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Neural correlates of temporal context retrieval for abstract scrambled phrases: Reducing narrative and familiarity-based strategies

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Abstract

Temporal context, memory for the timing of events, can be assessed using non-temporal strategies such as relative familiarity or inference from a semantic narrative. Neuroimaging studies, which have previously encouraged such strategies, find similar patterns of brain regions involved in both temporal and non-temporal context memory. The present study aims to investigate whether previous findings are driven by the use of non-temporal strategies or whether the same pattern of brain regions is identified when relative familiarity and semantic narrative strategies are discouraged. We used abstract phrases (e.g. alone me leave) created by scrambling familiar three-word phrases. The words in the phrases were less concrete than the object image stimuli used in previous studies of temporal context memory (Jenkins and Ranganath, 2010) and were presented quickly while participants read each word aloud. This differed from previous studies in which participants were encouraged to use narrative strategies during encoding (Tubridy and Davachi, 2011) and was designed to discourage use of narrative strategies. The relative familiarity of the words within each phrase was similar and likely not diagnostic of word order during encoding, in order to minimize the use of relative familiarity strategies. Neuroimaging results indicate that temporal context retrieval was associated with the hippocampus, parahippocampal cortex, ventromedial prefrontal cortex, and retrosplenial cortex, which are regions consistent with the retrieval of non-temporal context in episodic memory, suggesting that previous findings were not driven entirely by non-temporal strategies but rather that temporal memory relies on similar brain regions to non-temporal memory.

Keywords

Temporal context retrieval; Frontal cortex; Medial temporal lobe

1. Introduction

Temporal context refers to the timing or order in which events occurred. Temporal information is one of the key components of episodic memory (Polyn and Kahana, 2008). Given that episodic memory relies heavily on the medial temporal lobe (MTL) (Davachi,

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2006; Davachi et al., 2003; Diana et al., 2007; Eichenbaum et al., 2007, 1994), we might expect that temporal information is processed in MTL regions. The specific MTL subregions involved in temporal memory can be informed by the roles these subregions play in episodic memory in general. According to the “binding of item and context” (BIC) theory, perirhinal cortex (PRc) processes item information, parahippocampal cortex (PHc) processes context information, and the function of the hippocampus is to bind item and context into a single, holistic, event representation (Diana et al., 2007; Eichenbaum et al., 2007). BIC theory also proposes that if an item and its context are encoded as a single, novel, conceptual unit (unitized), retrieval of the context can be based on the familiarity of that item representation and therefore be driven by PRc (Diana et al., 2008, 2010). 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. Debate remains as to whether PHc processes specific forms of context (such as spatial) to the exclusion of others (Diana, in press; Epstein and Ward, 2010).

A variety of experimental paradigms have previously been used to study temporal context memory. Each of these paradigms has the potential to involve non-temporal strategies, with some explicitly encouraging non-temporal strategies, whereas the current study attempts to reduce non-temporal strategies. As previous studies have demonstrated, the brain regions involved in temporal context memory are likely to vary based on the strategy used to make the temporal judgment.

One common paradigm used to study temporal context memory is the recency judgment task. In this task, participants are tested with pairs of items that were previously encoded and asked to identify the item that was studied most recently. Early patient studies showed that prefrontal lesions led to impaired recency judgments (Milner, 1971; Milner et al., 1991; Kesner et al., 1994), whereas more recent patient and animal studies also identified a role for the hippocampus in recency judgments (Kesner et al., 2002; Mayes et al., 2001). Neuroimaging studies have implicated both the frontal lobe (Cabeza et al., 1997; Suzuki et al., 2002; Jacques et al., 2008) and the hippocampus (Agster et al., 2002; DuBrow and Davachi, 2014; Dudukovic and Wagner, 2007; Fortin et al., 2002; Jenkins and Ranganath, 2016; Kumaran and Maguire, 2006) in recency judgments. The involvement of the frontal lobe, might be driven by familiarity-based strategies. Accurate recency judgments can be based on the relative familiarity of two items with more familiar items inferred as being more recent. If the recency task relies on familiarity, the frontal lobe may provide monitoring or decision processes that are used to weigh the relative familiarity of the two items, which corresponds to the findings that frontal cortex plays an important role in evaluating retrieved information (Blumenfeld and Ranganath, 2007). A familiarity-based strategy for temporal judgments 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 level of familiarity should be similar for both items.

