Neural Correlates of Temporal Context Retrieval

Fang Wang

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Rachel A. Diana, Chair

Martha Ann Bell

Anthony Cate

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Abstract

Temporal context memory is memory for the timing of events. People can make temporal judgments based on strategies such as assessing the relative familiarity of events or inferring temporal order from the semantic associations among events. The purpose of present study is to investigate the brain regions that support temporal context retrieval in the absence of such non-temporal strategies (i.e. pure temporal context memory). We used three word familiar phrases (triplets) as stimuli. In study phase, three words were presented quickly consecutively in either familiar or scrambled order. Participants were instructed to read aloud each word and try to remember the order of the words. Then they were tested on their memory for the order of the words in each triplet. We propose that memory for the scrambled triplets reflects primarily temporal retrieval for two reasons. First, participants were prevented from using semantic strategies during encoding. Second, the relative familiarity of the words in each triplet was similar and not diagnostic of the order of the words during encoding. Neuroimaging results indicate that temporal context retrieval, memory for the order of words in scrambled triplets, was associated with the hippocampus, parahippocampal cortex, ventromedial prefrontal cortex, retrosplenial cortex, and posterior cingulate, which are consistent with the retrieval of non-temporal context in episodic memory. The results also suggest that temporal context retrieval could rely on familiarity, which was demonstrated by the higher accuracy and greater activation of PRc in familiar phrases and scrambled triplets presented in studied order in the test phase.

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Introduction

Episodic memory refers to the ability to internally re-experience events that happened in the past (Tulving, 2002; Hasselmo, 2009). Such memories include information about where and when these events occurred (Tulving, 2001, 2002). It has been well established that the medial temporal lobe (MTL) is critical for episodic memory (Eichenbaum & Cohen, 1988; Smith, 1988; Eichenbaum, Otto, & Cohen, 1992; Cohen, Poldrack, & Eichenbaum, 1997; Aggleton & Brown, 1999; Corkin, 2002; Diana, Yonelinas, & Ranganath, 2007; Squire, 2009). The MTL memory system includes the hippocampal region (CA fields, dentate gyrus, and subicular complex) as well as the entorhinal, perirhinal (PRc), and parahippocampal cortices (PHc) (Preston & Gabrieli, 2002; Squire, Stark, & Clark, 2004). Information enters the MTL memory system through PRc and PHc. Most of the inputs that PRc receives are from unimodal visual association areas and about one third of the inputs come from unimodal non-visual semantic association areas. PHc receives inputs from visuo-spatial areas in the posterior parietal cortex, dorsolateral prefrontal cortex and retrosplenial cortex. PHc and PRc project to entorhinal cortex separately. PRc projects to lateral entorhinal areas and PHc projects to medial entorhinal areas. The entorhinal cortex provides the vast majority of input to the hippocampus (with minor inputs coming from the fornix and the contralateral hippocampus). In addition, the entorhinal cortex receives reciprocal projections from the hippocampus (Preston & Gabrieli, 2002; Diana, Yonelinas, & Ranganath, 2007). Although the interconnections among these regions and the circuit of information flow are relatively clear to us, there are controversies about the functions of subregions in the MTL (Squire & Zola-Morgan, 1991; Eichenbaum, Yonelinas, & Ranganath, 2007; Squire, Wixted, & Clark, 2007).

One theory of subregion function in the MTL is the “binding of item and context” (BIC) theory. The foundation of the theory is the circuit of information flow from the cortex into MTL and within MTL. PRc receives inputs from the ventral visual stream that processes item information (the 'what' stream). PHC receives inputs from the dorsal visual stream that processes spatial information used for visually guided movements (the 'where/how' stream) (Witter et al., 1989; Burwell, 2000; Eichenbaum et al., 2007). The hippocampus therefore receives input from both streams and presumably allows these 'what' and 'where' streams to be integrated. Based on this circuit of information flow, the BIC theory proposes that PRc and PHc drive the encoding and retrieval of item and context information respectively. The function of the hippocampus is to associate an item with its context and thus bind the information into a unique representation.

BIC theory makes predictions about episodic memory retrieval based on the information that is thought to be processed in MTL subregions (Diana et al., 2007). The BIC theory predicts that the pattern of activation in the MTL at both encoding and retrieval depends on the cues that are presented and the way those cues are processed. Familiarity-based recognition only requires processing of item information, because it is defined as a judgment of item strength relative to expected baseline strength, so BIC theory predicts that it is supported by PRc. Recollection-based recognition requires retrieval of both an item-context binding and context information, because it is defined as retrieval of a context detail from an item cue. Therefore, BIC theory predicts that it is supported by the hippocampus and PHc. During *encoding*, PRc is more active for items that are subsequently judged as more familiar. When encoding trials are sorted according to recollection success, PHc and the hippocampus are more active for trials when recollection occurs and contextual information is retrieved. During item *retrieval*, a familiar item cue deactivates PRc. The size of the deactivation varies according to the degree of familiarity. If the input from PRc triggers retrieval of the item-context binding, the hippocampus shows increased activation, as does PHc, thereby leading to recollection.

An innovative prediction of the BIC theory is that the brain regions involved in retrieval will vary when items are encoded in a specialized manner. For example, if two items are encoded as a single, usually novel, conceptual unit (unitized), recognition of the two associated items can be based on familiarity and thereby driven by PRc. For instance, if the word egg and the color red are unitized in a way that the egg is red because the little girl colored it for Easter, the recognition of them should be based on familiarity. However, if they are encoded as separate items, the recognition will be based on recollection (Quamme et al., 2007).

Although the BIC theory predicts that the context of an event is processed in PHc, such context has been operationally defined from experiment-to-experiment. It is not known whether PHc processes particular forms of context (such as spatial) but not others. Diana et al. (2007) proposed that context could be defined as information encoded during an event that is peripheral to the study item and outside the primary focus of attention or encoding. In previous experiments relevant to the BIC theory, the manipulated context information has always been presented during the same temporal window as the item (Bar & Aminoff, 2003; Maki Suzuki, Tsukiura, Matsue, Yamadori, & Fujii, 2005; Davachi, 2006). However, some theories of context in episodic memory propose that events that happened before the event currently at the focus of attention can be encoded as contextual information (Kahana, 2002; Polyn & Kahana, 2008). This context can be used to identify the relative order of events and provide information about timing of an event that is being retrieved. For example, I remember that after I walked to campus, I read some papers in my office. Walking to campus provides temporal information for the critical event reading papers and can be used to infer the timing of that event. When associations between events include information about the timing or order in which events occurred, we define those associations as temporal context.

Different experimental paradigms have been used to study temporal context memory. Each of these paradigms may allow participants to use different strategies and therefore rely on different types of information to make temporal judgments. The most common paradigm used to study temporal context memory is the recency judgment task. In this task, participants are usually required to learn a list of items. At test, the participants are presented with two items that were previously encoded and asked to identify the item that was studied more recently. Although this task is used as a measure of temporal memory, this task does not require the retrieval of temporal context. That is, participants can use a strategy in which they weigh the relative familiarity of items and assume that the more familiar item is also the more recent item.

One of the first temporal context memory experiments was a modified recency judgment task, conducted by P.Corsi, and reported by Milner (1971). Patients with either left frontal brain lesions or left temporal brain lesions participated in the experiment. Pairs of words were shown on the screen one after another in a continuous recognition task. When a question mark appeared between two words participants were asked to make either a recognition judgment or a recency judgment. In the relative recency task, the question mark indicated that both words were presented earlier in the list and participants should judge which of the two words was studied more recently. In the recognition task, the question mark indicated that one word was presented earlier in the list (old) and the other word had not been presented in the list (new). Participants were asked to indicate which word was old and which word was new. Patients with left frontal lesions were impaired in the recency judgment task but showed normal performance in the old/new recognition test. In contrast, patients with left temporal-lobe lesions showed normal performance in the recency judgment task but were impaired in the old/new recognition test. This double dissociation demonstrated the contribution of frontal cortex and the temporal lobe to recency judgments and episodic recognition respectively. These results have also been replicated using non-verbal items as stimuli, with lesions occurring in the right hemisphere rather than the left hemisphere (Milner, 1971; Milner, Corsi, & Leonard, 1991; Kesner, Hopkins, & Fineman, 1994). These experiments provide strong evidence that the frontal lobe drives memory for relative familiarity and the temporal lobe drives episodic recognition.

Although recency judgments seem to rely on the frontal lobe, the patient experiments described above do not explain *how* frontal cortex contributes to recency judgments. One possible explanation for frontal involvement in recency judgments is that it arises from a confound in levels of difficulty between the item recognition and recency judgment test (Cabeza et al., 1997). If this is the case, frontal cortex is not uniquely related to recency but rather reflects the increased difficulty in distinguishing between two familiar items as compared to distinguishing between a familiar item and an unfamiliar item. In a test of this hypothesis, Cabeza and colleagues (1997) manipulated the level of difficulty in a recognition task and a recency judgment task by varying list length and item duration in the study phase. If the levels of difficulty are reversed for the recognition task and the recency judgment task but the brain regions involved remain the same as previous studies, the different patterns of brain activation cannot be explained by the difficulty of task. Although the task difficulty was successfully matched, such that the resulting proportion of correct responses in the low performance item recognition task was not significantly different from that in the high performance temporal-order judgment task, there was still a dissociation between the brain activation related to item recognition and brain activation related to recency judgments. Item recognition was associated with increased activity in PRc, and basal forebrain regions. Recency judgments were associated with increased activity in dorsal frontal regions. These results demonstrated that the involvement of frontal cortex in relative recency judgments is not due to a higher level of difficulty.

