CHAPTER FIVE

The role of context in episodic memory: Behavior and neurophysiology

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Abstract

There is broad agreement that context plays a role in episodic memory. There is less agreement on the nature and centrality of this role. Retrieved context models specify a set of computational mechanisms that place context at the very heart of episodic memory processes. They assume that an internal context representation updates, or drifts, whenever new events are experienced and that these events form associations to this representation. They further assume that memory search proceeds by using the

Psychology of Learning and Motivation, Volume 75
ISSN 0079-7421
https://doi.org/10.1016/bs.plm.2021.06.003

context representation as a cue and that recalled memories reinstate their own context which then forms part of the cue for the next recall. When applied to laboratory tasks such as free recall, these models make specific testable predictions about not only recall behavior but also to the neurophysiology of memory search. Specifically, they predict that the brain should maintain a representation that changes gradually during study and that new events should become associated with this context representation. Most critically, they predict that during memory search successfully recalling one item should trigger reinstatement of the state of context associated with that item. If true, this should manifest in subjects' behavior as a tendency for items experienced nearby in time to cluster together during recall (i.e., a contiguity effect) and in neurophysiological recordings as a temporally graded pattern of reinstatement. We review the evidence for each of these predictions. We also discuss a range of related issues including group and individual variation in contextual processing and different types of context, such as temporal and source.

1. Introduction

Context is what makes an episodic memory episodic. For example, if your parents have always told you that you visited a particular beach as a child, but you cannot mentally reinstate any of the details of the experience, then to you the beach vacation remains just a fact. If, however, you can reinstate the mental representations of contextual details, like a mental image of the view of the lighthouse in the distance, the sound of the waves crashing, the smell of the sea, or the emotions you experienced, then the vacation becomes an episodic memory. Theories of memory have long incorporated the idea of a context representation (McGeoch, 1932; Tulving, 1972) that carries these episodic details and these ideas have been formalized in computational models (Bower, 1967; Estes, 1955 b; Howard & Kahana, 2002; Mensink & Raaijmakers, 1989). Although the predictions of these models have been shown to be in close agreement with behavioral data, historically it has been difficult to test what is perhaps their most central prediction: the brain should maintain a slowly changing neural representation to which new events become associated and, critically, that upon recalling an event it should trigger reinstatement of this temporal representation. Here, we will review the behavioral and neurophysiological evidence for this key prediction. We will begin by defining what we mean by context and introducing retrieved context models as a framework for understanding the role of context in memory encoding and search.

2. Defining context

Context has several definitions and countless operationalizations. Our working definition conceptualizes context as the representation of stimulus features surrounding, but not comprising, the stimulus itself. In this way, one can distinguish a stimulus's content from its context, yet the content and context of a stimulus are associated together in memory. Context may include external, environmental features—a type of *source* context. For instance, if a student is attempting to retrieve a fact for an exam, this may evoke memory of sitting in the classroom and learning this fact. Although such details may form a part of the memory representation or assist with remembering the fact; nonetheless, these details are not an essential part of the fact itself. Research studies typically manipulate external, source context features. In its simplest form, the context of a visual stimulus might be a background color or image. Researchers also sometimes manipulate external context by having different parts of the study take place in distinctive rooms.

Another type of context, *temporal* context, is often discussed in relation to episodic memories, which are defined by the time and place they occurred (Tulving, 1972). As the name suggests, temporal context refers to the information surrounding the content of a memory in time. Temporal context can be thought of as one's current position in psychological space, with drift occurring as one's mind meanders through this space. This drift occurs slowly over time such that the state at time t_1 tends to be more similar to the state at time t_2 than to the state at time t_3. A stimulus or episode experienced at a certain time point t_i is encoded as an episodic memory associated with the temporal context state at t_i. Thus, stimuli or events experienced close together in time are associated with similar temporal context states. This notion, of shared similarity in context states between items presented nearby in time, may also apply to other external features (e.g., two experiences occurring successively in the same environment will share similar source context). Yet, as we will discuss further below, more drastic changes to content or context features tend to lead to greater sudden shifts in context.

Rather than an external variable to be manipulated, it is more common to intuit internal temporal information as a vector. In an experimental study, each studied or retrieved item is associated with a temporal context vector, and like an internal clock, temporal context vectors tend to change slowly over time. In this way, temporal context vectors associated with nearby timepoints tend to be more similar to one another. In one popular definition, this vector is comprised of binary elements (1 or 0), fluctuating in value from moment to moment (Bower, 1967; Estes, 1955 a). Thus, a given temporal context vector tends to be similar to vectors from nearby moments, as fewer elements would have fluctuated. Building on these ideas, retrieved context models (Howard & Kahana, 2002) assume that the temporal context vector changes with each item in memory, whether it is being studied or retrieved. For the remainder of this paper, we will use this latter definition of temporal context, where context changes slowly with each experienced stimulus or item.

For any type of context, a critical question concerns its role in memory. It is undeniable that in certain circumstances memory retrieval is supported by reinstatement of the context in addition to the content of a memory. Yet, more generally, it remains debated whether context retrieval plays a primary, supporting, or negligible role in episodic memory retrieval. Further fueling this debate, context retrieval can vary by context type, by memory task demands (e.g., Polyn, Erlikhman, & Kahana, 2011; Tulving, 1985), by subject (e.g., Healey, Crutchley, & Kahana, 2014; Manning, Polyn, Baltuch, Litt, & Kahana, 2011), and even for individual stimuli for a given subject (e.g., Folkerts, Rutishauser, & Howard, 2018; Sadeh, Moran, & Goshen-Gottstein, 2015). Here we present evidence for a central role of context information in episodic memory organization, especially in recall tasks. Under the assumption that context plays a central role, the intuition is that context evokes the content of their associated memories, and memories promote reinstatement of their associated contexts. In the next section, we describe a model framework which formalizes these relationships between context and content. This model framework has fueled the debate and developments regarding the influence of context in episodic recall.

3. Retrieved context models

Retrieved context models assume context plays a central role in episodic memory tasks (Howard & Kahana, 2002). These models have had much success in accounting for memory phenomena in the free recall paradigm, in which a list of items is presented, and then the model (or a subject) must recall as many items as possible from the just-studied list. Fig. 1 shows a schematic illustration of the architecture of these models, using the Context Maintenance and Retrieval Version 2 (CMR2; Lohnas, Polyn, & Kahana, 2015) as an example.

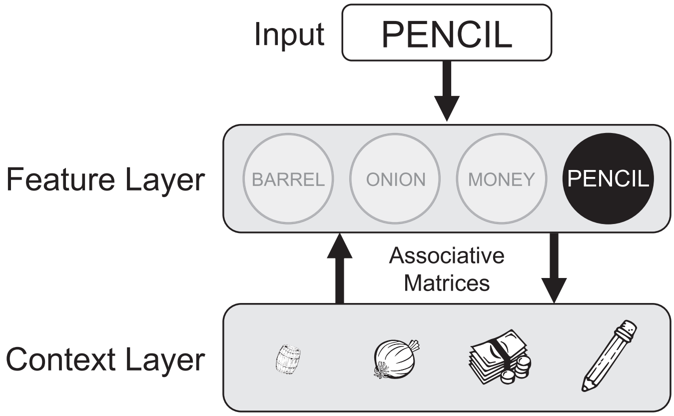

Fig. 1 Schematic of the Context Maintenance and Retrieval Version 2 model. The feature layer represents the identity of list items, with one node for each item. The context layer represents the ensemble of contextual associates that are activated when an item is presented; each item has a corresponding context node. Here, the item *pencil* is being presented to the model, which results in a state of context that incorporates *pencil*'s context with the context of previously presented items *money*, *onion*, and *barrel*. Note that due to context drift, the more recently presented items are more strongly active on the context layer (represented by the size of the icons). The two layers are connected by two associative matrices; one encoding feature-to-context associations and one encoding context-to-feature associations. Upon presentation of *pencil*, these matrices would update to store new associations between the *pencil* item representation and the active context.

As shown in Fig. 2, retrieved context models assume that new associations are formed between the studied item and the most recent context state and that the context state associated with each item is stored in memory (some implementations form associations before updating context, other update context before forming associations). Then, the presentation of an item updates context. The current context state is used to cue recall, and as a result, items more strongly associated to the current context state are more likely to be recalled. At the beginning of the recall period, this context state is a recency-weighted sum of the contexts from studied items. Recall of an item evokes retrieval of its associated context from study, and this retrieved context updates the current context state. The updated state of context is then used to cue recall of another item. Because the new recall cue incorporates the context from the just-recalled item, retrieved context models are more likely to successively recall items with similar contexts.