Another paradigm used to study temporal context memory is the temporal order or position task (Davachi and DuBrow, 2015). Participants are required to memorize a sequence of

several items (usually 3–5 items) and then are instructed to retrieve the studied order of these items. For example, in Jenkins and Ranganath's (2010) experiment, four object images were presented sequentially for 1.5 s each. Then, after an eight second delay, participants were tested on their memory for the temporal position of one studied object. Given the unfilled eight second delay between encoding and test in this paradigm, participants had the opportunity to create a narrative to incorporate the temporal order of events. That is, to remember the order of four objects: "bunny", "cooking pot", "paper bag", and "mushroom", one could create a story which includes the temporal order: "I came across a bunny on my way home. After I arrived at home I put the cooking pot on the stove and then opened the paper bag to get the mushroom." This story can then be used at retrieval to reconstruct the temporal order of the information (Friedman, 1993). Such temporal narrative strategies are likely to be used when the stimuli are concrete nouns or object pictures and when participants are given sufficient time during encoding (Ekstrom et al., 2011; Ekstrom and Bookheimer, 2007; Jenkins and Ranganath, 2010). Other studies of temporal order have used instructions that explicitly ask participants to imagine interactions between the items being presented (Tubridy and Davachi, 2011). The hippocampus and PHc have been found to contribute to temporal context memory in such temporal order or position memory tasks (Ekstrom et al., 2011; Ekstrom and Bookheimer, 2007; Jenkins and Ranganath, 2010; Tubridy and Davachi, 2011; Hsieh et al., 2014), which is consistent with the pattern of brain activation associated with memory for context information in general. The contribution of temporal narrative strategies may explain the involvement of the hippocampus and PHc in these studies of temporal context. To our knowledge, no prior study has discouraged the use of narrative strategies for temporal information other than Lehn et al. (2009), which is described below.

Lehn et al. (2009) used a paradigm designed to isolate temporal memory from non-temporal retrieval strategies. In their study, participants were instructed to watch a 90-min movie and then either retrieve the temporal order of four events presented in the movie or logically infer the order. The subtraction of logically inferred trials from temporal retrieval trials was intended to serve as a measure of brain activation specifically related to temporal context memory in the absence of non-temporal strategies. Results showed that right hippocampus was related to accuracy in temporal retrieval, as opposed to temporal inference. Bilateral PHc activation was also related to retrieval of temporal order, as opposed to inference, but this activation was not correlated with performance. However, when interpreting these results it should be noted that the four testing events in the inference condition always occurred more closely in time than the four testing events in the retrieval condition. It is possible that differing temporal distances, rather than inference vs retrieval, caused the different brain activation patterns in the two conditions. The longer temporal distance among testing events in the retrieval condition might have increased the likelihood that participants would apply relative familiarity-based strategies in this condition. Therefore, this study does not provide clear conclusions with respect to the difference between temporal and non-temporal memory strategies and further research is needed to determine whether memory for temporal information in the absence of temporal narrative strategies is also supported by MTL subregions.

One way to avoid non-temporal cognitive strategies is to use an implicit test to study temporal context processing. Because participants do not consciously retrieve the temporal order, contamination from non-temporal strategies is unlikely. In Turk-Browne et al.'s experiment (Turk-Browne et al., 2012), participants were instructed to give indoor/outdoor responses to consecutively presented pictures. All pictures were grouped into triplets, with the first two items being defined as the temporal context for the third, target, item. The triplets were then repeated or altered such that novel items replaced the context items that preceded the target item. Repetition attenuation, a decreased blood oxygen level-dependent (BOLD) response for repeated stimuli as compared to novel stimuli, was measured as an indicator of similarity in the neural representations of the target items. 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 a repeated scene as more similar when it is preceded by the same context than when it is preceded by a new context. The authors interpreted this to mean that PHc processes the connection between context and the item across time. Although the implicit memory paradigm prevents the contamination of non-temporal strategies, the paradigm is designed to measure the influence of temporal context on item processing rather than explicit temporal context retrieval. Explicit temporal context retrieval in response to an item may involve different brain regions than implicit temporal context processing.

These previous studies inform our understanding of temporal memory, but have not yet compared active retrieval of temporal context with temporal judgments based on other strategies. Therefore, the primary aim of the current study was to identify brain regions driving explicit temporal context retrieval with reduced contributions from non-temporal strategies such as familiarity-based or temporal narrative strategies. The second aim was to compare temporal context retrieval with temporal judgments that are based on unitization of temporal order with the item. We designed a paradigm to discourage participants from using temporal narrative and familiarity based strategies. Temporal narrative strategies were discouraged by presenting each item quickly (700 ms in the current study versus more than 1 s in previous studies), using a distractor task during encoding (requiring participants to read each item aloud versus unconstrained encoding in previous studies), and using a combination of abstract nouns (e.g. "thought" and "justice"), concrete nouns, and other parts of speech as stimuli (as opposed to object pictures or concrete nouns only). The intention was that participants would be discouraged from developing stories to associate the items and that the items themselves would not lend themselves to a semantic narrative. Therefore, the current study provides a comparison point for prior studies that allowed for or encouraged narrative strategies (e.g. Jenkins and Ranganath, 2010; Tubridy and Davachi, 2011) by reducing the influence of narrative strategies. If temporal context memory in the absence of narrative strategies does rely on a distinct set of brain regions from other types of context memory then we should see a different pattern of results in the current study than that seen in previous temporal context memory studies. If temporal context memory relies on the same neural mechanisms as other types of context memory, reducing the influence of narrative strategies should produce a similar pattern of results in the current study to those seen in previous temporal context memory studies.

