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Learning across experiences: an ERP study of memory integration.

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Abstract

This study investigated how individuals combine information learned across temporally separate events in order to make novel inferences through memory integration, utilising EEG to provide a novel investigation with high temporal resolution. Participants completed an associative inference task (Zeithamova & Preston, 2010) modified for EEG across three experiments, during which they learned stimulus pairs that shared a common item (AB/CB) along with control stimulus pairs (XY) in two encoding windows before being tested for their memory of these premise associations and, crucially, their ability to infer relationships between stimuli whose previous associated pairs shared a stimulus, but had not been viewed together (AC inference). Experiments 2 and 3 included novel auditory context manipulations to investigate the influence that novelty and familiarity has on the memory integration process when the context is or is not task-relevant. Despite previous memory integration research highlighting the significance of the neural activity differences in the time window where participants encode overlapping stimuli pairs (e.g. Backus et al., 2016; Zeithamova, Dominick & Preston, 2012), the current research found limited evidence of memory integration processes in the second encoding window. During the context manipulation experiments, no evidence of the encoding-retrieval (E-R) overlap effect was found for the context congruent ERPs. Implications of the findings and avenues for future research are discussed.

Keywords: memory integration, context reinstatement, episodic memory, EEG, inference, hippocampus.

Introduction

Utilising past experiences to inform behaviour in different situations is crucial to human life. The ability to draw information from past experiences and apply it to new situations allows individuals to adapt to an ever-changing environment by learning to navigate based on their surroundings (Schinazi, Nardi, Newcombe, Shipley & Epstein, 2013), become aware of irregularities that may signal upcoming danger (Schomaker & Meeter, 2015), and infer novel relationships between things they have not seen together (Shohamy & Wagner, 2008), granting the individual an understanding of the world that is greater than the sum of its parts.

This dynamic interaction between the reactivation and reconsolidation of past experiences with current experiences allows the brain to employ a variety of processes to best serve the current situation. One of these processes, memory integration, allows the individual to compare what is being experienced with past events that have shared context (landmarks, people, items), binding overlapping neural representations of the temporally separate events into a single, integrated memory trace. Neuroimaging research has identified key areas of the brain that interact to make this process possible- mainly the anterior hippocampus and the medial prefrontal cortex (mPFC)- through functional magnetic resonance imaging (fMRI) studies. However, although research has revealed the “where” of the process, fMRI studies cannot fully provide an answer to “why” the process happens, and it is particularly lacking in the “when” the process begins and ends.

The current study aimed to provide some insight into these questions through the analysis of behavioural and electrophysiological data. By adapting a modified memory integration paradigm (Backus, Schoffelen, Szabényi, Hanslmayr & Doeller, 2016) for electroencephalography (EEG), the current study was able to capitalise on the high temporal resolution of the brain data across 3 separate experiments to acutely measure at what time point over the course of the experiments that the memory integration process began, and how it developed over time. To address the question of why the integration process occurs, this base experiment was built upon by including context conditions that either increased or decreased the similarity between the two learning experiences, to investigate if novelty or familiarity between learning experiences resulted in an enhancement of the integration process, as measured by subsequent inference performance.

Memory Integration

Associative memory can refer to when two pieces of related information, such as a person and their name, are learned at the same time and remembered together (Palm, 1980), or to when two episodes that share overlapping elements are learned across two temporally separate experiences and integrated into a relational network of episodic memory (Schlichting & Preston, 2015). The latter of these two associative memories occurs through a process known as memory integration. This ability to recombine and link episodes with overlapping content allows us to make sense of the world through processes such as inferential reasoning (Shohamy & Wagner, 2008) and spatial navigation (Schinazi et al., 2013), which expand our knowledge base and influence current and future decision-making behaviour.

Theories of memory integration are built upon the premise that new experiences that share context with prior experiences interact with the previous memory traces in order to extract information from both, and form a new, overlapping memory trace. Research into memory has demonstrated that reactivated memory traces are susceptible to distortion and updating in new situations (McKenzie & Eichenbaum, 2011; Nadel, Hupbach, Gomez & Newman-Smith, 2012), whilst reactivating memory traces can influence how new episodes themselves are encoded (Gershman, Schapiro, Hupbach & Norman, 2013; Zeithmova, Dominick & Preston, 2012). This ability to influence both incoming memories and previously stored traces has been theorised to be due to relational memory networks, whereby memories are connected via shared content (Eichenbaum, 1999).

Functional magnetic resonance imaging (fMRI) studies have implicated areas of the anterior hippocampus and the medial prefrontal cortex (mPFC) as being key to the memory integration process in both animal lesion work and human studies (Bunsey & Eichenbaum, 1996; DeVito, Lykken, Kanter & Eichenbaum, 2010). The importance of these key nodes has been demonstrated by showing that damage in either leads to an impaired ability to combine information from separate episodes, despite memory for these episodes remaining intact (Bunsey & Eichenbaum, 1996).