Given that recency judgment tasks suggest a role for frontal cortex in temporal context memory, further research has investigated the specific function of frontal cortex in temporal context memory. In Mangels' experiment (1997), patients with frontal lobe lesions learned the temporal order of a word list either through intentional or incidental learning. At test, they were required to reconstruct the sequence of words that appeared during encoding. In the incidental learning condition, patients had comparable performance to the control group. However, in the intentional learning condition, the control group exhibited much better performance than patients. These results suggested that patients with frontal lobe lesions can automatically encode some temporal information, but that they failed to use strategies to improve their memory as the control group did during the intentional task. Thus frontal cortex is not necessary for automatic encoding of temporal information (Milner et al., 1991; Schacter, 1987), but rather appears to control temporal encoding strategies. The control group was able to organize encoded information in a way that facilitated memory for temporal context.

It is important to note that the frontal lobe is not a homogeneous structure. Different regions within frontal cortex have different functions and there may be hemispheric differences in function (as found with respect to stimulus type) (Milner, 1971; Milner, Corsi, & Leonard, 1991; Kesner, Hopkins, & Fineman, 1994). Cabeza and colleagues (2000) studied age-related differences in neural activity during the same recency judgment vs. recognition judgment task used in Milner's patient studies (described above) (Milner, 1971). Results showed that activation in the right frontal cortex was lower for older adults than for young adults during recency judgments. At the same time, activation in the left frontal cortex was higher for older adults than for young adults during recency judgments. This increase in left frontal activation was interpreted as compensatory activation due to the decreased function of right frontal cortex. The differences between right and left frontal cortex activity may also reflect age-related differences in strategies for recency judgments. In contrast to recency judgments, the ventromedial temporal regions involved in item recognition had similar levels of activation for two age groups.

In another experiment investigating hemispheric differences in frontal lobe function, participants were instructed to learn a list of pictures in the morning and another list in the afternoon (Suzuki, 2002). Following these encoding sessions, they were required to do three tasks: a between-list task, a within-list task and an item recognition task. In the between-list task, participants were asked to decide which of two studied pictures had appeared in the afternoon encoding list. In the within-list task, participants were asked to decide which of two studied pictures appeared later within a single list. In the item recognition task, participants were instructed to choose the old picture from a pair of pictures. A direct contrast comparing the between-list and within-list tasks showed that between-list judgments were associated with right prefrontal activity and within-list judgments were associated with left prefrontal activity. These differences could be explained by different strategies used in the between-list and within-list tasks. In between-list judgments, each picture was associated with relatively different episodes: morning or afternoon whereas pictures in the within-list task had similar episodes. Hemispheric differences have also been found in a study of autobiographical temporal memory (St Jacques, Rubin, LaBar, & Cabeza, 2008). In that experiment, participants took pictures throughout their day and were later given a relative recency task in the lab. Recency judgments about pictures that were taken closer to one another in time were associated with left dorsolateral prefrontal cortex. Recency judgments about pictures that were taken further from one another in time were associated with right dorsolateral prefrontal cortex. The authors interpreted this result as indicating that recency judgments for pictures that were taken close to each other involved a construction process in which contextual details, but not necessarily temporal details, of each study event are retrieved and these details are used to infer the order of pictures (Friedman, 1993). Temporal order judgments for pictures further away from each other involved a process that relies on the strength of each memory trace (Friedman, 1993). This interpretation is consistent with the results of Suzuki's (2002) study.

Subregions of frontal cortex with dissociable functions have also been identified within-hemispheres when working memory for temporal information was tested. In Amiez and Petrides' experiment (2007), abstract black and white designs were used as stimuli in order to discourage the use of verbal repetition. A series of four pictures were presented, which were followed by a cue (1,000ms). Immediately after the cue, a pair of test pictures was presented for 2,000ms. Participants were asked to indicate which picture appeared earlier in the sequence. Results showed that when the pair of pictures came from end positions (first and fourth pictures), there was greater activity in mid-*dorso*lateral prefrontal cortex. When the pair of pictures came from middle positions (second and third pictures), there was greater activity in mid-*ventro*lateral prefrontal cortex. Since pictures from middle positions were viewed more closely in time, mid-*ventro*lateral prefrontal cortex was interpreted to process precise order. In contrast, mid-*dorso*lateral prefrontal cortex was interpreted as responding primarily to the more salient first and last stimuli.

Although the contribution of frontal cortex to temporal context memory has been supported by many experiments, other studies using relative recency judgments have found the involvement of the hippocampus in temporal context memory. For instance, the activation of the hippocampus was associated with successful encoding the temporal order of items in sequences, especially the order of items that were repeated in multiple sequences (Kumaran and Maguire, 2006; Agster et al., 2002). Rats with hippocampal lesions were impaired at making relative recency judgments, even though they demonstrated normal familiarity-based recognition of studied vs. unstudied items (Fortin, Agster, & Eichenbaum, 2002; Kesner, Gilbert, & Barua, 2002).

Recency judgment paradigms suggest that both frontal cortex and the hippocampus are likely to contribute to temporal context memory (Milner, 1971; Schacter, 1987; Milner, Corsi, & Leonard, 1991; Kesner, Hopkins, & Fineman, 1994; Cabeza et al., 1997; M Suzuki, 2002; Amiez & Petrides, 2007; St Jacques, Rubin, LaBar, & Cabeza, 2008). However, it should be noticed that only a small number of studies found hippocampal involvement in relative recency judgments. Lehn et al. (2009) pointed out that the use of recency discrimination paradigms may explain why hippocampal activation has not been implicated in temporal context memory as reliably as frontal activation. In the recency discrimination task, participants do not necessarily need to remember the order of events. Accurate recency judgments can be based solely on the relative familiarity of the two items: more familiar items can be inferred as being more recent. Many theories attribute familiarity-based memory to PRc. If the recency task relies on familiarity rather than temporal context, the frontal lobe probably functions to provide monitoring or decision processes that are used to weigh the relative familiarity of the two items. Many studies have demonstrated that frontal cortex plays an important role in evaluating retrieved information (Blumenfeld & Ranganath, 2007).

If the recency judgment task measures only one of the many strategies that can be used to give temporal judgments, the brain regions driving recency judgments are not necessarily the neural basis of temporal context encoding and retrieval. Rather, the brain regions contributing to temporal context memory may differ depending on strategies. The strategies people use are influenced by the task.

For instance, strategies may be influenced by the scale of the temporal judgments being made. A familiarity-based strategy may be particularly useful when the interval between items is long because the level of familiarity of each item differs to a greater degree than when the interval between the tested items is short. In particular, relative familiarity is unlikely to be useful in judging the order of items that follow one another immediately in a list of many words, as the degree of familiarity should be similar for both items.

If a task requires binding of temporal context information to the item representation, rather than item familiarity alone, we would expect more involvement of the hippocampus (Lehn et al., 2009). One way to form such temporal bindings is to build semantic associations. For instance, in order to remember the order of three words: “apple”, “table” and “boy”, I could remember them as “an apple on the table was eaten by a boy”. These semantic associations can then be used at retrieval to reconstruct the temporal order of the information (Friedman, 1993). This type of strategy is likely to be used when participants are encouraged to imagine interactions between the items being presented, especially when these items are concrete nouns or object pictures (Tubridy & Davachi, 2011; Jenkins & Ranganath, 2010). The hippocampus and PHc were found to contribute to temporal context memory in these experiments. Thus, the pattern of brain activation associated with memory for temporal context in these experiments was consistent with the pattern of brain activation associated with memory for context information in general. However, the semantic strategies used in these studies may mask the difference between temporal context memory and other types of episodic context retrieval. The unique feature of temporal context memory is that events are distributed across the time. Semantic strategies align the events that were distributed in time such that they are encoded as one event through the construction of a story. In this case, temporal context memory is the same as general context memory. From this perspective, it is not surprising that the hippocampus and PHc were found to drive temporal context memory as those regions are involved in retrieval of non-temporal context in episodic memory.

Besides studies that found either prefrontal activation or the activation of the hippocampus and PHc, some experiments have demonstrated the involvement of both of these areas within a single temporal context memory task (Konishi et al., 2002; Jenkins & Ranganath, 2010). For instance, in Jenkins and Ranganath's experiment (2010), they distinguished two types of temporal context memory: fine temporal memory and coarse temporal memory. Fine temporal memory was tested by requiring participants to recall the order of three objects that were presented within one trial, close together in time. In the coarse temporal memory test, participants were instructed to indicate objects' temporal position within the entire study list. Results showed that the activation of PHc was related to fine temporal memory accuracy, whereas several regions in PFC and the hippocampus predicted coarse temporal memory accuracy. The activation of both PFC and MTL supports our claim that different types of temporal order judgments can be based on different types of information and therefore be associated with activation in PFC and/or MTL.