Familiarity-based strategies were discouraged by testing the temporal order of items that occurred consecutively during the study trials. The relative familiarity of these consecutive items should be similar and therefore not diagnostic of the order of the stimuli during encoding. By minimizing these two non-temporal strategies, the brain activity related to memory for item order should reflect the brain regions driving temporal context memory rather than other types of contextual or item familiarity-based information. We then contrasted temporal memory with the familiarity-based strategy of temporal context unitization. Stimuli whose representations require a specific order, such as familiar phrases (“see you later”), should be retrievable in that order using non-temporal, familiarity-based strategies whereas stimuli whose order is random should require additional retrieval processes beyond familiarity (“later you see”).

In the current experiment, participants studied three word phrases that were encoded as one of two types: familiar phrases and scrambled familiar phrases. Familiar phrases included both idioms and common phrases. We propose that the words in familiar phrases are unitized with their familiar temporal order. That is, the temporal order of the words is determined by their existence as a familiar phrase. According to the BIC theory and previous studies of unitization, PRC drives recognition when item and context are unitized, so we predicted that this would also be the case for temporal context unitization. Thus PRC should be involved in temporal context memory when order information is unitized with item information (Ford et al., 2010; Giovanello et al., 2006; Haskins et al., 2008). Scrambled familiar phrases were derived from the *same* set of idioms and common phrases, but with the order of the words within the phrase being randomly changed. We predicted that the brain activity related to scrambled familiar phrases should reflect temporal context memory in the absence of non-temporal strategies because participants should not be able to rely on familiarity for the phrase or temporal narrative 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 mechanisms than other context details, we expect to identify other regions, outside the typical recollection network, that support temporal context memory.

2. Results

2.1. Behavioral results

In the current experiment, temporal order judgments may involve retrieving two types of information: source/general context (was the phrase presented in its familiar order or a scrambled order?) and temporal order (what was the specific order of the words?). We did not ask participants to explicitly retrieve source/general context but rather inferred that judgment based on the temporal order response. Successful retrieval of source information (familiar or scrambled) influenced temporal context accuracy but that influence varied between the familiar phrase and scrambled familiar phrase conditions. When the phrase was studied in a familiar order, participants could easily retrieve the preexisting temporal order based on correct retrieval of its study condition. For familiar phrases whose source information was correctly retrieved, the temporal order response may not require temporal

context retrieval processes because the order is inherent within the phrase. That is, processing of the “item” alone, the unitized representation of the phrase, can support accurate retrieval. Therefore, correct temporal order retrieval for familiar phrases may rely on non-temporal context retrieval strategy: temporal context unitization.

For scrambled familiar phrases, incorrect source memory was indicated by a temporal order response that placed the words in their familiar order. For example, if “moons many ago” was presented in the study, it is a scrambled familiar phrase. If participants incorrectly respond that the studied order was “many moons ago” (the familiar order), their source memory was incorrect because the phrase was not presented in familiar order in the study. If participants correctly think that the phrase was studied in scrambled order, they then need to retrieve the temporal order of words in the study, because correct source retrieval does not necessarily lead to correct temporal order retrieval for scrambled phrases. For instance, “moons many ago” is a correct temporal response but “moons ago many” is not, although both of them correctly identify the study condition/source information (scrambled familiar phrase). In order to investigate temporal memory without the involvement of non-temporal strategies, we used only phrases that were assigned one of the five possible scrambled orders in our analysis of temporal context retrieval. These scrambled judgments were then further divided into those assigned the correct scrambled order and those assigned the incorrect scrambled order.

Behavioral accuracy and reaction time are presented in Table 1. Source judgment accuracy was 84.26% for familiar phrases and 81.7% for scrambled familiar phrases. This difference is not statistically significant ($t(21) = -.89$, $p = .19$). Therefore, the difficulty of source retrieval was approximately the same for both familiar phrases and scrambled familiar phrases and any brain activation differences between them is not likely to be due to source retrieval difficulty. 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. The accuracy of temporal context judgments for scrambled familiar phrases was 38.54%. The percentage of correct temporal order judgments was significantly higher for familiar phrases than scrambled phrases ($t(21) = 18.71$, $p < .001$).

