fMRI data. *Trends Cogn. Sci.* 10, 424–430
- 27 Sederberg, P.B. *et al.* (2007) Gamma oscillations distinguish true from false memories. *Psychol. Sci.* 18, 927–932
- 28 Naya, Y. *et al.* (2001) Backward spreading of memory-retrieval signal in the primate temporal cortex. *Science* 291, 661–664
- 29 Seung, H.S. *et al.* (2000) Stability of the memory of eye position in a recurrent network of conductance-based model neurons. *Neuron* 26, 259–271
- 30 Aksay, E. *et al.* (2001) *In vivo* intracellular recording and perturbation of persistent activity in a neural integrator. *Nat. Neurosci.* 4, 184–193
- 31 Miller, P. *et al.* (2003) A recurrent network model of somatosensory parametric working memory in the prefrontal cortex. *Cereb. Cortex* 13, 1208–1218
- 32 Hanks, T.D. *et al.* (2006) Microstimulation of macaque area LIP affects decision-making in a motion discrimination task. *Nat. Neurosci.* 9, 682–689
- 33 Gold, J.I. and Shadlen, M.N. (2007) The neural basis of decision making. *Annu. Rev. Neurosci.* 30, 535–574
- 34 Postle, B.R. (2006) Working memory as an emergent property of the mind and brain. *Neuroscience* 139, 23–38
- 35 Miller, E.K. and Cohen, J.D. (2001) An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* 24, 167–202
- 36 Braver, T.S. *et al.* (2001) Context processing in older adults: evidence for a theory relating cognitive control to neurobiology in healthy aging. *J. Exp. Psychol. Gen.* 130, 746–763
- 37 Frank, M.J. *et al.* (2001) Interactions between the frontal cortex and basal ganglia in working memory: a computational model. *Cogn. Affect. Behav. Neurosci.* 1, 137–160
- 38 McClelland, J.L. *et al.* (1995) Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychol. Rev.* 102, 419–457
- 39 Diana, R.A. *et al.* (2007) Imaging recollection and familiarity in the medial temporal lobe: a three-component model. *Trends Cogn. Sci.* 11, 379–386
- 40 Schacter, D.L. (1987) Memory, amnesia, and frontal lobe dysfunction. *Psychobiology* 15, 21–36
- 41 Shimamura, A.P. (1994) Memory and frontal lobe function. In *The Cognitive Neurosciences* (Gazzaniga, M.S., ed.), pp. 803–815, MIT Press
- 42 Norman, K.A. and Schacter, D.L. (1996) Implicit memory, explicit memory, and false recollection: a cognitive neuroscience perspective. In *Implicit Memory and Metacognition* (Reder, L.M., ed.), pp. 229–259, Lawrence Erlbaum and Associates
- 43 Moscovitch, M. and Winocur, G. (2002) The frontal cortex and working with memory. In *Principles of Frontal Lobe Function* (Stuss, D.T. and Knight, R.T., eds), pp. 188–209, Oxford University Press
- 44 Shimamura, A.P. *et al.* (1995) Susceptibility to memory interference effects following frontal lobe damage: findings from tests of paired-associate learning. *J. Cogn. Neurosci.* 7, 144–152
- 45 Wheeler, M.A. *et al.* (1995) Frontal lobe damage produces episodic memory impairment. *J. Int. Neuropsychol. Soc.* 1, 525–536
- 46 Gershberg, F.B. and Shimamura, A.P. (1995) Impaired use of organizational strategies in free recall following frontal lobe damage. *Neuropsychologia* 33, 1305–1333
- 47 Becker, S. and Lim, J. (2003) A computational model of prefrontal control in free recall: strategic memory use in the California verbal learning task. *J. Cogn. Neurosci.* 15, 821–832
- 48 Blumenfeld, R.S. and Ranganath, C. (2007) Prefrontal cortex and long-term memory encoding: An integrative review of findings from neuropsychology and neuroimaging. *Neuroscientist* 13, 280
- 49 McGeoch, J.A. (1942) *The Psychology of Human Learning: An Introduction*, Longmans
- 50 Estes, W.K. (1955) Statistical theory of spontaneous recovery and regression. *Psychol. Rev.* 62, 145–154
- 51 Estes, W.K. (1959) Component and pattern models with Markovian interpretations. In *Studies in Mathematical Learning Theory* (Bush, R.R. and Estes, W.K., eds), pp. 9–52, Stanford University Press
- 52 Bower, G.H. (1972) Stimulus-sampling theory of encoding variability. In *Coding Processes in Human Memory* (Melton, A.W. and Martin, E., eds), pp. 85–121, John Wiley and Sons
- 53 Yntema, D.B. and Trask, F.P. (1963) Recall as a search process. *J. Verbal Learn. Verbal Behav.* 2, 65–74
- 54 Loess, H. and Waugh, N.C. (1967) Short-term memory and intertrial interval. *J. Verbal Learn. Verbal Behav.* 6, 455–460
- 55 Ceraso, J. and Henderson, A. (1965) Unavailability and associative loss in RI and PI. *J. Exp. Psychol.* 70, 300–303
- 56 Underwood, B.J. and Freund, J.S. (1968) Effect of temporal separation of two tasks on proactive inhibition. *J. Exp. Psychol.* 78, 50–54
- 57 Ceraso, J. (1967) The interference theory of forgetting. *Sci. Am.* 217, 117–121
- 58 Mensink, G.-J.M. and Raaijmakers, J.G.W. (1988) A model for interference and forgetting. *Psychol. Rev.* 95, 434–455
- 59 Murdock, B.B. (1997) Context and mediators in a theory of distributed associative memory (TODAM2). *Psychol. Rev.* 104, 839–862
- 60 Brown, G.D.A. *et al.* (2000) Oscillator-based memory for serial order. *Psychol. Rev.* 107, 127–181
- 61 Sirotnin, Y.B. *et al.* (2005) Going beyond a single list: modeling the effects of prior experience on episodic free recall. *Psychon. Bull. Rev.* 12, 787–805
- 62 Davelaar, E.J. *et al.* (2005) The demise of short-term memory revisited: Empirical and computational investigations of recency effects. *Psychol. Rev.* 112, 3–42
- 63 Burgess, N. and Hitch, G. (2005) Computational models of working memory: putting long-term memory into context. *Trends Cogn. Sci.* 9, 535–541
- 64 Luce, R.D. (1959) Detection and recognition. In *Handbook of Mathematical Psychology* (Luce, R.D. *et al.*, eds), pp. 103–189, Wiley
- 65 Usher, M. and McClelland, J.L. (2001) The time course of perceptual choice: the leaky, competing accumulator model. *Psychol. Rev.* 108, 550–592
- 66 Unsworth, N. and Engle, R.W. (2007) The nature of individual differences in working memory capacity: active maintenance in