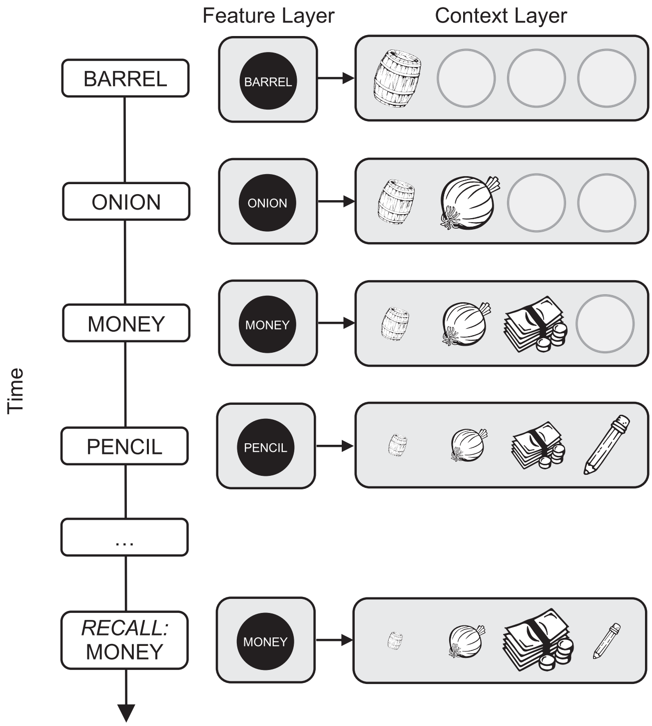

Fig. 2 Schematic illustration of how the feature and context representations of the Context Maintenance and Retrieval Version 2 model evolve during study and recall. Each row of the figure represents a different time point. The left column shows the input to the model at a given time point, the middle column shows the activity on the feature layer resulting from this input (note to save space we show only the active node of the feature layer), the right column shows the state context after projecting the feature layer through the feature-to-context associative matrix and updating context. When the first item, *barrel* (first row), appears its feature layer node is activated, which in turn activates its context representation by projecting through the feature-to-context matrix. When the next item, *onion*, appears its feature layer node is activated which causes its context representation to be activated and incorporated to the existing context representation so that both *barrel* and *onion* are active on the context layer. When the next item, *money*, appears, its context representation is activated and incorporated with the *barrel* and *onion* representation. Critically, as each new item's context is activated on the context layer, the activation of earlier items' contexts decreases (i.e., context drifts), illustrated here via the diminishing size of earlier pictures in the context layer. The final row shows how context evolves during memory search. The model has successfully recalled *money*, which activates, or reinstates, its representation on the feature layer which in turn activates the state of context associated with *money*. Due to learning during study, *money*'s context representation is now associated with items presented both before and after it in the list. Thus, when used as a cue, the reinstated context will provide support for temporally contiguous items.

4. Key behavioral evidence for retrieved context models

To make this model framework more concrete, Fig. 3 represents predictions from a retrieved context model (with temporal context only, as opposed to other types of context discussed in further sections) in a classic free recall paradigm (Howard & Kahana, 2002; Sederberg, Howard, & Kahana, 2008).

4.1 Serial position effects

Fig. 3A presents the probability of recalling each item as a function of its position in the studied list, termed serial position. Because context is updated with each studied item, at the end of a list, temporal context is a recency-weighted sum of the studied items. More recently presented items are associated more strongly to the current context, and thus are more likely to be recalled. This recall advantage for items presented near the end of the list is termed the recency effect. The simulated data in Fig. 3A also shows the increased probability of recalling early list items, termed the primacy effect.

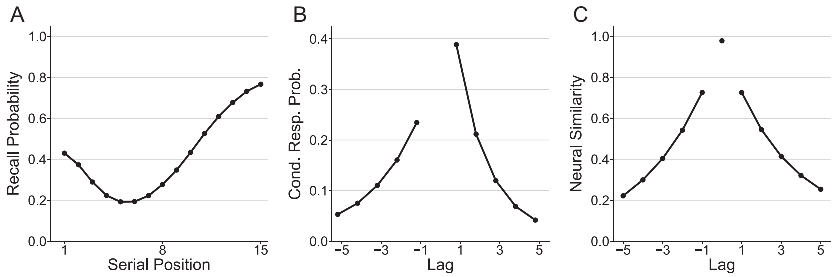

Fig. 3 Predictions of a retrieved context model in immediate free recall. For 1000 simulated subjects, the model studied and retrieved 50 lists of 15 items. Rather than presenting fits from an existing data set, predictions were generated using a generic set of parameters informed by prior work. (A) Serial position curve. The model predicts a strong recency effect and a modest primacy effect (due to an in-build primacy gradient as implemented in Sederberg et al. (2008)). (B) The model predicts a temporal contiguity effect in the form of a lag-conditional response probability (lag-CRP) function that is highest for absolute values of lag with a forward asymmetry. (C) The model also predicts that recalling an item should activate a representation that is similar to the study-phase representations of items presented nearby in time with the degree of similarity decreasing with the distance between items (see Section 5 for a detailed description of this analysis).

This occurs because the model assumes that earlier list items form stronger associations to context due to either greater attention or lack of competition (Sederberg et al., 2008).

4.2 The temporal contiguity effect

Once an item is recalled, this updates the current context state such that context has a stronger representation of the just-recalled item. When this updated state of context is used to cue recall, this promotes recall of items associated with similar temporal contexts to the just-recalled item. This property can be characterized by plotting the probability of a recall transition as a function of the difference in serial positions, or lag, between two items conditional on the second item's availability to be recalled (in the literature these functions are referred to as lag-conditional response probabilities or lag-CRPs). In these functions, positive lags correspond to transitioning forward in the list (e.g., a transition from the item in serial position 5 to the item in serial position 9 would be a lag of $9 - 5 = +4$), whereas negative lags correspond to backward transitions (e.g., a transition from the item 9 to 2 would be a lag of $2 - 9 = -7$).

As shown in Fig. 3B, retrieved context models predict a peak in lag-CRP for smaller absolute values of lags with transitions being more likely between items from nearby serial positions due to their shared temporal context states. Because the predicted lag-CRP shows a tendency for items that were temporally contiguous in the study list to be recalled together, we refer to the effect as the *temporal contiguity effect*. For reasons we will discuss below, the model predicts that the lag-CRP should be asymmetric, with forward transitions being more likely than backward transitions.

These predictions about the behavioral dynamics of memory search have been tested, and confirmed, in many studies—here, we will provide an overview of this behavioral literature (for a more extensive review, see Healey, Long, & Kahana, 2019). In reviewing the behavioral evidence for retrieved context models, we will focus on the contiguity effect as it, in particular, has several features that are naturally predicted by retrieved context models that help distinguish them from competing models. We will organize our review around three key properties of the contiguity effect: forward asymmetry, time scale similarity, and automaticity.

4.3 Competing accounts of the temporal contiguity effect

Some of the findings we will review below can be explained by theories other than retrieved context models. Thus, before we begin, we briefly outline some competing theories. Because space does not allow a comprehensive treatment of all theories of episodic memory, we will focus on four general categories of noncontextual mechanisms that could produce contiguity. First, *dual-store* perspectives assume that associations are formed between items that cooccupy a short-term buffer and can thus create strong associations among items presented close together in time (Davelaar, Goshen-Gottstein, Ashkenazi, Haarmann, & Usher, 2005; Kahana, 1996; Lehman & Malmberg, 2013; Phillips, Shiffrin, & Atkinson, 1967). Second, *positional coding* models assume that the brain associates events with an internal representation either of time itself (Brown, Neath, & Chater, 2007; Howard, Shankar, Aue, & Criss, 2015) or position within a sequence (such as an item list; e.g., Farrell & Lewandowsky, 2002; Oberauer, Lewandowsky, Farrell, Jarrold, & Greaves, 2012) in which representations of adjacent times/positions are somewhat confusable and thus will tend to produce a temporal gradient (i.e., a contiguity effect). Third, *chunking* mechanisms assume that items are associated with a group, or chunk, representation such that when a group representation is used as a cue, it tends to retrieve items from temporally proximate serial positions (Farrell, 2012). Fourth, *strategic processing* refers to the fact that subjects can deploy ad hoc strategies to meet the demands of a particular task, and these strategies rather than core principles of the memory system may generate contiguity. It is widely acknowledged that subjects engage in strategies like the method of loci or telling a story to link items in a list (Bouffard, Stokes, Kramer, & Ekstrom, 2018; Delaney & Knowles, 2005), and it has been argued that this might create a contiguity effect that has little to do with the dynamics of context drift and reinstatement (Hintzman, 2016). The evidence for and against these perspectives has been discussed in depth elsewhere (Dester, Lazarus, Uitvlugt, & Healey, in press; Healey et al., 2019). Nonetheless, in the course of our review below, we will briefly note data points that, in our view, are inconsistent with the predictions of these competing theories.