However, is not completely clear as to when this process occurs, with respect to both purpose- it remains to be shown if these representations are stored primarily as separate memory traces in a relational memory network (Eichenbaum, 1999) or if related traces are bound upon encoding and stored as a single, integrated representation- and to the mechanistic timeline of the process once it has begun. One way to uncover this is to investigate brain wave data with high temporal resolution, such as EEG data, during tasks that require

individuals to reactivate and compare temporally separate experiences to gain new information from them.

Task-relevant memory reactivation

Memory integration is an inherently task-based process. Whilst it can occur entirely outside of the conscious experience (Mullen & Dymond, 2014; Shohamy & Wagner, 2008; Wimmer & Shohamy, 2012), the purpose of memory integration is to extract information from the memories of prior events and the current experience in order to assist with current tasks such as spatial navigation (Schinazi, Nardi, Newcombe, Shipley & Epstein, 2013), decision making (Wimmer & Shohamy, 2012), constructing new ideas (Schacter, Addis, Hassabis, Martin, Spreng & Szpunar, 2012), and inferring novel relationships (Zeithamova, Dominick & Preston, 2012).

One area of the brain that has been linked to this behaviour-based approach to memory is the mPFC. It's been suggested that the mPFC has the ability to bias memory reactivation towards memories that are currently task-relevant, thus influencing the memory integration process (Kroes & Fernández, 2012; Preston & Eichenbaum, 2013). The mPFC is said to use mnemonic content in order to form mental models that guide behaviour (St. Jacques, Olm, Schacter, 2013; Roy, Shohamy & Wagner, 2012), including selecting appropriate responses and relevant behaviours in situations (Kroes & Fernández, 2012).

When the mPFC has selected the task-relevant memories for reactivation, the hippocampus may use pattern completion and pattern separation mechanisms to integrate the new experience into the stored memory trace, storing the new trace as an overlapping representation in the associative memory network. This would then allow for memory models to be updated through the hippocampus as needed (Van Kesteren, Ruiter & Fernández, 2012). This theory suggests that even if the mPFC does have an influence over which memories are reactivated, it still relies on the hippocampus to reactivate and integrate the prior experience with the current situation. However, it is under some debate as to why the hippocampus would trigger integration to begin with- whether it is due to the novelty of the new experience situation, which calls for a search for an appropriate response, or whether familiarity with past experiences is the key to integrating memories.

Novelty, similarity, and the hippocampus

As all memories are theorised to be stored in a relational memory network, the brain has a vast pool of experiences to compare when faced with new situations. The relational

memory network is said to be supported by the hippocampus, which allows for the extraction of information from previously stored memories to make it possible for the brain to perform behaviours such as making novel inferences between the current experience and a past experience (Zeithamova, Schlichting & Preston, 2012), and creating new, overlapping representations in the brain (McKenzie, Frank, Kinsky, Porter, Rivière & Eichenbaum, 2014).

Some studies suggest that it is the irregularities of the new experience compared to the prior that leads to memory integration. Sensitivity to novel stimuli and situations allows for an individual to adapt to and learn irregularities in an ever-changing environment (Schomaker & Meeter, 2015), and novelty has been shown to enhance attention (Schomaker & Meeter, 2014), ultimately leading to an improvement in the memory potentiation for novelty (Uncapher & Wagner, 2009; Wimmer & Shohamy, 2012).

When a new experience that shares content with a previously stored memory is experienced, pattern completion mechanisms in the hippocampus reactivate the previous memory (Preston & Eichenbaum, 2013), and hippocampal areas CA₁ and CA₃ have been implicated as being the drivers for this process. Area CA₁ is thought to act as a novelty detector by comparing what is being experienced in the current environment with the expectations of how the experience should progress, based from the related prior experience stored in memory, with recent fMRI work relating a behavioural measure of memory integration with the activation of area CA₁ during encoding of experiences that share content with previous experiences (Schlichting, Zeithamova, & Preston, 2014). This suggests that area CA₁, activated through novelty experienced during an event, is the trigger for the memory integration process. When a violation of the memory-based predictions of the current experience occurs, it acts to increase plasticity in hippocampal area CA₃, which is crucial to both initial pattern completion, and the formation of new memory traces through pattern separation, which are then stored as overlapping representations (Larkin, Lykken, Tye, Wickelgren & Frank, 2014; Rolls, 2013).

However, contrasting research has suggested that familiarity during an experience is critical for associative memory, with repetitive familiar items showing the most mnemonic benefit (Badham & Maylor, 2015; Craik & Tulving, 1975). Compared to novelty, familiarity was shown to evoke a mnemonic-processing bias that facilitated associative memory relying on pattern completion (Patil & Duncan, 2018). This effect lasted for a few seconds, as a result of a shift in cholinergic input that encouraged associative memory. Similarly, research into the mnemonic benefits of familiarity and novelty recently demonstrated that, when the novelty of stimuli is based on life-experience rather than the experimental context, it may not

result in mnemonic benefits of memory potentiation over stimuli that are conceptually familiar (Reggev, Sharoni, & Maril, 2018).