- primary memory and controlled search from secondary memory. *Psychol. Rev.* 114, 104–132
- 67 Egorov, A.V. *et al.* (2002) Graded persistent activity in entorhinal cortex neurons. *Nature* 420, 173–178
- 68 Fransen, E. *et al.* (2006) Mechanism of graded persistent cellular activity of entorhinal cortex layer V neurons. *Neuron* 49, 735–746
- 69 Manns, J.R. *et al.* (2007) Gradual changes in hippocampal activity support remembering the order of events. *Neuron* 53, 530–540
- 70 Howard, M.W. *et al.* (2006) Aging and contextual binding: Modeling recency and lag-recency effects with the temporal context model. *Psychon. Bull. Rev.* 13, 439–445
- 71 Cabeza, R. and Jacques, P., St (2007) Functional neuroimaging of autobiographical memory. *Trends Cogn. Sci.* 11, 219–227
- 72 Kreiman, G. *et al.* (2000) Category-specific visual responses of single neurons in the human medial temporal lobe. *Nat. Neurosci.* 3, 946–953
- 73 Quiroga, R.Q. *et al.* (2005) Invariant visual representation by single neurons in the human brain. *Nature* 435, 1102–1107

Have you contributed to an Elsevier publication? Did you know that you are entitled to a 30% discount on books?

A 30% discount is available to all Elsevier book and journal contributors when ordering books or stand-alone CD-ROMs directly from us.

To take advantage of your discount:

1. Choose your book(s) from www.elsevier.com or www.books.elsevier.com

2. Place your order

Americas:

Phone: +1 800 782 4927 for US customers

Phone: +1 800 460 3110 for Canada, South and Central America customers

Fax: +1 314 453 4898

author.contributor@elsevier.com

All other countries:

Phone: +44 (0)1865 474 010

Fax: +44 (0)1865 474 011

directorders@elsevier.com

You'll need to provide the name of the Elsevier book or journal to which you have contributed. Shipping is free on prepaid orders within the US.

If you are faxing your order, please enclose a copy of this page.

3. Make your payment

This discount is only available on prepaid orders. Please note that this offer does not apply to multi-volume reference works or Elsevier Health Sciences products.

For more information, visit www.books.elsevier.com