Although research has previously tested several strategies by which temporal context can be inferred through familiarity or reconstructed through recollection, little is known about purely temporal memory that does not involve such non-temporal strategies. Lehn and colleagues (2009) created a paradigm designed to isolate purely temporal memory in their study. On the first day of the experiment, participants watched a 90 minute movie. On the second day, they were instructed to give the order of four events from the movie either by retrieving the temporal order of events or by logically inferring the order. Researchers manipulated the type of test stimuli to promote participants either to retrieve or to infer. After reordering the events, participants were asked to indicate the strategies (retrieving/inferring/other) they used in the previous reordering trial. Subtraction of logically inferred trials from temporal retrieval trials was used as a measure of brain activation specifically related to temporal context memory. Results showed that right hippocampus was related to temporal context memory, as opposed to inferring, and positively correlated with accuracy. Bilateral PHc was also related to retrieval of temporal order, as opposed to inferring, but its activation was not correlated with performance. However, this experiment has limited generalizability because the four testing events in the inferring condition were studied more closely in time than the testing events in the retrieving condition. It is possible that different temporal distances, rather than inferring/retrieving, caused the different brain activation patterns in two conditions.

Another way to isolate temporal context retrieval from the involvement of non-temporal cognitive strategies is to use an implicit memory test. Because participants do not consciously encode and retrieve the temporal order, it is unlikely that cognitive processes such as monitoring or logical inference will be used. In Turk-Browne, Simon, and Sederberg's experiment (2012), participants were instructed to give indoor/outdoor responses to consecutively presented pictures. All these pictures were grouped into triplets, of which the first two items were seen as the temporal context for the third item. The triplets were then repeated in their original grouping or with novel items replacing the context items. Repetition attenuation was measured as an indicator of similarity in the brain representations of these stimuli. Repetition attenuation refers to the decreased BOLD response that is found for repeated compared to novel stimuli. Results showed that in PHc, the magnitude of the repetition attenuation effect was larger for repeated items that followed their original temporal context than for repeated items that followed a novel temporal context. This finding suggests that PHc treats two scenes as more similar when they are preceded by the same context than when they are preceded by different contexts. The authors interpreted this to mean that PHc processed the connection between context and the item across time. However, this experiment also has some limitations. First, temporal context memory was defined as the memory of context prior to the item. However, these contexts could also be considered as semantic or cognitive context for the item, so the experiment does not necessarily test temporal context memory. Also, increased repetition attenuation for items following same context compared to items following different context may reflect overall familiarity of the same context rather than the temporal relationship between items.

Although previous studies inform our understanding of temporal memory, such studies have not compared retrieval of purely temporal information with temporal judgments based on other strategies. The present study will test the following question: if participants are prevented from using familiarity-based or semantic strategies, which brain regions will drive temporal context memory? In other words, are there brain regions that uniquely contribute to temporal context memory rather than other types of episodic context? The design of the study is intended to compare pure temporal context memory, in the absence of semantic strategies, with temporal judgments that are based on non-temporal strategies.

In order to avoid semantic strategies, we will present each item in the study phase quickly and require participants to read each item aloud, with the intention that participants will not have enough time to develop stories to associate the items. We will also use stimuli that do not lend themselves to semantic associations (including abstract words.) In order to avoid familiarity-based strategies, we will only test the temporal order of items that occurred consecutively during the study trials. The relative familiarity of these consecutive items should be similar and will not be diagnostic of the order of the stimuli during encoding. Thus, by avoiding these two non-temporal strategies, the brain activity related to memory for item order should reflect the brain regions uniquely driving temporal context memory rather than other types of contextual or item familiarity-based information.

Participants will study triplets of three words, which are presented as one of two types: familiar phrases and scrambled familiar phrases. Familiar phrases include idioms and common phrases (see Appendix A). We propose that these familiar phrases have pre-existing representations as a single unit such that the order of the words is embedded within memory for the phrase, as in a unitized representation. According to the BIC theory, PRc drives recognition when items are unitized, so it should be the neural basis of temporal context memory when order information is unitized with item information. Therefore, we predict that retrieving the order of a familiar phrase will be based on PRc activation (Giovanello, Keane, & Verfaellie, 2006; Haskins, Yonelinas, Quamme, & Ranganath, 2008; Ford, Verfaellie, & Giovanello, 2010).

Scrambled familiar phrases come from the same set of idioms and common phrases, but with the order of the words within the triplet being randomly changed. We predict that the brain activity related to scrambled familiar phrases should reflect pure temporal context memory because participants will not be able to rely on familiarity for the phrase or semantic strategies to judge the order in which the words were studied. If temporal context information is encoded in the same way as other context details, we should find hippocampal and PHc activation for order memory in the scrambled condition. If temporal context information relies on different encoding and/or retrieval mechanisms than other context details, we expect to identify regions that support pure temporal context memory. Based on the results in Amiez and Petrides' experiment (2007) (described above), we hypothesize that mid-ventrolateral prefrontal cortex will drive pure temporal context memory. In their experiment, abstract black and white designs were used as stimuli, which ruled out the possibility of forming semantic strategies. Although relative recency paradigm brought confounding of familiarity monitoring, the greater activity of mid-ventrolateral prefrontal cortex observed in the memory of precise order may indicate the pure temporal context memory. These hypotheses will be tested in an fMRI study.

Hypothesis

Based on above analysis, we hypothesize that:

1. For scrambled familiar phrases, the contrast between correct temporal context responses and incorrect temporal context responses will indicate the brain regions related to pure temporal context memory. We hypothesize that mid-ventrolateral prefrontal cortex will be the brain region driving pure temporal context memory. We might find hippocampal and PHc activation if temporal context retrieval relies on same mechanisms as non-temporal context retrieval.
2. For the contrast between the familiar phrases condition and scrambled familiar phrases condition, we predict that PRc will be more active for familiar phrases given correct order responses than scrambled familiar phrases given correct order responses. The brain regions related to pure temporal context memory will be more activated for scrambled familiar phrases with correct order responses than familiar phrases with correct order responses.

Materials and Methods

Participants

Twenty five participants were recruited from the Virginia Tech student community by posting fliers on campus. Since familiar phrases were used as stimuli, in order to make sure that participants can recognize the familiar phrases, only English native speakers who grew up in US were included. All participants were right handed. The range of the age was from 19 to 32, with a mean age of 21. Four participants were male. All participants were paid $100 for participation. 3 participants were excluded from fMRI data analysis due to excessive movement during scanning.

Experimental Procedure

Stimuli included 120 word triplets that are familiar phrases heard in normal conversation. The familiar phrases were selected from idioms and common words. In a pilot study, college students were asked to recognize a set of familiar phrases and make judgment about whether they have heard the familiar phrases in daily life. 120 familiar triplets that were most often recognized by students were selected as stimuli. The concreteness and imagability of each word in each triplet was obtained from MRC Psycholinguistic Database (http://websites.psychology.uwa.edu.au/school/MRCDatabase/uwa_mrc.htm). The range of concreteness and imagability is from 100 to 700. The higher value indicates greater concreteness and imagability. The average concreteness of words in our study is 427 and the average imagability of words is 454. It indicates that concreteness value and imagability value are not very high, which means that stimuli did not lend themselves to semantic associations.

The triplets were randomly assigned into 5 blocks of 24 triplets for each participant. Half of the triplets were presented in their familiar order. The words in the remaining triplets were randomly scrambled. Each of the 5 blocks included both a study phase and a test phase and both familiar and scrambled triplets appeared on all lists. All phases were completed in the scanner, however imaging data were not recorded during study trials. (In order to record functional images from the study phase for analysis we would need to insert delays between each study trial, thus lengthening the experiment beyond tolerable levels for our participants.)

During the study trials, the individual words in each triplet were presented one by one on a computer screen for a duration of 700 ms. Participants were instructed to say each word aloud when it was on the screen. In order to make sure that participants say each word aloud, they were told that their responses would be monitored by the experimenter. This presentation of individual words was repeated twice. After the second presentation of the triplet, a question mark appeared on the screen for 2000 ms during which participants were instructed to repeat aloud the triplet from their own memory. Repetitive presentation and retrieval practice at encoding was designed to help participants remember the order of words in triplets. The purpose of saying each word aloud was to prevent participants from using other types of strategies to encode the order of the words.

fMRI scanning took place during the test phase. During each test phase, all triplets studied on the previous list were presented again in one of six possible orders. For instance, if a triplet was presented as A, B, and C in the study phase, at test the triplet may be presented as A-B-C, A-C-B, B-A-C, B-C-A, C-A-B, or C-B-A in the test. The whole triplet was presented vertically on the screen simultaneously for 8 seconds. Each word in the triplet was represented by a letter (T, or M, or B) on the left side of it. “T” means top and it corresponds to the top button on the button box in participants’ right hand. “M” means middle and it corresponds to the middle button on the button box in participants’ right hand. “B” means bottom and it corresponds to the bottom button on the button box in participants. Participants were instructed to press top, middle and bottom button to indicate the original order of each word from the study phase. For instance, three words which were presented as “Leave”, “Only”, and “Me” in the study phase were presented as “Me”, “Only”, and “Leave” in the test phase. The word “Me” corresponds to the top button; the word “Only” corresponds to the middle button; the word “Leave” corresponds to the bottom button. Because “Leave” was presented first in the study phase, participants should press the bottom button firstly to move “Leave” to the first position. “Only” was presented secondly in the study phase, so participants should press the middle button secondly to move “Only” to the second position. “Me” was presented thirdly in the study phase, so participants should press the top button lastly to move “Me” to the third position. Participants could see the order they were selecting as they pressed the buttons. They cannot change their answer after they pressed the button. The question would be replaced by fixation screen after participants finished indicating the order of words from the study phase or would disappear after 8 seconds.