4.4 Forward asymmetry

As seen in Fig. 3B, the model predicts that forward transitions are more likely than backward transitions, especially for smaller lags. This *forward asymmetry* arises from a key property of retrieved context models: rather than context drifting as a result of random fluctuations (cf. related context models; e.g., Mensink & Raaijmakers, 1988), context drifts because each newly studied item activates its own contextual associates which are then incorporated into the current state of context (Fig. 2). In consequence, any item studied after item *i* becomes associated with *i*'s context, whereas items studied before *i* are not. Thus, when *i* is recalled and its context is reinstated, it serves as a better cue for items presented after *i*, thus generating a forward asymmetry.

Whereas the forward asymmetry effect arises naturally from the contextual dynamics of retrieved context models, most of the noncontextual mechanisms outlined above require additional assumptions to produce such asymmetry. A dual-store model with a short-term buffer can produce forward asymmetry under the assumptions that associations formed in the buffer are themselves asymmetric (Kahana, 1996). Positional coding mechanisms that rely on a logarithmically spaced temporal representation where each item is associated with a region of the representation (rather than a single point) could also produce asymmetry (Brown, Chater, & Neath, 2008; Brown et al., 2007; Murdock, 2008). Farrell (2012) developed a chunking model that produces forward asymmetry when items within a chunk are cued in serial order. Strategies that entail forward serial recall could also produce forward asymmetry. While the evidence for asymmetry in standard free recall is quite strong, as we will see, it remains unclear whether asymmetry emerges in other paradigms or in neural dynamics.

4.5 Time scale invariance and similarity

The temporal contiguity effect has been most thoroughly explored in studies where items are presented one after the other separated by at most a short interstimulus interval. At these short time scales, it is possible to explain contiguity using noncontext mechanisms. For example, under models that include a limited capacity short-term memory buffer (Davelaar et al., 2005; Lehman & Malmberg, 2013; Raaijmakers & Shiffrin, 1981), contiguity could arise because items presented close together in time are simultaneously held in short-term memory and thus form item-to-item associations (Kahana, 1996). Such short-term memory-based accounts of the contiguity effect predict the effect should disappear (i.e., the lag-CRP in Fig. 3B should not vary by lag, and thus be flat) at longer time scales in the absence of other model mechanisms that can produce contiguity (Davelaar et al., 2005). By contrast, retrieved context models predict that a contiguity effect should be observed at a variety of time scales (i.e., the lag-CRP should look like Fig. 3B even if lag was on a longer time scale, as described in the next section, Howard, 2004).

4.5.1 Evidence for time scale similarity

Although this remains an area of active investigation, the existing data suggest that the contiguity effect is indeed robust at time scales ranging from minutes to months. At the shorter end, continual distractor free recall inserts a demanding distractor task, such as 12 s of solving math problems, between each word (Bjork & Whitten, 1974). This distractor should be sufficient to displace list items from short-term memory and thereby prevent direct associations among items, yet a strong contiguity effect emerges (Bhatarah, Ward, & Tan, 2006; Howard & Kahana, 1999).

Contiguity also emerges at long time scales in final free recall where, after having spent an experimental session studying and recalling multiple free recall lists, subjects are then asked to try to recall all the words presented during the session, regardless of list. Here, subjects not only show the typical list-level contiguity effect (successively recalling items that were presented near together in a given list, producing a peaked lag-CRP), but also show an across-list contiguity effect such that when they successively recall two items from different lists. To illustrate, imagine a subject who has spent a session studying and recalling 16 different lists each with 16 items and then receives a final recall test where they are asked to recall all the items they can from the entire session, regardless of list. This subject will tend to show two distinct contiguity effects. First, they will show a *within-list* contiguity effect such that when they successively recall two items that had been studied in the same list, say list 10, they will tend to be from similar serial positions in that list, say transitioning from recalling the item from serial position 13 of list 10 to next recalling the item from position 14 of list 10. Second, they will show an *across-list* contiguity effect. For example, if the subject has just recalled an item they originally studied in list 5, and the next item they recall is from a *different* list, it is more likely to be from list 6 than from list 7 or list 8. In general, this *across-list* contiguity effect means the probability of transitioning between list i and list $i + lag$ is a decreasing function of the absolute value of list lag in much the same way it is for within-list lag (Healey et al., 2019; Howard, Youker, & Venkatadass, 2008; Unsworth, 2008). We note that this across-list contiguity effect tends to be more symmetric than the within-list effect—we return to this observation below.

To investigate even longer time scales, Cortis Mack, Cinel, Davies, Harding, and Ward (2017) used subjects' smart-phones to present 8- to 10-item lists at a rate of 1 word per hour spread over an entire day. They found clear contiguity effects, including forward asymmetry, very similar to those found with continual distractor recall tasks where the separation between items is on the order of seconds rather than an hour. Contiguity has been observed at still longer time scales. Uitvlugt and Healey (2019) asked subjects to recall news events that had occurred over the course of the 2-year long 2016 presidential election campaign. For example, one subject recalled that "Trump won't accept the results of election," which referred to a story that first appeared on October 9, 2016 and then next recalled "Trump invites Obama's half-brother to third debate," which also happened on October 9, for a lag of zero days. Another subject recalled that "Trump's Access Hollywood hot mic," which appeared in the new on October 7, and next recalled "FBI re-opens Clinton's e-mail investigation," which happened on October 28 for a lag of $28 - 7 = 21$ days. After finding the lags for each transition, they found that when subjects recalled one event they had a strong tendency to next recall another event that had happened within 10 days of the first, with decreasing probabilities for longer lags. Moreton and Ward (2010) found a similar long-range contiguity effect when asking subjects to recall autobiographical memories that had occurred in the last 5 weeks, months, or years. The contiguity effect observed in these latter two studies (Moreton & Ward, 2010; Uitvlugt & Healey, 2019) did not show consistent evidence of forward asymmetry.

4.5.2 Theoretical implications of time scale similarity versus invariance

All of the studies reviewed above show a clear contiguity effect at time scales that make it hard to attribute the effect to binding in short-term memory—contiguity seems to be relatively robust to time scale. Nonetheless, we note that it is an open question whether the magnitude and functional form of the effect are truly *invariant* across time scales or are merely *similar* across time scales. For example, although the existing data from long time scales show a clear bias for short lags, unlike short time scales, long time scales do not consistently show a forward asymmetry (Healey et al., 2019; Howard et al., 2008; Moreton & Ward, 2010; Uitvlugt & Healey, 2019; Unsworth, 2008). Certain positional coding mechanisms are inherently time scale similar (e.g., Brown et al., 2007) and chunking mechanisms can incorporate a hierarchy of chunk representations at different time scales, which could allow them to account for this property of the contiguity effect. But time scale similarity poses difficulties for dual-store and strategic processing accounts of the contiguity effect as it is unclear how such mechanisms would facilitate associations between items separated months or years.

The question of whether the contiguity effect is truly time scale invariant, or merely time scale similar, is a critical issue for future research. The observation that the contiguity effect is less symmetric in immediate free recall than it is in final free recall or in the recall of news events suggests that at least the asymmetry component of the contiguity effect is not fully time scale invariant. This is actually, at least qualitatively, consistent with some versions of retrieved context models that are themselves *not* time scale invariant because they assume context drifts at a single rate (Howard, 2004). To make the model truly scale-invariant would require adding set of integrators with a range of rates. Howard and colleagues have proposed that the brain maintains a representation of "internal time" that has this property (Howard et al., 2015; Shankar & Howard, 2012, 2013). Their representation relies on a set of nodes that each represent a different "where" and a different "what." For example, one node might represent 10 s in the past (i.e., when) and the word *money* (i.e., what) and another might represent 15 s in the past and the word *onion*. By assembling a set of these nodes into a time × item "sheet" the representation can precisely encode which items were presented when. This functions in some respects like a set of context vectors each with a different drift rate. Howard et al. (2015) showed that such a model could account for a range of findings from areas including judgments of recency and classical conditioning. Most critically for our current purposes, they showed that a version of the temporal context model that used this time scale invariant representation was able to account for both the asymmetric contiguity effect observed in free recall as well as the more symmetric contiguity effect found in across-list transitions during final free recall. This representation across time scales is consistent with properties of neurons in hippocampus of the medial temporal lobe. In particular, an individual "time cell" fires action potentials at a prescribed time after the beginning of a memory delay period, yet each neuron tends to have a different time scale, leading to a "sheet" of time scales across neurons (MacDonald, Lepage, Eden, & Eichenbaum, 2011). Further, there is evidence suggesting that different brain regions may keep track of information across different time scales (Hasson, Chen, & Honey, 2015; Honey et al., 2012; Lerner, Honey, Silbert, & Hasson, 2011). However, it remains to be determined whether and how additional temporal representations contribute to provide a more accurate account of memory than a retrieved context model with simpler assumptions of temporal context.