2.2. fMRI analyses

The first fMRI analysis assessed the neural correlates of temporal context retrieval by contrasting correct and incorrect temporal context retrieval for scrambled familiar phrases which were correctly identified as scrambled. We predicted that if temporal context memory involves the same brain regions as other types of context retrieval, there would be greater activation in the hippocampus and PHc for scrambled phrases with correct temporal context retrieval (scrambled correct temporal) compared to scrambled phrases with incorrect temporal context retrieval (scrambled incorrect temporal). We also predicted greater activation in prefrontal cortex for the scrambled correct temporal condition relative to the scrambled incorrect temporal condition if temporal context retrieval involves the same brain regions as recency judgments. Consistent with our prediction, correct temporal context retrieval was associated with 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 Fig. 1a). In addition to activation in the MTL, we also observed greater activation in ventromedial pre-frontal cortex (vmPFC) [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 the scrambled correct temporal and scrambled incorrect temporal conditions were extracted from the hippocampus, PHc, and PRc based on anatomical masks of each region (see Fig. 1b). The voxel-wise analyses presented above identify spatially localized regions of activation regardless of how those regions are situated within anatomical borders. The beta value analyses presented next identify whether activation within an anatomical region as a whole varies with the contrasted conditions. All MTL regions showed significant beta value differences between correct and incorrect trials (Hippocampus: $t(16) = 3.82$, $p = .002$; PHc: $t(16) = 2.46$, $p = .026$; PRc: $t(16) = 4.21$, $p = .001$) and there were no significant differences between the regions. Therefore, the beta analysis supports the conclusions from the voxel-wise analysis, that all three MTL regions: hippocampus, PRc, and PHc were involved in successful temporal context retrieval to a greater degree than unsuccessful temporal context retrieval, and suggests that the activation extends broadly throughout the anatomical borders of each subregion.

Although we did not expect it, we did find greater activation in PRc for the scrambled correct temporal memory versus incorrect temporal memory contrast. One explanation for the PRc activation might be that temporal order retrieval relied on familiarity or item processing to some extent. Further analysis of the behavioral data showed that scrambled phrases tested in the original studied order (e.g. the studied phrase “moons many ago” being tested with the cue “moons many ago”, $M = 59\%$) were significantly better remembered than scrambled phrases tested in the non-studied order (e.g. the studied phrase “moons many ago” being tested with the cue “ago many moons”, $M = 35\%$) ($t(21) = 6.11$, $p < .001$). This finding suggests that test presentation in the studied order allowed familiarity for the scrambled order to improve retrieval. An alternative explanation for the finding of higher accuracy to scrambled phrases tested in the original studied order might be that participants were biased to accept the test probe as given, regardless of its accuracy. We tested this alternative explanation by comparing the rate at which scrambled phrases were ordered to match the test-presented order when it was *incorrect* ($M = 18.8\%$) with an expected false alarm rate of 20% if all five possible incorrect response options were selected equally. This difference was not statistically significant ($t(21) = -.69$, $p = .25$). Therefore, we conclude that the increase in hit rates to test scrambled phrases presented in studied order was primarily driven by increased mnemonic information rather than an overall bias to accept the presented order regardless of its correctness. In order to reduce the involvement of familiarity in our analysis of temporal order judgments, we did a follow-up analysis of scrambled correct temporal memory vs scrambled incorrect temporal memory in which we excluded trials on which the scrambled phrases were presented in the studied order on the test. Given our stated minimum trial number of 15 trials to include participants in the group-

level analyses, the N for this contrast was 14. As we predicted, the activation of PRc was reduced in this analysis and restricted to the right hemisphere [peak voxel $x = 31$, $y = -17$, $z = -26$, $t(13) = 5.39$, $p < .001$] (See Fig. 1a). We still identified activation in bilateral hippocampus in this analysis [left: peak voxel $x = -20$, $y = -1$, $z = -19$, $t(13) = 4.46$, $p < .001$; right: peak voxel $x = 27$, $y = -3$, $z = -13$, $t(13) = 7.14$, $p < .001$] but not in PHc.

Beta value differences in the hippocampus, PHc, and PRc were also extracted for this modified contrast using anatomical masks (See Fig. 1b). All three regions showed significant beta value differences between correct and incorrect trials (Hippocampus: $t(13) = 3.39$, $p = .005$; PHc: $t(13) = 2.34$, $p = .036$; PRc: $t(13) = 2.61$, $p = .022$). In addition, the difference between correct and incorrect judgments was significantly greater in the hippocampus than that in PRc ($t(13) = 2.60$, $p = .022$). Although there were no significant clusters of activation in PHc after excluding the scrambled phrases presented in the studied order on the test, the average beta values for PHc as a whole were significantly different between the scrambled correct condition and scrambled incorrect condition.