The interval between each word order memory test question was filled by fixation and odd/even judgments. The mean length of the interval was 8 seconds. The length of the interval was determined by an optimization simulation using the optseq program (http://surfer.nmr.mgh.harvard.edu/optseq/). The fixation was presented for the first one second and the last two seconds. The odd/even judgment task was presented during the rest of the interval. In the odd/even judgment task, participants indicated whether the single-digit number on the screen is an odd number or an even number. If the number is even, participants should press the top button on the button box in participant’s left hand. If the number is odd, participants should press the top button on the button box in participant’s left hand. Each odd/even question was presented for 1 second whether participants made a judgment or not. The odd/even judgment task was used as baseline and was intended to prevent participants from mind wandering, which might result in increased MTL activity during the baseline period.

After participants finish five study-test blocks they were taken out of the scanner and given all the triplets in familiar order again. They were instructed to mark any of the familiar phrases from the experiment that were not familiar to them personally prior to the experiment. Those phrases that were not familiar to an individual participant were then excluded from analysis of that participant's data.

MRI data were acquired at Virginia Tech Carilion Research Institute using a 3T Siemens Trio scanner equipped with a 12-channel head coil. Prescreening interviews ensured safety in the scanner, and headphones were provided to attenuate acoustic noise from the scanner. Padding and adjustable head restraints were used to minimize head movement. A gradient echoplanar imaging (EPI) sequence was used to collect functional data (repetition time/TR, 2,000 ms; echo time/TE, 25 ms; field of view, 220). Each volume included 38 slices with a thickness of 3.4 mm and no interslice gap. Voxel size for functional images was 3.4×3.4×3.4 mm. Anatomical images were collected using an MPRAGE sequence (voxel size=.475×.475×.95).

Preprocessing was performed using Statistical Parametric Mapping (SPM8) software. EPI data were slice-time corrected with sinc interpolation to account for differences in the timing of adjacent slice acquisition. Then, functional images were brought into spatial alignment by using a six-parameter, rigid-body transformation. Following realignment, the high-resolution MPRAGE structural image for each participant was then co-registered to the mean EPI for each participant. Spatial normalization was conducted using a segmentation-based procedure. First, the unified segmentation tool in SPM8 was used to calculate normalization parameters based on each participant's co-registered high-resolution MPRAGE. These normalization parameters were then applied to the EPI images to transform them into Montreal Neurological Institute (MNI) template space. Finally, the images were spatially smoothed with an 8 mm full-width at halfmaximum Gaussian filter.

GLM analyses of the fMRI data during the test lists were conducted using SPM8. Outliers were identified at the individual-subject level using the Artifact Detection Tools (http://gablab.mit.edu/index.php/software) in SPM8 with thresholds for global signal intensity (z = 5), translational movement (0.5 mm), and rotational movement (0.005 rad). TRs identified as outliers were modeled as covariates of no interest. Each test trial was modeled based on the reaction time of the memory response immediately following presentation of the test item. The unit of reaction time was transformed into TRs. All analyses used an uncorrected threshold of $p < .001$.

Results

Behavioral Results

In the current experiment, temporal order judgments may involve two steps: source retrieval and temporal order retrieval. Source retrieval means that participants retrieve general context information in order to determine whether the triplet was presented in its familiar order at study or a scrambled order at study (1st step). Retrieval of this information will improve temporal context accuracy but does not require retrieval of temporal information. When the triplet was studied as a familiar phrase, participants can easily retrieve the preexisting order if they correctly retrieve its study condition. For familiar phrases, if participants' incorrect response indicates that they thought the triplet was studied as a scrambled familiar phrase, source memory was incorrect. For scrambled familiar phrases, if participants' incorrect response indicates that they thought the triplet was studied as a familiar phrase, source memory was incorrect. For example, if the triplet "Moons Many Ago" was presented in the study, it is considered as a scrambled familiar phrase. If participants falsely remember that the studied order was "Many

Moons Ago" (familiar phrase), their source memory is incorrect because the triplet was not presented as a familiar phrase in the study. If participants incorrectly think that the correct order is "Ago Moons Many" (scrambled familiar phrase), they have correct source memory although their temporal context memory is incorrect.

If the triplet was a scrambled familiar phrase, participants then need to retrieve the temporal order of words in the study (2^{nd} step). In order to investigate pure temporal memory, we will use only triplets that were given the correct source judgment in our analysis of temporal order. For scrambled familiar phrases, the contrast between correct temporal context judgments and incorrect temporal context judgments will indicate pure temporal context retrieval.

All 25 participants' behavioral results were included in the analysis and the results are presented in Table 1. Those familiar phrases that participants have never heard before the experiment were excluded from analysis. After exclusion, there were 55 familiar phrases and 56 scrambled familiar phrases on average. For familiar phrases, source judgment accuracy was 84.76% and the average number of correct trials per participant was 48. The accuracy of temporal context judgments in the familiar phrase condition is the same as source judgment accuracy, because familiar phrases that are given correct temporal context judgments are by definition also categorized as source correct. For scrambled familiar phrases, source judgment accuracy was 81.67% and the average number of correct trials was 45. The accuracy of temporal context judgments for scrambled familiar phrases was 38.85% and the average number of correct trials was 21.

fMRI Analyses

The first fMRI analysis assessed the neural correlates of temporal context retrieval by contrasting correct and incorrect temporal context retrieval within scrambled familiar phrases which were given correct source retrieval. We predicted that if temporal context memory is same as other types of episodic memory, there would be greater activation in the hippocampus and PHc for scrambled triplets with correct temporal context retrieval (scrambled correct temporal) compared to scrambled triplets with incorrect temporal context retrieval (scrambled incorrect temporal). We also predicted higher activation in mid-ventrolateral prefrontal cortex for scrambled correct temporal condition relative to scrambled incorrect temporal condition according to previous studies. Consistent with our prediction, correct/incorrect temporal context retrieval identified widespread activation in medial temporal lobe, including left hippocampus and left PRc [peak voxel x=-24, y=-17, z=-19, t(16)=5.40, p<.001], right hippocampus [peak voxel x=24, y=-3, z=-19, t(16)=3.84, p=.001], right PRc [peak voxel x=21, y=-24, z=-19, t(16)=4.83, p<.001], and right PHc [peak voxel x=34, y=-30, z=-13, t(16)=5.15, p<.001] (see Figure 3). Besides MTL, we also observed greater activation in ventromedial PFC [peak voxel x=0, y=55, z=4, t(16)=6.86, p<.001] and posterior cingulate including retrosplenial cortex [peak voxel x=-3, y=-24, z=38, t(16)=7.75, p<.001]. Table 2 lists the significant clusters found in the whole-brain analysis for this contrast. Beta value differences between scrambled correct temporal condition and scrambled incorrect temporal condition were extracted from the hippocampus, PHc and PRc (see Figure 4). All the beta value differences between correct and incorrect trials are significantly different from zero (Hippocampus: t(16)=3.82, p=.002; PHc: t(16)=2.46, p=.026; PRc: t(16)=4.21, p=.001) and there is no significant difference between any two of them.

We did not expect to have greater activation of PRc in the scrambled correct versus incorrect temporal contrast. One reason for the observed activation of PRc is that temporal order retrieval may have relied on familiarity to some extent. Further analysis of the behavioral data revealed higher accuracy of scrambled triplets presented in the studied order in test phase compared to scrambled triplets presented in the non-studied order (t(21)=6.047, p<.001), suggesting that presentation in the studied order allowed familiarity to contribute to retrieval. In order to reduce the involvement of familiarity in our analysis of temporal order judgments, we did another contrast between scrambled correct temporal condition and scrambled incorrect temporal condition without including those scrambled triplets that were presented in the studied order on the test. As we predicted, the activation of PRc was reduced and was only shown on the right [peak voxel x=31, y=-17, z=-26, t(13)=5.39, p<.001] but not left hemisphere (See Figure 3). We still identified activation in bilateral hippocampus [left: peak voxel x=-20, y=-1, z=-19, t(13)=4.46, p<.001; right: peak voxel x=27, y=-3, z=-13, t(13)=7.14, p<.001]. However, there was not any activation in PHc after we excluded the scrambled triplets presented in their studied order in the test. Beta value differences in the hippocampus, PHc, and PRc were also extracted in this contrast. All beta value differences are significantly different from zero (Hippocampus: t(13)=3.39, p=.005; PHc: t(13)=2.34, p=.036; PRc: t(13)=2.61, p=.022) and the difference in the hippocampus is significantly greater than that in PRc (t(13)=2.60, p=.022). The beta value differences reveal a different pattern from what we observed in brain activation (See Figure 4). In contrast to the decreased activation in PRc, there was not significant decrease in the beta value difference in PRc. Although there was no activation in PHc after excluding the scrambled triplets presented in the studied order in the test, there was still a significantly difference of beta values between scrambled correct condition and scrambled incorrect condition.