4.6 Automaticity

Retrieved context models suggest that the contiguity effect occurs because memory fundamentally depends on associations between items and the mental context in which they occur. But most of the work reviewed in this section relies on tasks where subjects deliberately memorize lists of items for a test, which has been argued to not generalize to everyday life, where encoding tends to be more passive. Further adding to the unrealistic nature of these studies, items are generally words and often chosen randomly from a word pool such that the list has little structure other than the order in which they were presented. In this way, these "impoverished" stimuli may have too few intrinsic associations in comparison to everyday experiences. Some have argued that these features (deliberate learning of impoverished stimuli) force subjects to rely on temporal information and that in more realistic situations, context plays a less important role (e.g., Hintzman, 2011). Recent work directly addresses both of these concerns.

Diamond and Levine (2020) addressed the issue of impoverished stimuli by moving beyond lists of discrete items and instead using an audio walking tour of artwork on the museum-like first floor of a large hospital. After the tour, subjects recalled the tour in a free-form way ("Tell me everything you can remember about the tour"). Once scored using well-established autobiographical memory interview techniques (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002), subjects' recalls showed a strong contiguity effect that was remarkably similar in shape—including strong forward asymmetry—and magnitude to the effect typically seen with word lists. Similarly, the Moreton and Ward (2010) study discussed above asked subjects to recall events from their own lives and the Uitvlugt and Healey (2019) asked subjects to recall news events. Both studies showed clear contiguity. These findings suggest that contiguity is not limited to situations where stimuli are impoverished.

The Moreton and Ward (2010) and Uitvlugt and Healey (2019) studies also help address the concern that laboratory tasks are overly reliant on deliberate learning by using "stimuli" that were not presented in the context of a learning task, but rather were events naturally experienced and encoded as part of real life with no expectation of a memory task. This suggests that contiguity does not depend on deliberate encoding processes (cf. Nairne, Cogdill, & Lehman, 2017). To test this more directly, Healey (2018) had subjects view lists of words under incidental encoding instructions (e.g., under the ploy of a judgment task, such as determining whether the item would fit in a shoebox) and then administered a surprise free recall test, thus eliminating any reason for subjects to engage in deliberate encoding. Even under these incidental encoding conditions a significant contiguity effect was observed, although the effect was smaller and more symmetric than under intentional encoding. Recently Dester et al. (in press) not only replicated this incidental contiguity effect but also included a continual distractor condition, thus showing that the time scale similarity of the contiguity effect does not depend on any intentional encoding process. Moreover, they showed through a series of simulations that, by varying parameters, retrieved context models can account for the level of contiguity under both intentional and incidental encoding. One open question raised by Dester et al. (in press) is whether the retrieved context models are able to fully account for the difference in asymmetry between intentional and incidental encoding—it may be that the asymmetry effect is partly due to strategic processes, such as rehearsal, that are not implemented in current versions of the models.

The apparent automaticity of the contiguity effect is perhaps the most challenging property for competing theories, especially when combined with time scale similarity, as most rely on deliberately linking items either to each other or a hierarchical representation. The strongest candidate for being able to handle an automatic and time scale similar contiguity effect is a positional coding mechanism based on a logarithmic representation of time (Brown et al., 2007). Directly pitting such a model against retrieved context models is an important target for future research.

As one attempt to test qualitatively different predictions of item-based and context-based accounts of contiguity, Lohnas and Kahana (2014) examined contiguity not by considering each temporal transition but rather by considering pairs of successive transitions. If an item is recalled and this item serves as the retrieval cue for the next recall, then the next recall should not be influenced by other items recalled prior to the most recent recall. By contrast, according to retrieved context models, if each recalled item retrieves its associated context from study, then the retrieval cue will be a recency-weighted sum of the contexts of recalled items. As a result, the context of the most recently recalled item dominates the retrieval cue, but the context studied with the preceding recalled item should influence context as well. Comparing transitions following a remote temporal transition (i.e., $|lag| > 3$) versus $lag = +1$, subjects made significantly more transitions of $lag = +1$ at the current transition, suggesting that the prior transition influenced the current transition (Lohnas & Kahana, 2014). This effect was predicted by a retrieved context model variant, as well as a model which assumes the retrieval cue is a compound cue comprised of past recalled items (Kimball, Smith, & Kahana, 2007). However, this effect was not predicted by a model assuming that the most recently recalled item cued the next recall (Sirotin, Kimball, & Kahana, 2005). Ruling out a rehearsal-based account, this effect is still present in a continual distractor condition in which subjects' rehearsals are greatly reduced. Taken together, this contiguity-based effect implicates the role of a cue comprised of prior recalled items, naturally explained by retrieved context models. We next review work also aimed to distinguish predictions of retrieved context models from item-based models, moving away from pure behavior and rather based on neural representations of context states.

5. Neurophysiological measures of temporal context

To characterize the role of temporal context in episodic memory tasks, another approach examines neural measures of temporal context representations. With this approach, one can ask whether neural activity exhibits properties consistent with retrieved context models, as well as whether these context states relate to memory performance. Posited temporal context states can be calculated from neural patterns of activity which change slowly over time during study. This means that the context state during presentation of item i, denoted t_i, will be similar to the context state during presentation of item $i + 1$, t_{i+1}, and somewhat less similar to the context state during presentation item $i + 2$, t_{i+2}. Critically, during a memory retrieval test, if a subject recalls an item i or recognizes i with high confidence, then the neural measure of the temporal context state t during retrieval of an item studied in position i, t_{ri}, should exhibit properties consistent with temporal context reinstatement (cf. Manning et al., 2011). This context is termed t_{ri} to indicate **r**etrieval of item ***i***, distinct from t_i, the context when i is originally studied. To appreciate these properties, t_{ri} was compared not only to the context of item i as it was studied but also to the items studied nearby in time to item i. One can measure similarity between t_{ri} and t_{i+lag} as a function of *lag* in a way analogous to the behavioral lag-CRP. Fig. 3C shows what this neural similarity function should look like according to a retrieved context model.

It is noteworthy that t_{ri} is most similar to the context state during study of item i because this rules out the possibility that the slowly changing neural activity from study—posited to reflect temporal context—may just be noise which changes slowly over time. If the neural activity associated with a studied item was in fact noise, unrelated to and thus not encoded into memory, then this neural activity would not be reinstated during a memory recall test. As a result, t_{ri} would not be most similar to t_i, but rather t_{ri} would be most similar to the states of items presented near the end of the list. As another alternate explanation to context reinstatement, if there were simply increased similarity between the context of item i at study and item i at retrieval, this may seem more consistent with retrieval of the *content* of item i rather than its temporal *context*. The critical distinction between content reinstatement and context reinstatement lies in the similarity of t_{ri} to the context states of items studied before i, as these items dominate the temporal context representation when item i is studied. During study, the context associated with item i is most similar to the context of $i - 1$; similarity decreases as a function of lag. If t_{ri} reflects reinstatement of the temporal context of item i at study, then this context state should also be more similar to the context during study of item $i - 1$ than to more distant items. The presence of this property is interpreted as evidence of temporal context reinstatement. Providing support for evidence of temporal context, this property has been found in neural activity in several studies (Folkerts et al., 2018; Howard, Viskontas, Shankar, & Fried, 2012; Manning et al., 2011).

More specifically, Manning et al. (2011) examined electrical activity recorded from electrodes directly on or in the brain, termed intracranial electroencephalography (EEG) or electrocorticography. They found that patterns of oscillatory activity exhibited all of the expected properties of temporal context: Their posited neural measure of temporal context changed slowly with each studied item, and during free recall, the retrieved temporal context of a recalled item, t_{ri}, was more similar to the context states of its neighbors from study. Oscillatory activity from electrodes recording across the entire brain was consistent with their posited neural measure of temporal context. When performing the same analyses on subsets of electrodes by lobe, they found that activity in the temporal lobe exhibited properties of temporal context.

Howard et al. (2012) have also provided evidence for a measure of temporal context in the temporal lobe using single-unit intracranial recordings, assumed to reflect activity from individual neurons. In the first demonstration of this work, subjects performed a continuous recognition task, indicating whether each presented item was also presented earlier. During this task, firing rates of action potentials from medial temporal lobe neurons changed slowly with each presented item. In addition, during the presentation of previously studied items, activity across the ensemble of neurons exhibited the desired properties of temporal context: Ensemble activity was most similar to activity from the first presentation of the item, and ensemble activity decreased in similarity as a function of lag from when the item was last presented. Building on this work, in an item recognition task, medial temporal lobe neurons only exhibited activity consistent with temporal context reinstatement—with similarity greatest for the test item and decreasing with lag—for items which subjects recognized with high confidence but not low confidence (Folkerts et al., 2018).

Although this neural measure exhibits properties consistent with temporal context, one could argue that this measure is an epiphenomenon, unrelated to memory performance. However, in free recall, subjects exhibiting a greater reinstatement in the neural measure of temporal context reinstatement also exhibited greater temporal clustering scores (Manning et al., 2011), suggesting that temporal context reinstatement influenced temporal memory organization. In addition, temporal context reinstatement is found when items are recognized with high, but not low, confidence (Folkerts et al., 2018), suggesting that these neural measures relate to the level of retrieval of mnemonic information. We revisit variability in reinstatement of temporal context across subjects and across items in Section 6.2.