The second fMRI analysis assessed the contrast between familiar phrases that were given correct temporal responses (familiar correct temporal) and scrambled phrases that were given correct temporal responses (scrambled correct temporal). It should be noted that accuracy in these two conditions varied greatly, with familiar temporal judgments being correct on 84% of trials and scrambled temporal judgments being correct on 39% of trials. We predicted that there would be higher activation in PRc in the familiar correct temporal condition compared to the scrambled correct temporal condition based on the assumption that the temporal order and the word were unitized for phrases studied in their familiar order. Consistent with our prediction, there was significantly greater activation in right PRc [peak voxel $x = 27$, $y = -7$, $z = -19$, $t(18) = 6.61$, $p < .001$] in the familiar correct temporal condition than in the scrambled correct temporal condition (See Fig. 2a). Other regions also produced greater activation for the familiar correct temporal condition than the scrambled correct temporal condition: bilateral hippocampus [left: peak voxel $x = -27$, $y = -17$, $z = -19$, $t(18) = 4.00$, $p < .001$; right: in the same cluster as PRc], left PHc [peak voxel $x = -27$, $y = -41$, $z = -9$, $t(18) = 4.41$, $p < .001$], vmPFC [peak voxel $x = -3$, $y = 51$, $z = -13$, $t(18) = 6.95$, $p < .001$], and posterior cingulate including retro-splenial 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 once again using anatomical masks (See Fig. 2b). As we expected, the PRc beta value for the familiar correct temporal condition was significantly higher than that for the scrambled correct temporal condition ($t(18) = 2.47$, $p = .024$). Although the beta value differences between familiar correct temporal and scrambled correct temporal retrieval in the hippocampus ($t(18) = 2.06$, $p = .055$) and PHc ($t(18) = 1.02$, $p = .322$) were not significant, these regions show a numerical effect that is similar to PRc. These findings suggest that temporal order memory for familiar phrases may be more supported by PRc than temporal order memory for scrambled phrases but do not provide a definitive conclusion regarding the specificity of PRc involvement as compared to other MTL subregions in this contrast. It should also be noted that there were voxel-wise clusters of activation in each MTL

subregion. We also assessed activation in the reverse contrast: greater in the scrambled correct temporal condition than the familiar correct temporal condition (See Fig. 2a). There were no significant differences in MTL activation in this contrast. However, we found a large cluster of increased activation in bilateral dorsolateral prefrontal cortex (DLPFC) for the scrambled temporal correct condition as compared to the familiar temporal correct condition (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.

3. Discussion

The current experiment was designed to identify brain regions associated with temporal context retrieval when there was minimal opportunity to apply common non-temporal strategies. In order to obtain temporal context memory without the involvement of familiarity-based strategies, we tested the temporal order of words that occurred consecutively during the study trials. We also discouraged participants from using temporal narrative strategies by using more abstract stimuli than previous studies and requiring participants to read each phrase aloud during study. With these characteristics in place to minimize non-temporal strategies, we can compare our results to the results of previous studies that allowed or encouraged temporal strategies and determine whether our findings differ from the previous literature.

The contrast between correct and incorrect temporal retrieval within the scrambled phrases condition indicates the neural correlates of temporal context retrieval without non-temporal strategies. We found greater activation in bilateral hippocampus and PRc, left PHc, vmPFC, retrosplenial cortex, and posterior cingulate in this contrast. These brain regions, aside from PRc, correspond to BIC theory predictions for context retrieval in general but also belong to one of the extended networks proposed by Ranganath and Ritchey (2012). Ranganath and Ritchey (2012) proposed that PHc and RSc are core components of a posterior medial (PM) network (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 mode 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 the associated context information which appeared simultaneously with the item during study. Based on the brain activation in the scrambled correct versus incorrect temporal retrieval contrast, it seems that temporal context retrieval as measured in the current experiment has a similar activation pattern to other types of non-temporal context retrieval even though non-temporal strategies were limited in this experiment. Therefore, even though temporal context is qualitatively different from other episodic context in the sense that temporal context occurs at different time point

from target event, temporal context retrieval and non-temporal context retrieval seem to share similar neural correlates.