The second analysis assessed the contrast between familiar triplets that were given correct temporal responses (familiar correct temporal) and scrambled triplets that were given correct temporal responses (scrambled correct temporal). We predicted that there would be higher activation in PRc in the familiar correct temporal condition compared to scrambled correct temporal condition, since the temporal order and the word was unitized. Consistent with our prediction, there was higher activation in right PRc (cluster = 41 contiguous voxels) [peak voxel x=27, y=-7, z=-19, t(18)=6.61, p<.001] in familiar correct temporal condition than in scrambled correct temporal condition (See Figure 5). However, some other regions we did not predict have also been identified: bilateral hippocampus [left: peak voxel x=-27, y=-17, z=-19, t(18)=4.00, p<.001; right: in the same cluster as PRc], bilateral PHc[left: peak voxel x=-27, y=-41, z=-9, t(18)=4.41, p<.001; right: peak voxel x=38, y=-37, z=-9, t(18)=4.31, p<.001], vmPFC [peak voxel x=-3, y=51, z=-13, t(18)=6.95, p<.001], and posterior cingulate including retrosplenial cortex [peak voxel x=-7, y=-51, z=25, t(18)=6.08, p<.001]. Table 3 lists the significant clusters found in the whole-brain analysis for this contrast. Beta value differences in the hippocampus, PHc, and PRc were extracted in this contrast (See Figure 6). As we expected, the beta value in familiar correct temporal condition is significantly higher than that in scrambled correct temporal condition in PRc (t(18)=2.47, p=.024). However, the beta value differences between familiar correct temporal and scrambled correct temporal in the hippocampus (t(18)=2.06, p=.055) and PHc (t(18)=1.02, p=.322) were not significant.

We also assessed activation greater in scrambled correct temporal condition in contrast to familiar correct temporal condition (See Figure 5). There was not any activation in MTL in this contrast. However, we found a large cluster of activation in bilateral dorsolateral PFC (left: cluster=1302 contiguous voxels; right: cluster= 874 contiguous voxels) [left: peak voxel x=-47, y=7, z=28, t(18)=11.53, p<.001; right: peak voxel x=48, y=10, z=28, t(18)=9.58, p<.001]. Table 4 lists the significant clusters found in the whole-brain analysis for this contrast.

Discussion

This study investigated the neural correlates of temporal context retrieval. Temporal context can be retrieved using different strategies. For instance, temporal information can be assessed by making recency judgments according to relative familiarity of events. That is, the more familiar the event the more recently it occurred. Temporal context retrieval can also be based on semantic associations among events and therefore inferring temporal order from remembering associated information. The use of these two strategies does not require retrieval of contextual information that appeared at different time points, which makes the temporal context retrieval same as other types of episodic memory retrieval. Therefore, it is not surprising that temporal context memory was associated with MTL in previous studies, since in almost all the studies participants could use strategies to help them remember the temporal information and retrieval of non-temporal context is known to involve PHc and the hippocampus.

The current experiment aims to find the brain regions associated with temporal context retrieval when participants cannot use non-temporal strategies (pure temporal context retrieval). The way we prevented participants from using relative familiarity strategies was to only test the temporal order of words that occurred consecutively during the study trials. In order to rule out semantic association-based judgments, we used abstract words as stimuli and presented each word in the study quickly and required participants to read each item aloud.

We presented familiar phrases in either familiar or scrambled order in the study and asked them to retrieve the order in the test. We assumed that it took 2 steps for participants to retrieve the temporal order. The first step is general context retrieval, which means participants should recollect whether the triplet was studied as a familiar phrase or scrambled familiar phrase. If participants thought a triplet was presented in familiar order in the study, the second step, temporal context retrieval, would be very easy since the order of words is “built in”. If participant thought a triplet was presented in scrambled order in the study, they should try to retrieve the exact order they studied. We did not explicitly ask participants to retrieve the temporal order in 2 steps. Instead, we did the analysis based on their responses. We only included trials that were given correct general context retrieval in the contrasts in order to prevent any confound from general context retrieval.

We hypothesized that the contrast between correct and incorrect temporal retrieval within scrambled triplets indicated the neural correlates of pure temporal context retrieval. We found greater activation in bilateral hippocampus and PRc, left PHc, vmPFC, retrosplenial cortex, and posterior cingulate in the contrast. These brain regions belong to two dissociable and extended networks proposed by Ranganath and Ritchey (2012). Ranganath and Ritchey (2012) proposed that PRc is a core component of an extended anterior temporal (AT) system that also includes the ventral temporopolar cortex, lateral orbitofrontal cortex and amygdala. One of the AT system's functions is familiarity-based recognition memory. The activation of PRc is not what we expected since we were trying to rule out non-temporal retrieval strategies. However, the activation of PRc suggests that familiarity was involved in the temporal context retrieval process. This is consistent with behavioral results which showed that when the scrambled triplets were presented in their studied order in the test, the accuracy is significantly higher than the accuracy of scrambled triplets presented in non-studied order in the test. That is, when the scrambled triplets were presented in their studied order in the test, participants tended to make their judgment based on familiarity.

In order to test our hypothesis of the involvement of familiarity, we did another contrast analysis between scrambled correct versus incorrect temporal condition without including those scrambled triplets presented in the studied order on the test. As expected, there was only greater activation in right PRc in this contrast rather than widespread activation in bilateral PRc when we included all scrambled triplets. The activation of PRc indicates that even though we tried to eliminate the involvement of non-temporal strategies, there was still some involvement of familiarity based judgments.

PHc and RSc are core components of an extended posterior medial (PM) network according to Ranganath and Ritchey (2012). The PM network also includes the mammillary bodies and anterior thalamic nuclei, pre- and parasubiculum and the default network (including the posterior cingulate, precuneus, lateral parietal cortex and medial prefrontal cortex). The hippocampus is an anatomical convergence for connections from PRc and PHc. Consistent evidence from fMRI studies have shown that activation in the hippocampus, PHc and RSc, as well as anatomically connected regions in the default network, is associated with successful memory of the context of an event. Most of this evidence came from non-temporal context memory studies in which lists of words, objects or other stimuli are studied and then memory is tested for each item and its associated context information which appeared simultaneously with items in the study. Based on the brain activation in scrambled correct versus incorrect temporal retrieval contrast, it seems temporal context retrieval has the same activation pattern as in other types of non-temporal episodic memory retrieval even though non-temporal strategies have been prevented. What we found here is similar to results in some studies in which researchers tried to prevent non-temporal strategies. For instance, in Lehn et al.'s (2009) experiment, they asked participants to either infer or retrieve temporal order of events. They used subtraction of logically inferred trials from temporal retrieval trials as a measure of brain activation specifically related to temporal context memory. Their results showed that right hippocampus and bilateral PHc were related to retrieval of temporal order. Turk-Browne, Simon, and Sederberg's (2012) experiment used implicit memory test in which participants were not explicitly told that the order of pictures were manipulated. They found that PHc is related to temporal context. One limitation of the current study is that we are unable to directly compare the brain regions associated with temporal context retrieval to brain regions associated with non-temporal context retrieval (general context retrieval), since there was an insufficient number of trials with incorrect general context retrieval.

One interesting result is that after we excluded the scrambled triplets which were presented in studied order in test phase, the beta value difference between scrambled correct and incorrect temporal retrieval contrast was still significant in PHc. However, there was not any activation above the statistical threshold in either right or left PHc in scrambled correct versus incorrect temporal retrieval contrast. The inconsistent result may indicate that the function of PHc in temporal context retrieval is different from its function in non-temporal context retrieval. Mixed evidence has been found about the function of PHC in temporal context memory. For instance, in Turk-Browne et al.'s (2012) study, PHc has been found to treat two identical scenes as more similar when they were preceded in time by the same stimuli compared to when they were preceded by different stimuli. The temporal context in Turk-Browne et al.'s study is "relative" information, which means that it is the scene that appeared before the critical scene matters. They did not take into account the "absolute" position of the scene in the list. Hsieh, Gruber, Jenkins, and Ranganath (2014) studied the memory of objects and its absolute position in the list. They found that PHc activation carried absolute position information and the function of the hippocampus is to bind object with position information, which are consistent with the prediction of non-temporal context retrieval based on BIC theory (Diana et al., 2007). One difference between the present study and Turk-Browne et al., Hsieh et al.'s study is that they recorded the brain activity associated with each stimulus; the present study recorded the brain activation when participants retrieved order information of all three words together. In present experiment, Participants could retrieve either absolute or relative temporal information to help them make judgments, so our data do not indicate the exact functions of PHc.