Further relating neural measures of temporal context to memory performance, Kragel and Polyn (2015) examined whether incorporating functional magnetic resonance imaging (fMRI) activity into a retrieved context model would improve model predictions. First, they fit a model to behavioral performance as a baseline of model performance without incorporating neural data. Next, they altered this model such that the extent of temporal context retrieval was proportional to the fMRI signal in posterior medial temporal lobe. This latter model provided a better fit to behavioral data than the baseline model, suggesting that the posterior medial temporal lobe mediates temporal context reinstatement. This finding is consistent with studies querying neural correlates of temporal context in the medial temporal lobe (Folkerts et al., 2018; Howard et al., 2012; Jenkins & Ranganath, 2010; Manns, Howard, & Eichenbaum, 2007). Also consistent with this finding, Manning et al. (2011) incorporated brain activity from electrodes recorded in all lobes of the brain, when examining activity from each lobe separately, only the temporal lobe yielded significant measures of temporal context on its own. Further, Kragel and Polyn (2015) found that fMRI activity in the hippocampus reflected retrieval of temporal context and item content. This is consistent with the posited role of the hippocampus to bind item and context information together (Davachi, 2006; Diana, Yonelinas, & Ranganath, 2007; Qin et al., 2007; Staresina & Davachi, 2009) and to represent temporal information of episodic events (Hsieh, Gruber, Jenkins, & Ranganath, 2014; MacDonald et al., 2011; Mankin et al., 2012; Nielson, Smith, Sreekumar, Dennis, & Sederberg, 2015).

Taken together, we have reviewed evidence of neural measures of temporal context and the influence of temporal context on episodic memory performance. Beyond a proof of concept, these neural measures can also be leveraged to examine changes to temporal context. For instance, by "brain mapping" these cognitive representations to specific brain regions, researchers can interpret activity in such regions to reflect temporal context (e.g., Ezzyat & Davachi, 2014). Having established behavioral and neural measures of temporal context, we next examine how these measures may vary by individual, by item, and by memory demands.

6. Variability in temporal context representations

Whereas neural measures of temporal context retrieval may vary by item and by subject, most simulations of retrieved context models make the simplifying assumption that temporal context retrieval measures remain at a constant level across items and subjects. Given that these models can make accurate predictions of data averaged across subjects and items, presumably if there were interitem variability, a case can be made that interitem variability averages out, and the model is capturing the general properties of the data.

6.1 Group and individual differences

Healey and Kahana (2014) directly investigated this issue by examining lag-CRPs from 126 young adults in an immediate free recall task. They found that, depending on encoding task condition, 96%–100% of subjects showed a contiguity effect, defined as the CRP for $lag = +1$ being greater than the CRP for $lag = +2$ *and* the CRP for $lag = -1$ being greater than the CRP for $lag = -2$. The asymmetry effect was also robust with 95% of subjects having higher CRPs for $lag = +1$ than for $lag = -1$. Moreover, a retrieved context model was able to fit the individual subject data. Yet, even though the average reasonably describes the behavior of individual subjects, variation around the average, in the form individual differences and differences between subgroups, is theoretically meaningful and related to other variables.

Individuals who show larger contiguity effects, as measured by temporal factor scores which express the lags of subjects' actual transitions as a percentile of the transitions they could have made, tend to also show higher overall recall performance (i.e., recall more items; Healey et al., 2014; Healey & Uitvlugt, 2019; Sederberg, Miller, Howard, & Kahana, 2010; Spillers & Unsworth, 2011). But the size of this correlation between contiguity and recall depends on the nature of the task. In tasks with lists of largely semantically unrelated items, the correlation is fairly high (e.g., $r = .51$ in Healey et al., 2019). By contrast, in tasks with lists of strongly related words, the correlation between temporal clustering and recall performance is actually negative (e.g., $r = -.44$ in Healey & Uitvlugt, 2019). This pattern suggests that recall success depends on the ability of the subject to selectively reinstate whichever sort of context (temporal or semantic) is most appropriate for the task. In addition to overall recall, contiguity is positively correlated with measures of fluid intelligence (at least for lists without strong semantic associations), perhaps suggesting that the ability to control context reinstatement contributes to general intellectual ability (Healey et al., 2014). To date, no work has tested the ability of retrieved context models to account for this pattern of correlations. Thus, accounting for individual differences remains an important target for future modeling work.

Consistent differences in the size of the contiguity effect have also been reported between various subgroups. One of the clearest examples is age. Compared to younger adults (i.e., aged ≤ 35), older adults (i.e., aged ≥ 60) show a smaller contiguity effect (Healey & Kahana, 2016; Kahana, Howard, Zaromb, & Wingfield, 2002; Wahlheim, Ball, & Richmond, 2017; Wahlheim & Huff, 2015). The age-related reduction in the contiguity effect takes the form of older adults having lower CRPs for small lags, especially for $lag = +1$ (i.e., reduced asymmetry). This age-related decline in the contiguity effect has been modeled as changes in CMR2 parameters, including those that control the effectiveness of context reinstatement (Healey and Kahana 2016, also see Howard, Kahana, & Wingfield, 2006). At the other end of the developmental spectrum, there is also some evidence that the contiguity effect increases from adolescence to young adulthood (Lehman and Hasselhorn 2012; Lehmann and Hasselhorn 2010, but see Jarrold et al., 2015). Some clinical conditions such as schizophrenia (Polyn et al., 2015; Sahakyan & Kwapil, 2018) or high trait worry (Pajkossy, Keresztes, & Racsmány, 2017) have also been linked to reduced contiguity. Note that in all these cases, decreases in the contiguity effect are associated with decreases in overall recall performance.

In one exception to the pattern of reduced overall memory performance being linked to reduced contiguity, Gibson, Healey, and Gondoli (2019) found that adolescents with ADHD showed reduced memory performance but *increased* contiguity and asymmetry. Modeling with a retrieved context model suggested that reduced memory resulted from reduced context drift and item-to-context association formation at study coupled with an *increased* rate of context drift during recall. The authors interpreted this as suggesting that ADHD was characterized by difficulty directing attention at external events (e.g., encoding words presented on a screen) but an intact and perhaps enhanced ability to direct attention to internal representations (e.g., reinstating mental context).

6.2 Variability across items

Above we reviewed evidence suggesting a role for context reinstatement in free recall. However, this does not mean that all items or subjects evoke context reinstatement to perform episodic recall tasks. Indeed, variability in context reinstatement for individual items also fuels the controversy regarding the role of context in episodic memory tasks. As one example, Tulving (1985) explored variability in the level of context retrieval across several types of retrieval tests and delays. For each tested item which a subject remembered as occurring on a previously studied list, the subject also responded "whether they actually 'remembered' its occurrence in the list or whether they simply 'knew' on some other basis that the item was a member of the study list." Tulving (1985) posited that when a memory test is more challenging, less retrieval information is provided to the subject, and so if a subject retrieves an item on a more challenging test, this more likely reflects more detailed information from study. Consistent with this finding, subjects classified more items with "remember" when the memory test was free recall, in comparison to a memory test in which the subject was provided with a word's category or the initial letter of the word and its category. From a retrieved context model perspective, if an item is remembered with better temporal precision in free recall, this suggests that successful free recall of an item evokes more retrieval of the item's temporal context. Thus, these results suggest a role for temporal context in free recall. Nonetheless, when subjects are asked for remember/know judgments on free recalled items, a significant number are classified as "know" (Arnold & Lindsay, 2002; McDermott, 2006; Read, 1996; Tulving, 1985), suggesting that subjects may associate these items only with temporal precision of the list level, and thus not more detailed temporal context information.

Sadeh et al. (2015) examined differences between free recalled items classified as "remember" versus "know," based on recall transitions from each class of items. According to retrieved context models, if an item evokes more temporal context retrieval, then the temporal context of this item should play a stronger role in the retrieval cue for the next item. Thus, temporal contiguity should be greater following items with greater temporal context retrieval. Consistent with this prediction, temporal contiguity was greater following recall of "remembered" items versus "know" items, suggesting that "remember" items evokes more temporal context reinstatement (Sadeh et al., 2015).