Contrary to our predictions, we also found PRc activation associated with temporal context retrieval for scrambled phrases. PRc is a core component of the 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 and item processing which we did not expect in the scrambled phrase condition (Ranganath and Ritchey, 2012). However, this neural finding is consistent with behavioral results demonstrating that when the scrambled phrases were presented in their studied order at test, accuracy was significantly higher than the accuracy of scrambled phrases presented in non-studied order at test. This suggests that familiarity for the scrambled triplet at test influenced participants' temporal order judgments. In order to test our post-hoc hypothesis, we created another contrast between the scrambled correct temporal and scrambled incorrect temporal conditions without including those scrambled phrases presented in the studied order on the test. This contrast should reduce any influence of familiarity in retrieval of scrambled phrase temporal order. Although PRc activation was reduced in the voxel-wise contrast relative to the contrast that included all scrambled phrases, the beta parameters extracted from the PRc anatomical ROI remained statistically significant suggesting that the role of PRc is not confined to scrambled phrases presented in the studied order but rather occurs across all types of scrambled correct temporal retrieval. This indicates one potential difference between temporal and non-temporal context retrieval: PRc may be involved in temporal context retrieval but not in other types of episodic context retrieval. This result is consistent with at least one prior study which showed the involvement of PRc neurons in signaling the conjunction of items and their temporal information (Naya and Suzuki, 2011).

In addition, after we excluded the scrambled phrases 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 the PHc as a whole. However, there were no individual voxels that exceeded the statistical threshold in either right or left PHc in this modified scrambled correct versus incorrect temporal retrieval contrast. These changes mirror the changes in PRc and suggest that the post hoc analysis produced an overall dampening of the effects across the brain.

The second purpose of the current experiment was to compare temporal context retrieval with temporal judgments that are based on unitization. Since PRc drives recognition when an item and context are unitized, we predicted that it would be the neural basis of temporal context memory when order information is unitized with words as in the familiar phrase condition. In order to address this question we contrasted the familiar correct temporal judgments with scrambled correct temporal judgments. We hypothesized that there should be greater activity in PRc for familiar correct temporal judgments than scrambled correct temporal judgments, if memory for order is based on pre-existing information within the representation of the familiar phrase. ROI analyses did identify greater activation in PRc for the familiar correct temporal condition than the scrambled temporal correct condition; however both the hippocampus and PHc showed a trend toward significance in this analysis as well. Significant clusters of activation were found in all three areas in the voxel-wise

analysis as well as in other parts of the default network including vmPFC, retrosplenial cortex, and posterior cingulate. The increased activation across brain regions likely corresponds to the substantially higher accuracy for familiar phrase temporal retrieval than scrambled phrase temporal retrieval. Therefore it is difficult to draw strong conclusions about the specificity of increased PRC activation in the familiar correct temporal retrieval condition as compared to the scrambled correct temporal retrieval condition. Interestingly, the brain regions that showed greater activation in the familiar versus scrambled correct temporal contrast also showed greater activation in the scrambled correct versus incorrect temporal contrast. Although some differences in statistical significance were identified, the numerical pattern of MTL subregion involvement appears to be similar in temporal context retrieval for both familiar and scrambled order phrases.

We found greater activation in DLPFC for the scrambled correct temporal condition compared to the familiar correct temporal condition. DLPFC has previously been associated with the re-organization of information in working memory. For instance, in Blumenfeld and Ranganath's (2006) study, participants were instructed to either "rehearse" or "reorder" a list of three words. The rehearse condition required subvocal rehearsal of a list of three words. The reorder condition required a mentally reordering of three objects based on their weight. Results showed that DLPFC activation is greater when participants reordered the words, relative to rehearsed words. The greater DLPFC activation observed in scrambled/familiar contrast is likely due to greater effort when participants reordered the words in scrambled phrases.

4. Conclusion

The present study investigated the brain regions that support temporal context retrieval in the absence of non-temporal strategies. We found that temporal context retrieval was associated with the hippocampus, parahippocampal cortex, ventromedial pre-frontal cortex, retrosplenial cortex, and posterior cingulate in both the familiar phrase and scrambled phrase conditions, which are regions consistent with the retrieval of non-temporal context in episodic memory. We therefore conclude that temporal context memory relies on similar brain regions to non-temporal context memory, even when non-temporal strategies are minimized. Given that PRC was involved in temporal context retrieval in our study, which is unusual when compared to non-temporal context retrieval, it is possible that temporal context memory recruits from a somewhat broader set of brain regions than non-temporal context memory. Finally, we found that temporal context retrieval could rely on familiarity, which was demonstrated by the higher accuracy and greater activation of PRC in familiar phrases (temporal context unitization based familiarity) and scrambled phrases presented in studied order in the test phase.