Another contrast in the current study is between familiar correct temporal condition and scrambled correct temporal condition. We hypothesized that there should be greater activity in PRc for familiar correct temporal condition than scrambled correct temporal condition, since the order the words in familiar triplets is “unitized”, or pre-existing within the representation of the triplet. Consistent with our prediction, we found greater activation in PRc for the familiar correct temporal condition. This result suggests that the item and temporal context information may have been unitized for familiar triplets. An alternative explanation for the greater activity in PRc in familiar correct temporal condition is the semantic memory of familiar triplets from pre-experimental experience. However, this is unlikely because scrambled triplets could automatically trigger the retrieval of familiar order, which means that the contribution of semantic memory of familiar order to PRc activation should be almost same for familiar and scrambled triplets in the test.

We also observed greater activation in the hippocampus, PHC, and other parts of the default network including vmPFC, retrosplenial cortex, and posterior cingulate for the contrast of familiar correct temporal and scrambled correct temporal. The greater activations in these brain regions correspond to the overall higher accuracy for the familiar triplets than the scrambled triplets. Interestingly, the brain regions show greater activation in familiar versus scrambled correct temporal contrast are also involved in scrambled correct versus incorrect temporal contrast, although the beta value difference in PRc is significantly greater in the familiar versus scrambled correct temporal comparison than the scrambled correct versus incorrect temporal comparison. That is, temporal context retrieval of familiar and scrambled order involved the same brain regions with familiar triplets producing more activation in PRc.

We found greater activation in DLPFC for the scrambled correct temporal condition compared to the familiar correct temporal condition. It has been found that DLPFC is association with the re-organization of information in working memory. For instance, in Blumenfeld and Ranganath's (2006) study, participants were instructed to either "rehearse" trials or "reorder" trials. Rehearse means that participants should subvocally rehearse a list of three words. Reorder indicates that participants were instructed to mentally rearrange three words based on the weight of the objects that the words referred to. Results showed that the activation of DLPFC is greater when participants reordered the words, relative to rehearsed words. And DLPFC activation is correlated with following memory performance. The greater DLPFC activation observed in scrambled/familiar contrast should be due to greater effort when participants reordered the words in scrambled triplets.

Conclusion

The present study investigated the brain regions that support temporal context retrieval in the absence of non-temporal strategies (i.e. pure temporal context memory). We found that temporal context retrieval was associated with the hippocampus, parahippocampal cortex, ventromedial prefrontal cortex, retrosplenial cortex, and posterior cingulate in both the familiar triplet and scrambled triplet conditions, which are consistent with the retrieval of non-temporal context in episodic memory. We also found that temporal context retrieval could rely on familiarity, which was demonstrated by the higher accuracy and greater activation of PRc in familiar phrases and scrambled triplets presented in studied order in the test phase.

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Table 1.

Accuracy for Familiar Phrases and Scrambled Familiar Phrases in General Context Retrieval and Temporal Context Retrieval

	General Context Retrieval		Temporal Context Retrieval	
Familiar phrases	Correct	84.76%(48)	Correct	84.76%(48)
			Incorrect	0
	Incorrect	15.24%(8)		
Scrambled familiar phrases	Correct	81.67%(45)	Correct	38.85%(21)
			Incorrect	42.82%(24)
	Incorrect	18.34%(10)		

Note. The number in parentheses is the average number of trials in each condition.

Table 2.

Peak Voxels at $P_{Uncorrected}$<.001 for Whole-Brain Analyses of Scrambled Correct Temporal Condition Versus Scrambled Incorrect Temporal Condition Analysis

Brain region	x	y	z	t	Cluster
Posterior cingulate gyrus	-3	-24	38	7.75	1137
	38	-41	59	6.73	
	4	-27	45	6.21	
Right superior temporal sulcus	41	-47	15	7.31	616
	55	-54	8	7.14	
	55	-41	18	6.28	
Left superior temporal sulcus	-51	-68	15	7.05	366
	-44	-51	32	6.45	
	-41	-71	32	6.11	
Superior frontal gyrus	0	55	4	6.86	356
	-13	44	-6	6.37	
	7	55	21	5.48	
Right caudate nucleus	14	24	8	6.69	139
	21	27	15	6.38	
	17	41	11	5.45	
Right circular insular sulcus	38	0	11	6.25	81
	27	4	-26	5.03	
	17	-7	-16	4.47	
Left middle temporal gyrus	-64	-17	-19	5.98	249
	-44	-34	-13	5.65	
	-24	-17	-19	5.40	
Left middle frontal gyrus	-30	24	52	5.82	65
	-27	21	35	4.20	
Left lateral fissure	-58	-3	4	5.45	40
	-58	-17	8	4.65	
Right lateral fissure	58	0	8	5.00	30
Right superior frontal gyrus	21	38	45	4.60	19
Posterior cingulate gyrus	-7	-58	15	4.58	20

Note. Peak voxel for each cluster is listed in bold followed by other peaks within the same cluster.

Table 3.

Peak Voxels at $P_{Uncorrected}$<.001 for Whole-Brain Analyses of Familiar Correct Temporal Condition Versus Scrambled Correct Temporal Condition Analysis

Brain region	x	y	z	t	Cluster
Left transverse temporal sulcus	-44	-13	15	7.57	31
Left superior temporal gyrus	-54	-24	8	7.09	43
Superior frontal gyrus	-3	51	-13	6.95	419
	4	58	-6	6.65	
	10	51	-2	6.56	
Left superior temporal sulcus	-54	-68	18	6.78	135
	-58	-61	21	5.77	
	-47	-71	32	5.51	
Left superior frontal gyrus	-24	38	45	6.70	56
Right anterior hippocampus	27	-7	-19	6.61	41
	21	-7	-30	3.99	
Right lateral fissure	55	-30	25	6.22	270
	61	-17	4	5.93	
	65	-24	11	5.38	
Posterior cingulate gyrus	-7	-51	25	6.08	479
	-24	-41	69	5.84	
	-17	-27	55	5.73	
Right central sulcus	27	-27	55	6.03	138
	17	-30	59	5.20	
	21	-44	69	5.06	
Left inferior temporal sulcus	-64	-13	-23	5.80	94
	-51	0	-23	4.50	
Left subcentral gyrus	-54	-3	4	5.74	13
Right lateral occipitotemporal sulcus	51	-10	-33	5.45	51
	58	-10	-23	4.82	
Right superior parietal gyrus	14	-85	38	5.33	22
Right temporal stem	41	-17	-6	5.19	30
	41	-10	4	3.96	
	38	-17	-16	3.82	
Left temporal stem	-41	-17	-9	5.01	18
Right long insular gyri	44	-13	18	4.83	14
Left superior parietal gyrus	-10	-92	28	4.21	17
	-13	-81	32	4.19	

Note. Peak voxel for each cluster is listed in bold followed by other peaks within the same cluster.

Table 4.

Peak Voxels at $P_{\text{Uncorrected}}<.001$ for Whole-Brain Analyses of Scrambled Correct Temporal Condition Versus Familiar Correct Temporal Condition Analysis

Brain region	x	y	z	t	Cluster
Left dorsolateral prefrontal cortex	-47	7	28	11.53	1302
	-27	21	-6	10.76	
	-41	17	25	9.54	
Right dorsolateral prefrontal cortex	48	10	28	9.58	874
	44	27	25	7.77	
	31	21	-2	7.51	
Medial cingulate	10	10	55	9.03	437
	-3	0	52	7.36	
	10	21	28	7.14	
Right superior frontal sulcus	27	-3	52	7.96	87
	31	10	62	5.34	
Left middle occipital gyrus	-41	-71	-9	7.80	296
	-41	-64	-16	7.12	
	-30	-61	-13	7.03	
Right intraparietal	27	-64	32	7.53	1217
	21	-68	55	7.30	
	-27	-61	45	7.23	
Right caudate nucleus	14	7	1	7.10	387
	-17	0	11	7.01	
	-10	-13	4	6.91	
Right cingulate gyrus	-10	24	21	5.37	11

Note. Peak voxel for each cluster is listed in bold followed by other peaks within the same cluster.

Figure 1. Study phase. Subjects were instructed to say aloud each triplet for three times.