What might promote this variability in the success of encoding temporal context information? Several studies have implicated medial temporal lobe regions, including the hippocampus, consistent with its posited role in temporal context representations (Folkerts et al., 2018; Howard et al., 2012; Jenkins & Ranganath, 2010; Kragel & Polyn, 2015; Manning et al., 2011; Manns et al., 2007). These studies built on prior work establishing a role of the medial temporal lobe for episodic memory in general, by comparing brain activity during encoding for items which were later recognized with high confidence compared to those which were not (Kim, 2011; Paller & Wagner, 2002; Wagner et al., 1998). Staresina and Davachi (2006) also compared brain activity during encoding as a function of successful memory, yet critically considered successful "memory" for each item according to three types of memory tests. During encoding, subjects studied nouns associated with colors. Next, subjects performed free recall on these items. Then, subjects performed a two-step recognition test on these items, first indicating whether a test item was studied. If the subject indicated that they had studied the item, they were then probed to indicate its associated color. Staresina and Davachi (2006) examined fMRI activity for items which were successfully "remembered" during free recall, whether they were subsequently recognized along with their color (source recognition), or if the item was recognized but its color was not remembered correctly (item recognition). In the hippocampus as well as in regions of inferior prefrontal cortex, fMRI activity during encoding was significantly greater for items with correct source recognition than correct item recognition. Further, fMRI activity was significantly greater in these regions for items which were free recalled than items with correct source recognition. Whereas an increase in activity from item recognition to source recognition suggests that these regions support associations of features for a given item (Davachi, 2006; Diana et al., 2007; Qin et al., 2007; Staresina & Davachi, 2009), the increase in activity from source recognition to free recall suggests that activity in these regions promotes further associative processing. This may reflect stronger associations of items to their context states, which would be more important when subjects must retrieve the items themselves instead of being provided the items as test cues. This may also reflect better encoding of direct interitem associations. Regardless, the increase in encoding activity in the hippocampus, according to increasing associative demands of the memory tasks, has been taken as evidence for the role of the hippocampus in associating the features and context of an item together (Davachi, 2006; Diana et al., 2007; Polyn & Kahana, 2008; Qin et al., 2007; Staresina & Davachi, 2009). Further, due to the increase in activity in for free recall over recognition, these results may be taken as further evidence for the role of the hippocampus in supporting successful memory where temporal information is more critical for successful memory retrieval.

Jenkins and Ranganath (2010) took a more direct approach to examine temporal context representations and their relation to successful memory. They found that a medial temporal lobe region, specifically, the parahippocampal cortex, exhibited greater activity during encoding for those items which subjects could provide fine-grained temporal estimates of their list position. Regions in the hippocampus and inferior prefrontal cortex exhibited greater activity for items successfully remembered with a more coarse-grain temporal memory test. These results were also taken as evidence that the medial temporal lobe supports encoding of temporal information.

In addition to encoding, there is evidence that medial temporal lobe regions, including the hippocampus, support retrieval of temporal context during memory tests. Activity in the hippocampus is greater during free recall of items with the correct temporal context (i.e., items studied in the just-presented list) in comparison to free recall of items with incorrect temporal context (Long et al., 2017; Sederberg et al., 2007) or in comparison to deliberation periods without recall (Burke et al., 2014; Long et al., 2017). These results suggest variability in the amount of temporal context change during memory retrieval.

Taken together, these results highlight how the changes to, and the impact of, temporal context may vary by subject and may vary within a subject depending on task demands or even across items. Although medial temporal lobe regions seem to track variability in context drift, the origins of this variability remain to be fully characterized. Temporal context tends to be conceptualized as slowly drifting over time, yet there is also evidence suggesting that changes in stimulus features or task goals can lead to more drastic shifts in temporal context (for a recent review, see DuBrow, Rouhani, Niv, & Norman, 2017). Below we review how changes to stimulus features, reflected in other types of contexts beyond temporal context, influence memory organization, as well as how these types of contexts interact with temporal context.

7. Source context

We define source context features as those features of each studied item which are neither temporal nor unique to the item itself. For instance, some features of *onion* are unique to the word onion only, whereas *onion* and *garlic* are both odorous. It can be useful to define source context based on whether the features are extrinsic or intrinsic. By *extrinsic*, we refer to features that are more external and not a defining feature of the item itself. For instance, if source is operationalized as font color of studied words, any word may be presented in any color. By contrast, source features more *intrinsic* to the item itself cannot be applied to any item, but nonetheless apply to a set of items. As examples of intrinsic features, source context could be the semantic category or emotional valence of each word. Below we review the impact of source context on memory organization, viewed through the lens of retrieved context models.

7.1 Extrinsic stimulus features

Thus far, our retrieved context model simulations have not made explicit assumptions regarding source context. How might a retrieved context model be extended to incorporate source representation? Polyn, Norman, and Kahana (2009) examined this question by evaluating which of three potential model variants could best account for free recall dynamics. With this setup, each item was studied with one of two possible encoding tasks, and thus one of two possible source contexts. One model variant assumed that source features and source context were elements concatenated onto the vectors for item features and temporal context, respectively. This is illustrated schematically in Fig. 4. Unlike temporal context—comprised of a set of features changing slowly with each studied item—source context was represented as one of two possible encoding tasks. Yet just as temporal context reflects the temporal history of studied and recalled items, so too does source context reflect the history of the sources of prior items. In this way, a given source will have a stronger representation in source context if an item was studied with that task more recently. By this logic, recall of an item evokes retrieval of its source context, in addition to its temporal context.

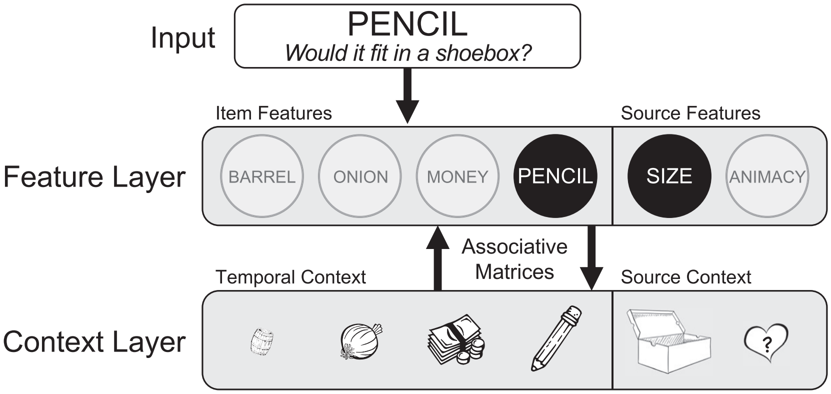

Fig. 4 Schematic of the context maintenance and retrieval model including source context. The feature layer represents the identity of list items, with one node for each item, but also includes nodes for each source (here two possible semantic encoding tasks—judging whether the presented item is alive or judging whether it would fit in a shoe-box). Similarly, the context layer not only represents the ensemble of contextual associates that are activated when an item is presented but also includes nodes for the contextual associates of the encoding tasks.

These retrieved context states update the context representation, and promote recall of items with similar source contexts to the just-recalled item. Depending on the experimental setup, items with the same source may or may not be presented nearby in time. Thus, this *source contiguity* effect may work in conjunction with, or against, the temporal contiguity effect. For instance, suppose in a list of 10 items, items 3 and 7 are studied with the same encoding task, and during the recall period, the subject recalls item 3. Retrieval of item 3's temporal context promotes recall of items presented nearby in time, such as items 2 and 4. However, recall of item 3 also evokes retrieval of its source context, including the source context shared with item 7. Thus, despite the temporal distance, recall of item 3 would promote recall of item 7 due to the shared source context between these items.

Polyn et al. (2009) assessed the predictions of this model in several measures of recall dynamics. Consistent with model predictions, subjects were more likely to recall items successively if they were associated with the same source context, in comparison to items associated with different source contexts (see also, Murdock & Walker, 1969; Puff, 1979). However, this model variant actually overpredicted such transitions between same-source items, particularly for transitions between two same-source items presented with at least one intervening subsequence of items from another source. (For instance, consider a sequence of 9 items each studied with an encoding task A or B with the following order: A-A-A-B-B-B-A-A-A. Item 2 shares the same source context with items 3 and 8. Yet whereas items 2 and 3 are within the same subsequence of same-source items, items 2 and 8 are separated by a subsequence of items from task B.) This suggests that, with this model variant, items with shared source information are too strongly associated together in memory, by which recall of an item from a specific source excessively promotes the recall of other items from the same source.

Why might items with the same source, but separated by source changes, be associated more weakly in memory? Prior work has suggested that changes to stimulus features, such as a change in source context, update context and thereby isolate items separated by the context change (Donchin & Coles, 1988). With respect to retrieved context models, where temporal context plays a central role, the intuition is that a change in source context evokes a greater change or drift in temporal context. Consistent with this intuition, if two items are separated by a change in source context, subjects perceive them as occurring farther apart in time, when compared to items *not* separated by such a change (Ezzyat & Davachi, 2014; Faber & Gennari, 2017; Lositsky et al., 2016). This suggests that temporal context might drift or update more between two items separated by a source change, thus leading to the perception that the two items' temporal context states are more distinct. Further, when compared to item pairs *not* separated by a source change, subjects exhibit reduced accuracy and increased response times when making temporal judgments for item pairs separated by a change in source context (DuBrow & Davachi, 2013, 2014, 2016; Heusser, Ezzyat, Shiff, & Davachi, 2018; Speer and Zacks, 2005). These results are also consistent with fewer shared temporal context features between items separated by a source change, thus disrupting temporal associations between those items.