5. Materials and methods

5.1. Participants

Twenty five members of the Virginia Tech community were recruited and given monetary compensation for participating. In order to ensure that participants recognized the familiar phrases, only native English speakers who grew up in the US were included. All participants

were right handed. Participant age ranged from 19 to 32, with a mean age of 21. Four participants were male. Three participants were excluded from fMRI data analysis due to excessive movement during scanning as determined during preprocessing artifact analysis for a final N of 22. In order to increase the signal-to-noise ratio, we excluded participants with fewer than 15 trials in a given contrast from the group-level analysis. Therefore, the scrambled correct versus incorrect temporal retrieval contrast had a final N of 17 participants and the familiar correct temporal retrieval versus scrambled correct temporal retrieval had a final N of 19 participants.

5.2. Experimental procedure

Stimuli included 120 three-word familiar phrases, including idioms, heard in normal conversation (e.g., leave me alone). Only phrases identified in a pilot study by participants from the same community as familiar were selected to be included in the stimulus set. The concreteness and imageability of each word in each phrase was obtained from the MRC Psycholinguistic Database (http://websites.psychology.uwa.edu.au/school/MRCDatabase/uwa_mrc.htm). Concreteness and imageability values in the MRC database range from 100 to 700. The average concreteness of words in our study was 427 and the average imageability of words was 454.

The stimuli were randomly assigned to 5 blocks of 24 phrases for each participant. Half of the phrases were randomly selected to be presented in their familiar order such as “leave me alone”. The words in the remaining phrases were randomly scrambled such as “moons many ago”. Each of the 5 blocks included both a study phase and a test phase, and both familiar and scrambled phrases appeared on all lists. There was a 2 min delay between study and test phase, during which participants were reminded about the instruction for the test. All blocks were completed in the scanner but 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 words in a phrase were presented one-by-one on a computer screen for a duration of 700 ms each and, upon completion of the three-word phrase, were immediately re-presented (See Fig. 3). Participants were instructed to say each word aloud when it was on the screen. In order to ensure that participants said the words aloud, they were told that their responses would be monitored by the experimenter. Immediately after the second presentation of the phrase, a question mark appeared on the screen for 2 s during which participants were instructed to retrieve the studied phrase from their own memory and say it aloud. The 2 s interval was chosen to be too short for additional effortful strategies to be applied after the phrase was retrieved and repeated aloud. The purpose of using repeated presentation and retrieval practice at encoding was to help participants remember the order of the words in phrases as this is a difficult task without the use of temporal narrative strategies.

fMRI scanning took place during the test phase (See Fig. 4). During each test phase, all phrases studied on the previous list were presented again in one of six possible orders. For instance, if a phrase was presented as A, B, and C in the study phase, at test the phrase may

be presented as A-B-C, A-C-B, B-A-C, B-C-A, C-A-B, or C-B-A. The whole phrase was presented vertically on the screen simultaneously. Each word in the phrase was represented by a letter (T, or M, or B) on the left side of it which stood for the top, middle, and bottom buttons on the response box. Participants were instructed to indicate the order of each word as they were presented in the study phase by pressing the three buttons in the correct sequence. For instance, a phrase presented as “leave me alone” in the study phase might be presented as “me alone leave” in the test phase. Because “leave” was presented first in the study phase, the bottom button should be pressed first to move “leave” to the first position. “Me” was presented second in the study phase, so the top button should be pressed second to move “me” to the second position. “Alone” was presented third in the study phase, so the middle button should be pressed third to move “alone” to the third position. Participants could see the order they were selecting as they pressed the buttons but could not change their answers after they pressed the button. Each phrase was presented for 8 s or until participants finished indicating the order of words from the study phase in which case the question was replaced by a fixation screen. The reaction time was defined as the time interval between the initial presentation of the test probe and the last button response.

The interval between each test trial was filled by an odd/even judgment active baseline tasks. The mean length of the intertrial interval was 8 s and varied according to the results of an optimization simulation using the optseq2 program (<http://surfer.nmr.mgh.harvard.edu/optseq/>). A fixation cross was presented for the first one second and the last two seconds of the intertrial interval. In the odd/even judgment task, participants indicated whether the single-digit number on the screen was an odd number or an even number. Each of the odd/even judgments was presented for 1 s.

After the participants finished the five study-test blocks they were taken out of the scanner and given a list of all phrases in the familiar order. They were instructed to mark any of the 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 the Virginia Tech Carilion Research Institute Human Neuroimaging Lab using a 3T Siemens Tim 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, 2,010 ms; echo time/TE, 23 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 $3.4 \times 3.4 \times 3.4$ mm. Anatomical images were collected using an MPAGE sequence (voxel size = $.475 \times .475 \times .95$).

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, the functional images for a single participant were brought into spatial alignment by using a six-parameter, rigid-body transformation. Following realignment, the high-resolution MPAGE structural image for each participant

was 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 half-maximum Gaussian filter.