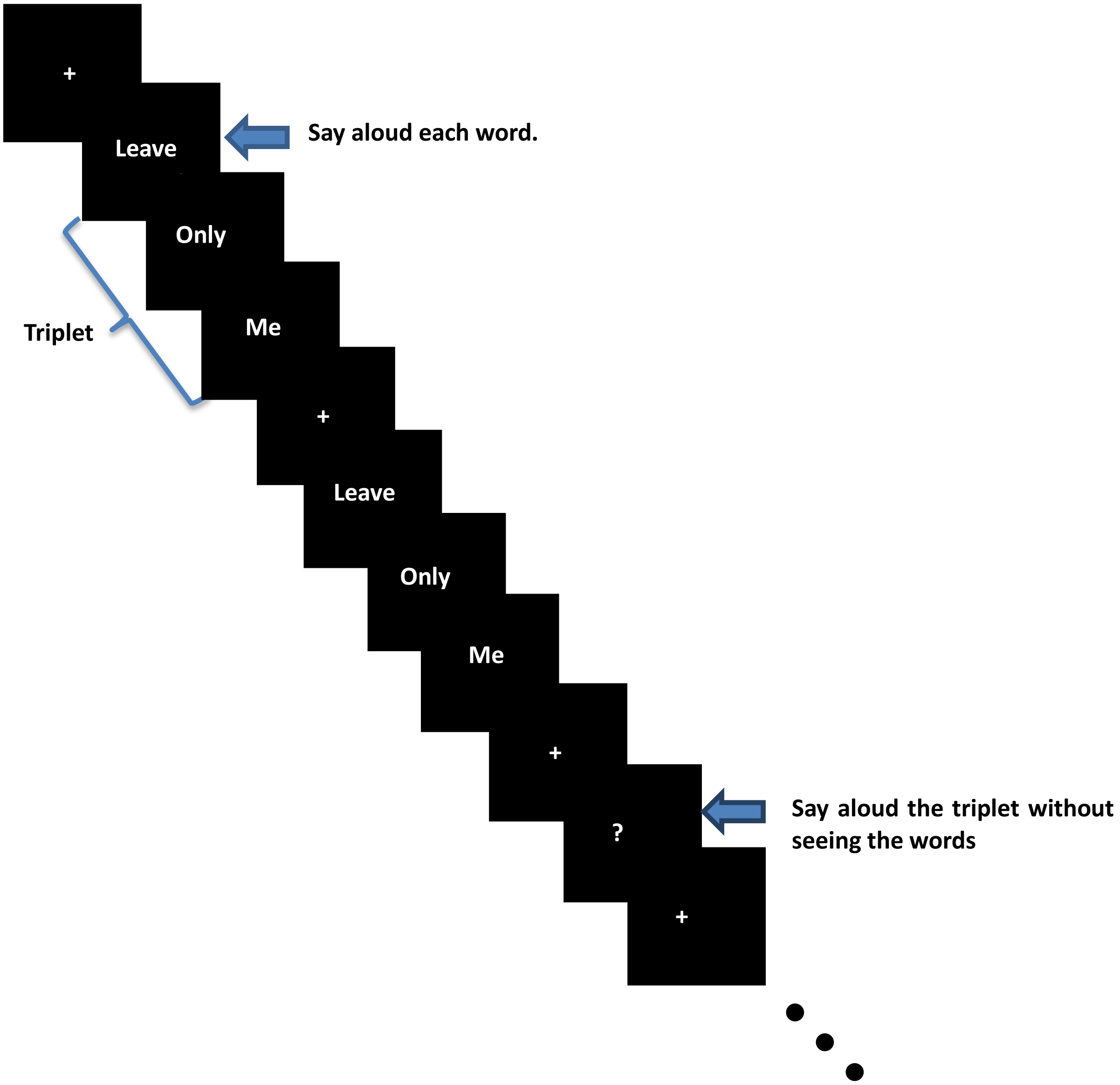
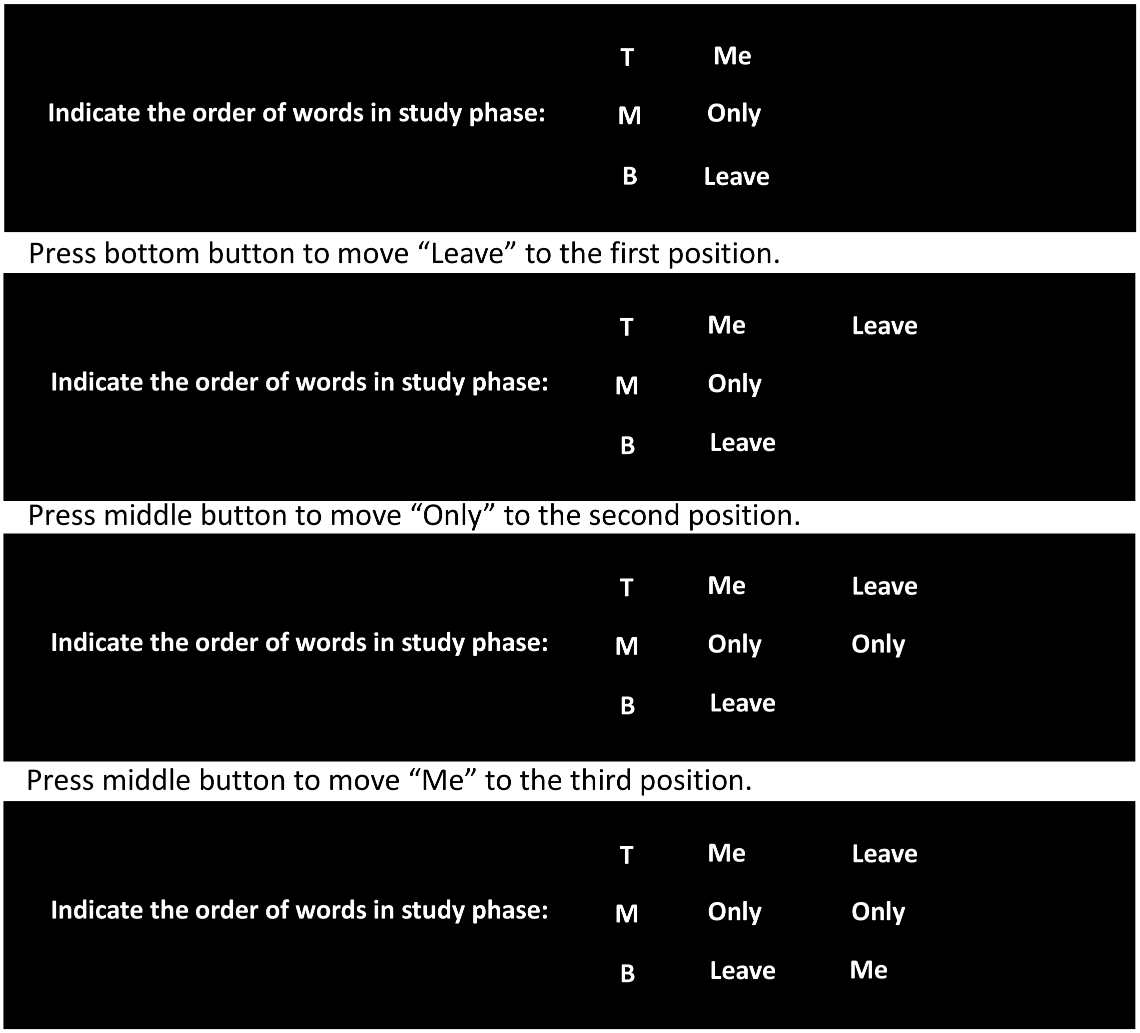


Figure 2. Test phase. Participants were instructed to reorder words into their studied order.



Indicate the order of words in study phase:
T Me
M Only
B Leave

Press bottom button to move “Leave” to the first position.

Indicate the order of words in study phase:
T Me Leave
M Only
B Leave

Press middle button to move “Only” to the second position.

Indicate the order of words in study phase:
T Me Leave
M Only Only
B Leave

Press middle button to move “Me” to the third position.

Indicate the order of words in study phase:
T Me Leave
M Only Only
B Leave Me

Figure 3. The contrast between scrambled correct temporal condition and scrambled incorrect temporal condition.