Retrieved context models can implement this property by assuming that each time there is a change in source context within a list (e.g., a subject switches encoding tasks), then an additional item is presented to the model, evoking further drift in temporal context. As a result, two items separated by a change in source context have fewer shared temporal context features. This "full model" variant, assuming representations of source context (Fig. 4), as well as a disruption to temporal context with each change in source context, provides more accurate predictions of recall dynamics (Polyn et al., 2009). In particular, this model predicts that subjects are more likely to transition between items of the same source context, due to their shared context states. Nonetheless, such transitions are less likely for same-source items separated by a change in source context. As a result, *temporal* transitions are less likely between two items—even if they are studied nearby in time—when separated by a change in source context. However, the presence of different encoding tasks in a list does not eliminate the temporal contiguity effect (Healey et al., 2019).

Thus far, we have reviewed two model variants, establishing that the assumption of separate source context representations does not suffice to account for subject data. Rather, the more accurate "full" model assumes that there is further drift in, or a "disruption" to, temporal context, each time there is a change in source context. Given the central role of temporal context in episodic memory, this raises the question of whether the temporal disruption mechanism on its own suffices to account for memory effects. However, if a retrieved context model assumes source information is only represented as a disruption to temporal context without separate source representations, this "pure disruption" model makes less accurate predictions than the full model, in particular when considering transitions between items with different source contexts. As noted above, subjects are less likely to successively recall items associated with different sources than items associated with the same source. Whereas the pure disruption model predicts a reduction of different-source item pairs due to the temporal disruption mechanism, it nonetheless does not predict as large a reduction as exhibited in subject behavior. By contrast, the full model variant does predict this larger reduction, presumably due to fewer shared temporal features as well as fewer shared source features.

A recent study provides further support for the critical role and properties of source context in memory search (Polyn, Kragel, McCluey, & Burke, submitted). First, they determined a correlate of source context by using multivariate pattern analysis with fMRI to extract brain activity which could distinguish between two encoding tasks (Duda, Hart, & Stork, 2001; Norman, Newman, Detre, & Polyn, 2006; Polyn, Natu, Cohen, & Norman, 2005). Brain activity in the same regions during recall could classify the associated encoding task with each recalled item, suggesting that subjects were reinstating source context representations. Interestingly, Polyn et al. (2012) found that source classification decreased as a function of position after a switch in source context. Although retrieved context models typically assume that context drifts at a constant rate for each studied item, this effect was best explained by a model assuming that temporal context drifts less with increasing position after a switch. Taken together, these results highlight the influence of source context on temporal context drift and on memory representations.

7.2 Intrinsic source context

Whereas some source context features could be applied to any studied item (e.g., a presented word could be presented in a red or a blue font), some source context features are more intrinsic to the items themselves. For instance, sometimes semantic categories of presented stimuli are operationalized as a type of source context. How might these intrinsic features influence source context and temporal context? In one approach, subjects are presented with labeled images from different semantic categories, including objects, locations, and celebrities. Items from each category are presented in each list, and subjects view sequences of items from one category at a time. These categories were sufficiently distinctive such that patterns of neural activity could classify the category of the viewed image during encoding, whether measured with fMRI (Polyn et al., 2005), intracranial EEG, or scalp EEG (Morton et al., 2013). In this way, each semantic category can be viewed as a different context. In these studies, after viewing the list of items, subjects performed free recall. Multivariate analyses of neural activity revealed retrieval of category context representations during recall (Morton et al., 2013; Polyn et al., 2005). Further, examining multivariate pattern classifier performance by position within a sequence of same-category items, Morton et al. (2013) found improved classifier performance for items later in a sequence. They interpreted this as evidence of category context changing slowly with each studied item, as predicted by retrieved context models. Interestingly, classifier performance was greater for subsequently remembered items than forgotten items, suggestive of the contribution of category context to memory representations (Morton et al., 2013). In addition, based on the brain regions from study, the neural classifier could also predict the category of each recalled item, underscoring the role and reinstatement of category context in memory search.

More recently, several studies have examined the impact of changes to source and category context on temporal context and temporal representations. Like Polyn et al. (2009), DuBrow and Davachi (2013) presented subjects with subsequences of items that were drawn from different semantic categories, and items from each category were associated with different encoding tasks. At test, subjects were presented with two same-category items from the studied list and had to indicate which item was studied more recently. Critically, recency judgments were more accurate for pairs of items presented within the same subsequence. This was interpreted as evidence that changes in task and category context disrupt temporal context. As further evidence of the contribution of category context representations influencing the temporal memory decision, DuBrow and Davachi (2014) examined fMRI activity while subjects deliberated their memory response. Although the item pairs were always from the same category, there was greater evidence for the displayed category when those items were presented from the same subsequence, suggesting that subjects were retrieving the category context of intervening items to make their response. Taken together, these results implicate the influence of category context on temporal context, even when category context is arguably more secondary to the memory task.

Ezzyat and Davachi (2014) examined more directly how changes to stimulus features influence temporal representations and judgments. Subjects viewed sequences of faces and objects (intrinsic semantic category context), each presented with an associated scene (extrinsic source context), and then made spacing judgments between pairs of studied items. Critically, item pairs were either presented with the source and semantic context or were from different source and semantic contexts. Controlling for absolute spacing, subjects judged items with the same contexts as being studied closer in time (Ezzyat & Davachi, 2014). Further, during study of items subsequently tested in different-context pairs, hippocampal activity was more strongly correlated between items judged as close than far. This suggests that hippocampal representations change slowly over time, whereby items perceived as occurring closer in time are represented more similarly. Thus, these results further implicate the role of the hippocampus and medial temporal lobe in temporal context representations. Building on this work in a more ecologically valid setting, Lositsky et al. (2016) had subjects view movie clips, then made temporal judgments between images drawn from a movie. Subjects perceived the two images as being farther apart in time—both based on absolute time and also based on how many changes in events took place between the scenes. Such event changes may reflect changes in scene, characters, and conversation topic, arguably reflecting changes to other extrinsic and intrinsic content and context distinct from temporal context. Lositsky et al. (2016) also related neural similarity between subsequently tested movie images to perceived temporal similarity, which provided further evidence of medial temporal lobe regions, including hippocampus and entorhinal cortex, in these effects.

Although the nature of emotional processing and representation remains debated, there is some evidence that the emotional valence of a stimulus (i.e., on a scale of positive to negative emotion) operates as a source context. Such a context may reflect more intrinsic features of individual stimuli (e.g., the word *rifle* generally evokes more negative feelings than the word *puppy*). However, emotional valence may also be operationalized as presenting subjects with neutral items alongside more emotional information (e.g., background music or images of scenes depicting emotional situations, such as a car accident or appetizing food). With emotional information, however, it is not as straightforward that the same emotional context among items leads to improved memory. Rather, regardless of whether items are intrinsically more emotional or neutral, memory tends to be greater when items are studied in an emotional context (Bower, 1981; Eich, 1995; Erk et al., 2003; Maratos & Rugg, 2001). Although there is a general consensus that emotional items are better remembered than neutral items (Dolcos, LaBar, & Cabeza, 2004; LaBar & Cabeza, 2006), if emotional items or neutral items are studied in separate lists, then there is generally no memory advantage for lists of emotional items over lists of neutral items (Barnacle, Montaldi, Talmi, & Sommer, 2016; Dewhurst & Parry, 2000; Talmi, Luk, McGarry, & Moscovitch, 2007). To account for these findings, Talmi, Lohnas, and Daw (2019) developed a retrieved context model which assumed emotional valence was represented as a source context. Like the full model of Polyn et al. (2009), the source context of each item was represented separate from temporal context, and a change in source context evoked a disruption to temporal context. Further, emotionally negative items benefited from stronger context-to-item associations, reflecting greater attention devoted to those items (cf. Sederberg et al., 2008). This model predicted that emotional items were more likely to be recalled in mixed lists of emotional and neutral items due to their stronger associations to the context cue. In pure lists of emotional items, however, all emotional items had an equal benefit of stronger associations, and so this model predicted similar recall probability between pure lists of emotional and neutral items. Also consistent with a retrieved context account of emotional representations, subjects are more likely to successively recall items of the same emotional valence (Long, Danoff, & Kahana, 2015; Siddiqui & Unsworth, 2011; Talmi et al., 2019). However, this model only touches upon the impact of emotion on longer time scales than a typical free recall experiment, so future work remains for retrieved context models to account for the role of emotion as well as episodic memory more broadly (see also Sederberg, Gershman, Polyn, & Norman, 2011).

Across intrinsic and extrinsic features of source context, there is accumulating evidence that source context influences memory organization, whereby subjects retrieve source context features during recall, and are more likely to recall items from the same source. Such organization may work against or with the temporal contiguity effect, depending, respectively, on whether items from the same source are presented far apart or nearby in time. Further attesting to interactions between source context and temporal context, there is behavioral and neural evidence that a change in source context leads to a greater change in temporal context. Retrieved context models help to clarify these interactions and their impact on recall dynamics.