GLM analyses of the fMRI data collected 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 (.5 mm), and rotational movement (.005 rad). TRs identified as outliers were modeled as covariates of no interest. The duration of each test trial was modeled based on the reaction time of the memory response to that test triplet with the onset being the appearance of the test probe.

All GLM analyses used a corrected threshold of $p < .05$. This threshold was determined by the 3dClustSim function in the AFNI software package. The function calculates Monte Carlo simulations to determine a combined p -threshold and cluster threshold that will produce a corrected threshold at the desired alpha level. Our whole-brain analyses were thresholded at $p < .001$ with a minimum cluster size of 22 (to produce a corrected $p < .05$). Our MTL analyses, based on a priori predictions for this region, were thresholded at $p < .001$ with a minimum cluster size of 4 (to produce a corrected $p < .05$).

Beta values were extracted from ROIs by drawing anatomical masks on the MNI template brain for the hippocampus, PHc and PRc in the MTL based on anatomical criteria described in previous studies (Buffalo et al., 2006; Insausti et al., 1998). The anterior limit of PRc was drawn 2 mm anterior to the limen insula. The posterior limit of PHc was defined as the posterior limit of the hippocampus. PHc and PRc included the cortex on the parahippocampal gyrus and on the banks of the collateral sulcus. The border between PRc and PHc was defined as the coronal slice containing the posterior limit of the hippocampal head. These analyses were assigned an alpha level of .05 based on a priori predictions for these regions.

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Fig. 1.

The contrast between scrambled correct temporal and scrambled incorrect temporal conditions (threshold, $p < .001$). (a) Both red and green activation indicate the contrast between scrambled correct temporal condition and scrambled incorrect temporal condition. The difference between red activation and green activation is that the former included all scrambled phrases that were given correct general context retrieval and the latter excluded phrases there were presented in studied order in the test. (b) Both red and green bars indicate beta value differences between correct and incorrect temporal context retrieval within scrambled phrases. All beta value differences between correct and incorrect condition are significant (bars indicate standard errors of the means). $*p < .05$.

Fig. 2.

The contrast between familiar correct temporal and scrambled correct temporal conditions (threshold, $p < .001$). (a) The blue activation indicates greater activation for scrambled correct temporal than familiar correct temporal. The yellow activation indicates greater activation for familiar correct temporal than scrambled correct temporal. The upper panel masked MTL activation only. The lower panel masked whole brain activation. (b) Beta value differences between familiar correct temporal condition and scrambled correct temporal condition (bars indicate standard errors of the means). * $p < .05$.

Fig. 3.

Study phase. At study, participants were instructed to say each word aloud when it was on the screen. This presentation of individual words was then repeated. After the second presentation of the phrase, a question mark appeared on the screen for 2000 ms during which participants were instructed to repeat aloud the phrase from their own memory.

Fig. 4.

Test phase. During test phase, all phrases studied on the previous list were presented again in one of six possible orders. The whole phrase was presented vertically on the screen simultaneously for 8 s. Each word in the phrase 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’ right hand. Participants were instructed to press top, middle and bottom button to indicate the original order of each word from the study phase.

Table 1

Accuracy for familiar phrases and scrambled familiar phrases in general context retrieval and temporal context retrieval (Reaction time in parentheses).

	General Context Retrieval		Temporal Context Retrieval	
Familiar phrases	Correct	84.26% (3409 ms)	Correct	84.26% (3409 ms)
	Incorrect		Incorrect	0
	Incorrect	15.74% (4488 ms)		
Scrambled familiar phrases	Correct	81.7% (4464 ms)	Correct	38.54% (4244 ms)
	Incorrect		Incorrect	43.16% (4675 ms)
	Incorrect	18.29% (4084 ms)		

Table 2

Peak voxels at $p_{\text{corrected}} < .05$ for whole-brain analyses of scrambled correct temporal condition versus scrambled incorrect temporal condition. Peak voxel for each cluster is listed in bold in bold followed by other peaks within the same cluster.

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

Table 3

Peak voxels at $p_{\text{corrected}} < .05$ for the whole-brain analysis of familiar correct temporal condition versus scrambled correct temporal condition. Peak voxel for each cluster is listed in bold in bold followed by other peaks within the same cluster.

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	
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	

Brain region					Cluster
x	y	z	t		
38	-17	-16	3.82		

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Table 4

Peak Voxels at $p_{\text{corrected}} < .05$ for the whole-brain analysis of scrambled correct temporal condition versus familiar correct temporal condition. Peak voxel for each cluster is listed in bold followed by other peaks within the same cluster.

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	