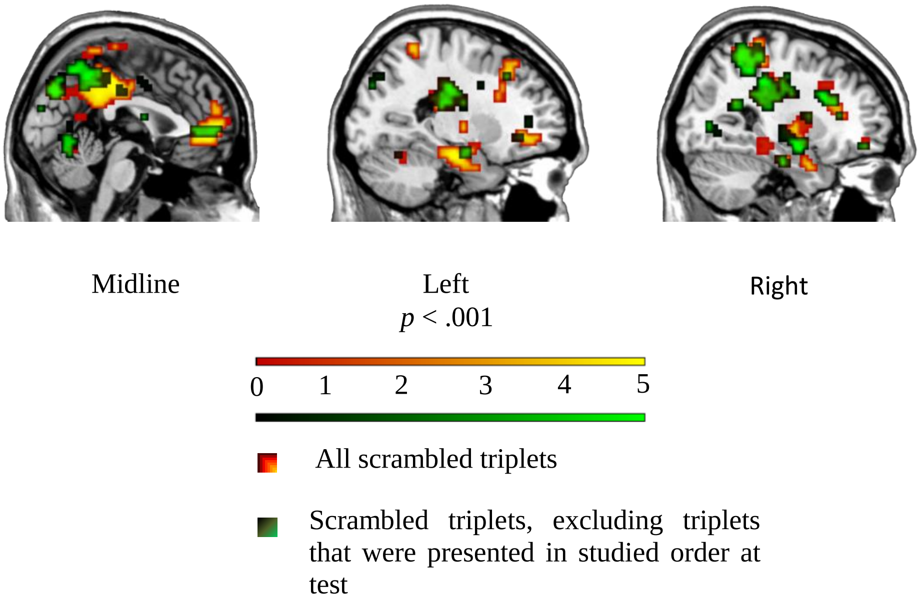
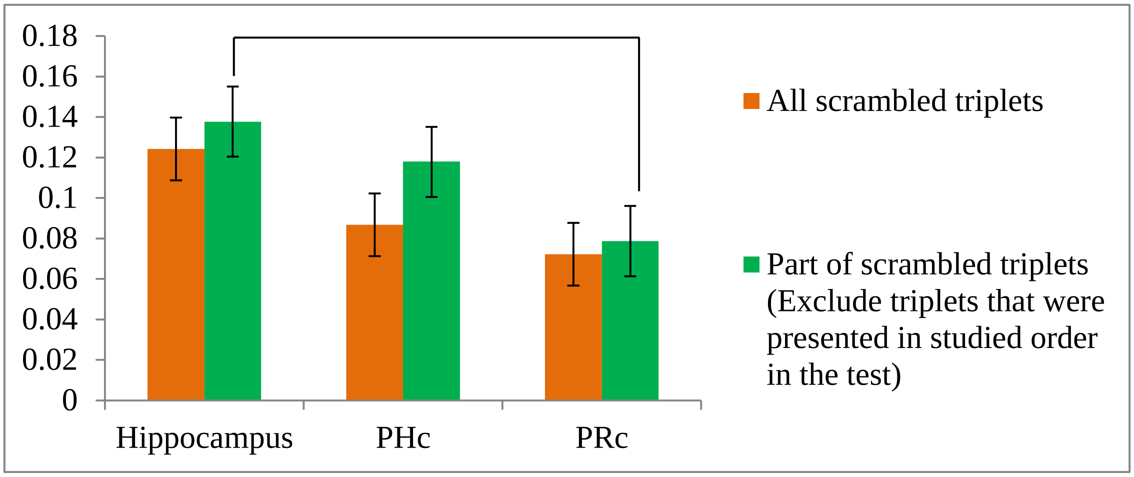
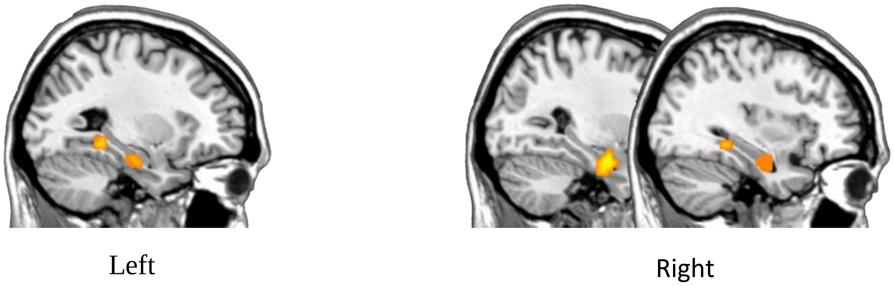


Figure 4. Beta value differences between correct and incorrect temporal context retrieval within scrambled triplets. All beta value differences between correct and incorrect condition are significant.



Note. *p<.05

Figure 5. The contrast between familiar correct temporal and scrambled correct temporal condition



Masked for MTL activation only

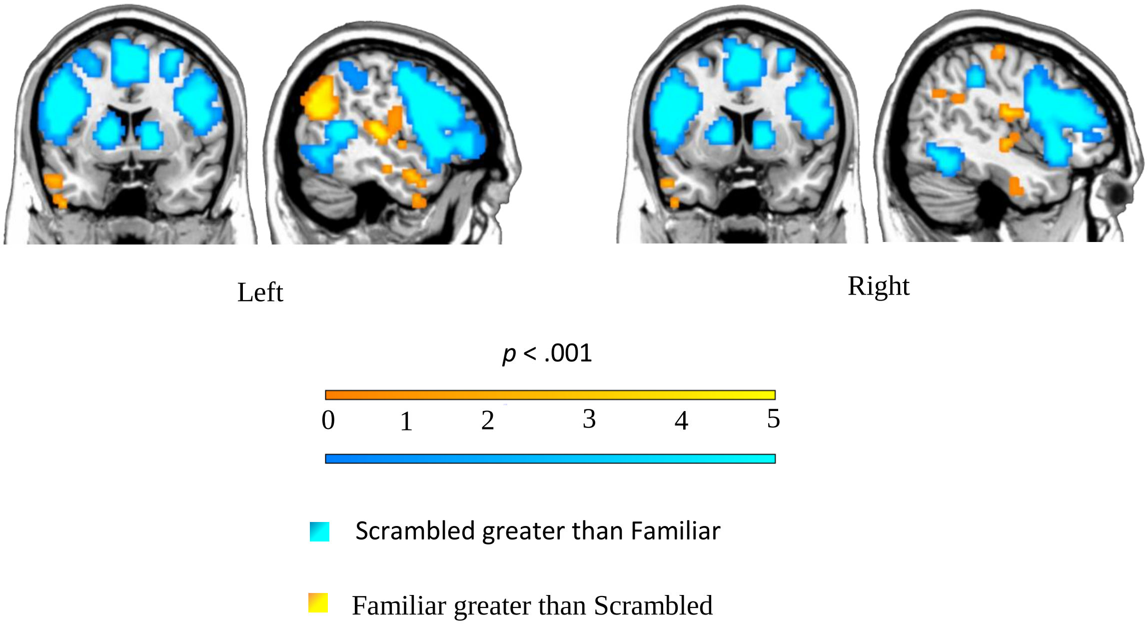
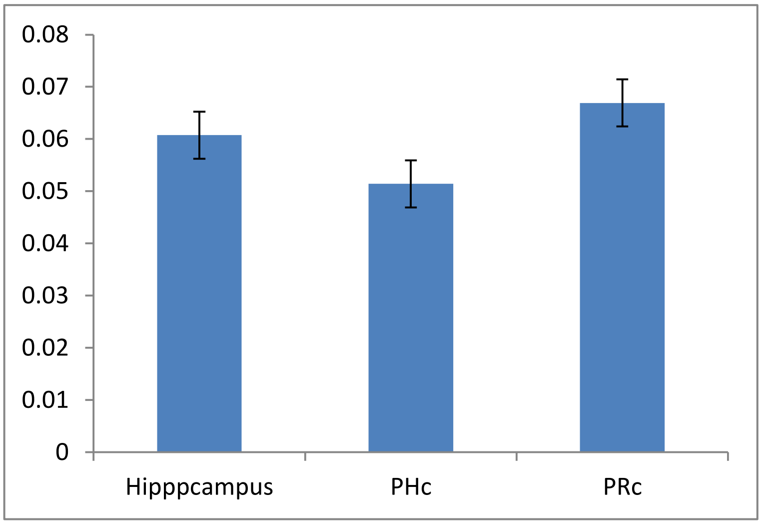


Figure 6. Beta value differences between familiar correct temporal condition and scrambled correct temporal condition.



Note. *p<.05

Appendix A

Many Moons Ago
Whisper Sweet Nothings
Reach First Base
Internet Service Provider
Leave Me Alone
Gross Domestic Product
Scream Bloody Murder
Emergency Medical Technician
Familiarity Breeds Contempt
Central Intelligence Agency
Start From Scratch
Have Broad Shoulders
Ram Down Throat
Big Bang Theory
Blessing In Disguise
Not Born Yesterday
Some other time
Honor Among Thieves
Martin Luther King
Zero Tolerance Policy
Chocolate Chip Cookie
Flat Screen Television
No Holds Barred
Blue Collar Job
Cast Iron Stomach
Six Feet Under
Glass Half Empty
Three Blind Mice
Heads Will Roll
Light Bulb Moment
Rush Hour Traffic
Slowly But Surely
Piece Of Cake
Wild Goose Chase
Wear Several Hats
Jump Through Hoops
Hit Rock Bottom
Two Strikes Against
Heaven Only Knows
Food For Thought
Best Foot Forward
Older Than Dirt
Ace Up Sleeve
Bad Hair Day
Ears Are Burning
Our Daily Bread
Sport Utility Vehicle
Never Say Die
Million Miles Away
Men At Work
Break A Leg
Apples To Oranges
See You Later
Fare Thee Well
Goodbye Cruel World
Sell Yourself Short
Knee Jerk Reaction
Fat Lady Sings
Jog My Memory
Saturday Night Live
Low Hanging Fruit
Show Good Faith
Look Both Ways
Bird's Eye View
Little Drummer Boy
Come Full Circle

When Pigs Fly
Mad Cow Disease
Level Playing Field
Fair Weather Friend
Famous Last Words
All Rights Reserved
Age Before Beauty
Pumpkin Spice Latte
Bite Your Tongue
Whole Nine Yards
Breathe Life Into
Black Friday Sale
Moral High Ground
Haste Makes Waste
Papa John's Pizza
Misery Loves Company
Happy New Year
Quid Pro Quo
Take The Reins
Driving While Intoxicated
Davy Jones' Locker
International Date Line
Let Freedom Ring
Behind Closed Doors
Winter Storm Warning
Fine Tooth Comb
Easy Does It
Law Abiding Citizen
Guilty As Charged
Without Further Ado
Ball Park Figure
Thar She Blows
Supreme Court Justice
Empire State Building
Key Lime Pie
Squires Student Center
Jungle Out There
Death Warmed Over
Saving Private Ryan
Most Valuable Player
Knock On Wood
Philly Cheese Steak
Long Road Home
Lock Horns With
Talk Is Cheap
Watching Paint Dry
And So Forth
Golden Gate Bridge
By Any Means
Red Nose Reindeer
Devil May Care
Wheels Fall Off
Rip Van Winkle
Dead Or Alive