7.3 Spatial context

Thus far, we have discussed properties of context relating to each presented item. However, context may reflect external information such as the spatial environment in which encoding and retrieval take place. Spatial context, like temporal context, comprises a critical component to episodic memory. In cognitive psychology, spatial context has received much less attention than temporal context. For most episodic memory tasks conducted in a laboratory, spatial context is assumed to remain constant because a subject is presented with information while seated in a single spatial location. Here, we focus not on studies of spatial navigation and representations of spatial information, but rather the influence of space as a context on episodic memory representations.

Like other types of context, in free recall subjects tend to cluster their recalls based on spatial similarities between studied words. In a study relying on known locations of famous landmarks (e.g., Eiffel Tower in Paris), they were more likely to successively recall landmarks located in nearby geographic locations (Miller, Lazarus, Polyn, & Kahana, 2013). Another approach considers how subjects associate items to spatial locations formed during the study itself. For instance, Gibson, Healey, Schor, and Gondoli (in press) had subjects study a list composed of identical squares presented sequentially in different cells of a 6 × 10 matrix and then after a 15-s delay recall the locations by clicking on the presented locations. Subjects clustered their responses not only by temporal order (i.e., they showed a temporal contiguity effect; also see Cortis Mack, Dent, & Ward, 2018) but also by spatial location (i.e., the were more likely to successively recall squares presented in nearby location than those that were farther apart on screen). In a similar way, Miller et al. (2013) had subjects perform a spatial navigation task with different to-be-recalled words presented at different spatial locations. In this set up as well, subjects are likely to successively recall items located nearby one another in space (Miller, Lazarus, et al., 2013). Neural evidence suggests that the hippocampus promotes reinstatement of relevant spatial information, and according to retrieved context models, such reinstatement would promote successive recalls of items with similar context states. In particular, when a subject recalls an item studied in a specific location, hippocampal activity is more similar to the activity during study of other spatially proximal than distal items (Miller, Neufang, et al., 2013). In this way, the hippocampus is hypothesized to support associating episodic memories to both the spatial and temporal components of context (Howard & Eichenbaum, 2013; Poppenk, Evensmoen, Moscovitch, & Nadel, 2013).

Although within a studied list, subjects organize their recalls based on spatial similarity, the results are more complex when manipulating spatial context between study and test. According to retrieved context models, recall of an item evokes retrieval of its contexts, including spatial context, and this updates the context used to cue another recall. In this way, recall of an item from one spatial context promotes recall of items with similar spatial contexts. By this logic, suppose a list of items is studied in one spatial context, such as inside an experiment testing room in a psychology building. If the memory test is administered in the same spatial context, then the subject is cued with the spatial context from study. By contrast, if the memory test is administered in another spatial context (e.g., outside on a lawn in front of the psychology building), there is less overlap in spatial context between study and test, and thus memory performance should be worse. Consistent with this intuition, episodic memory tends to be worse when context differs between encoding and test (Smith, Glenberg, & Bjork, 1978; Smith & Vela, 2001). Even if subjects change spatial contexts between study and test, the negative effects of context change can be counteracted by guiding subjects to mentally reinstate the spatial context from study (Smith 1979; see also Sahakyan & Kelley, 2002). With respect to retrieved context models, reexperiencing the spatial context from study, whether provided externally or generated internally, can support retrieval of items with similar spatial contexts.

Building on these findings, Brinegar, Lehman, and Malmberg (2013) hypothesized that if the spatial contexts differed between study and test, then memory might also be modified by "preinstating," a spatial context prior to list encoding. Subjects were familiarized with two environments, then studied two lists of items, with each list in a different environment. Subjects who spent 30 s thinking about the environment of List 2 prior to studying List 1 exhibited recall patterns consistent with successful "preinstatement" of the List 2 spatial context. Further, these effects were predicted by a model assuming that each item is associated with a temporal context and spatial context (Criss & Shiffrin, 2004; Lehman & Malmberg, 2009; Malmberg & Shiffrin, 2005). Although each spatial context was represented more distinctly, the spatial context could be reinstated internally, leading to more shared contexts between items from different lists, and thus the pattern of recalls exhibited in this study.

Nonetheless, if prior to studying a list, a subject reinstates the spatial context in which they will be tested, it is not a simple story such that the more reinstatement of the test context, then the more improvement in memory due to shared context. Indeed, (Brinegar et al., 2013) did not find improved correct memory when subjects reinstated the test context of List 1 prior to studying List 1. Building on these findings, Masicampo and Sahakyan (2014) had all subjects imagine a context before study (termed A or B), study a list of items, then perform free recall in the same or different environment (A, B, or C). If subjects imagined and familiarized themselves with the context at study, Context A, then they recalled proportionally more items if tested in Context A in comparison to a different Context B. Yet, remarkably, if subjects imagined Context B during study, free recall performance was even greater than imagining, and remaining, in Context A. Further, as long as subjects imagined a context other than A, recall was not significantly different between subjects tested in Contexts A, B, or a new Context C. If these effects were purely driven by shared retrieved context of recalled items, then imagining and being tested in the same contexts (either A or B) should lead to the highest level of recalls. Instead, Masicampo and Sahakyan (2014) posited that these results were most consistent with a facilitated-reinstatement account, whereby the active imagination of a different context at study makes it more likely for subjects to reinstate the study context at test. This increased likelihood of reinstatement may be a conscious process made easier by practice, or may make it more likely for context reinstatement to happen more naturally. Regardless, these findings highlight a critical role for context, as well as unexplored factors influencing the ease and extent of context reinstatement across environments and test conditions. Further, these serve as a challenge for retrieved context models to explain how shared context may not always benefit memory performance.

8. Concluding remarks

Here, we have reviewed the evidence supporting retrieved context models. The models assume that events activate their contextual associates which are then incorporated into the state of drifting mental context representation. The models further assume that episodic memories are formed by creating new associations between event representations and the current state of the mental context representation. During memory search, context is used as a retrieval cue. Once an event is recalled, it reinstates its associated context which then forms part of the cue for another recall attempt. Together, these assumptions predict that recall behavior should be characterized by a strong temporal contiguity effect—the tendency for items experienced nearby in time to be recalled together. They also predict that neural recordings should contain signatures of context reinstatement in the form of similarity between neural activity during recall of an event and the neural activity during study not just of the recalled event *but also* study of temporally adjacent events.

We reviewed studies showing that the predicted behavioral contiguity effect is extremely robust, appearing across a wide range of experimental situations, stimuli types, and individuals. The effect shows three key characteristics predicted by retrieved context models: forward asymmetry, time scale similarity, and automaticity. We then reviewed studies showing the predicted neural signature of context reinstatement across several different types of paradigms. We then discussed different types of context representations such as temporal versus source context. We argue that taken together, these findings provide strong support for retrieved context models.

8.1 Open questions and future directions

The various effects, both behavioral and neurophysiological, that we have reviewed here are natural predictions of the retrieved context framework. Nonetheless, as we have noted throughout the chapter, other theoretical perspectives are also consistent with many of these findings. Our view is that retrieved context models provide the most parsimonious account as they require relatively few ad hoc assumptions or mechanisms to account for the data. But this view should be pressure tested. A competitive modeling exercise in which retrieved context models along with promising alternatives, such as temporal coding models (e.g., SIMPLE, Brown et al., 2007) or chunking models (Farrell, 2012) must be tested for their ability to simultaneously account for a set of benchmark findings, such as those reviewed here. Similar competitive, benchmark-based approaches have been fruitful in other areas (e.g., Oberauer et al., 2018).

Relatedly, it is noteworthy that the term we have used throughout this chapter to describe our theoretical framework, retrieved context model*s* is plural. That is, there are different versions of implementations of the modeling framework that make different assumptions and design decisions. For example, most implementations of the model use a single context vector that drifts at a single rate, but some versions have used a single context vector but allow a variable rate (Kragel & Polyn, 2015), and others have used a set of time-cell-like integrators with a range of rates (Howard et al., 2015). Similarly, there are different ways that semantic information can be integrated into the model's cognitive representations (Morton & Polyn, 2016) and different ways the models can selectively retrieve from specific time periods (e.g., the list-before-last paradigm; Healey & Wahlheim, 2020; Lohnas et al., 2015). There may be value in working toward a common implementation by determining which existing version, or hybrid of versions, provides the best simultaneous account of the available data.

Although model assumptions, and the role of context, may vary across items, subjects, and episodic memory tasks, understanding the limitations of retrieved context models still furthers our understanding of the role of context in memory encoding, organization and retrieval. Despite the model variants, all retrieved context models share the core principles that context changes slowly with each studied or retrieved item, and the current context serves as the memory cue. We view the success of the class of retrieved context models as strong evidence that context plays a central role in episodic memory.

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