Clearly, the relationship between novelty, familiarity, and the mechanisms leading to successful memory for and integration of temporally separate events is still to be fully clarified. One way that researchers can experimentally influence the familiarity or novelty of a situation to investigate the effect this has on the memory integration process is through the manipulation of the background context during learning.

Context reinstatement

Context is an extremely important factor in episodic memory. When forming memories of events, people encode not only information about the items or events occurring, but also information about the context in which they occur (Howard & Kahana, 2002; Lehman & Malmberg, 2013). This means that contextual information present at encoding can be used as a retrieval cue to the encoding event through reinstatement. According to the encoding specificity principle, when the encoding context is reinstated at retrieval the overlap of the encoding and retrieval (E-R) conditions will lead to a significant increase in memory performance (Tulving & Thomson, 1973). This idea has been widely supported by empirical research (for a review, see; Smith & Vela, 2001). Recent research has expanded on these findings, demonstrating that the improvement in performance for retrieving a specific memory is only experienced if the reinstated context is diagnostic of the memory that is being searched for (Bramão & Johansson, 2017; Nairne, 2002, 2006; Raaijmakers & Shiffrin, 1981), the more diagnostic the retrieval cues being are, the more likely a related target memory will be found due to a higher level of accessibility.

Stark, Reagh, Yassa & Stark (2017) recently posited 3 tenets for operationalising context in the experimental setting: 1) contexts must be stable over time along an experimental dimension; 2) contexts must be moderately complex in nature and their representations must be modifiable or adaptable; and 3) contexts must have behavioural relevance so that their role can be measured. This operationalisation of context fits both with traditional studies, that inferred that the current spatiotemporal context was of key importance (Goddon & Baddeley, 1975), and recent studies investigating the benefits of reinstating internal state contexts (Klein, Shiffrin & Criss, 2007), such as mood (Lewis & Critchley, 2003; Xie & Zhang, 2018), physiology (Miles & Hardman, 1998), and the language being used (Marian & Neisser, 2000), all of which resulted in significant improvements in memory performance. It has even been shown that mentally reconstructing a context can have

comparable results to physically reinstating the context in subsequent memory performance (Bramão, Karlsson & Johansson, 2017), further eluding to how robust the E-R overlap effect is.

Up until now, there have been a limited amount of studies investigating context reinstatement within a memory integration paradigm, and the research that is available focuses primarily on the visual modality of context reinstatement, such as reinstating a background scene behind a to-be-remembered word. This leaves room to investigate different modalities, and how they can influence the memory integration processes, and subsequent inference performance.

Background music as a context

Although the effect that background music has on learning and memory has been investigated in a variety of different paradigms and situations in previous literature, the results are inconsistent. There is some evidence that background music improves memory (de Groot, 2006; Eschrich, Münte & Altenmüller, 2008; Nguyen & Grahm, 2017; Richards, Fassbender, Bilgin, & Thompson, 2008), yet other research has found that there is no effect between music and non-music groups (Hirokawa, 2004; Jäncke & Sandmann, 2010; Kou, McClland & Furnham, 2018; Miller & Schyb, 1989; Nguyen & Grahm, 2017), or that music worsens memory (Hallam, Price, & Katsarou, 2002; Iwanaga & Ito, 2002; Reaves, Graham, Grahm, Rabannifard, & Duarte, 2015).

One potential reason for the discrepancies between the results could be that participants have differing experiences to working with background noise, and thus some are more suited- or at least have adapted- to working with sound in the background than others. In their recent paper, Kou et al. (2018) found no main effect of background sound conditions on performance between music, office noise and silence conditions. One explanation the authors provide for this is that their sample of Chinese students are likely used to working in noisy environments when working on complex cognitive problems due to larger class sizes of 50-80 students per classroom. This suggests that the participants could inhibit the non-task-relevant music and noise stimuli in the background, allowing for comparable memory performance across the conditions- a finding that supports previous research (Reaves, Graham, Grahm, Rabbanifard & Duarte, 2015).

Whilst the effect of background music on the first type of associative memory has been previously researched using paired-associates learning tasks- where subjects learn pairs of items with background music present at learning and at test (Nguyen & Grahm, 2017;

Reaves et al., 2015)- there has not, at the time of writing, been any research conducted that investigates the effect of background music in a memory integration paradigm.

Associative inference task

A standard paradigm for studying the memory integration process is through an associative inference task (Zeithamova & Preston, 2010). As shown in Figure 1A, in this paradigm participants intentionally learn item pair associations (AB) and overlapping associations (CB) that share a common stimulus. Once all of the stimuli pairs have been encoded, participants are then tested through the crucial inference test, and a test of the direct associations (Figure 1B).

The participant's ability to successfully infer the relationship between item A and item C, that share a common stimulus in their respective pairs but are never shown together, is seen as a reflection of the memory traces for the two learned associations having been successfully integrated. The direct association test acts as a validity measure of integration by ensuring that participants have successfully encoded the necessary associations required for the integration to be due to memory processes, so that the inference can be shown to be made based from the combination of previously learned information rather than either guesswork or chance.

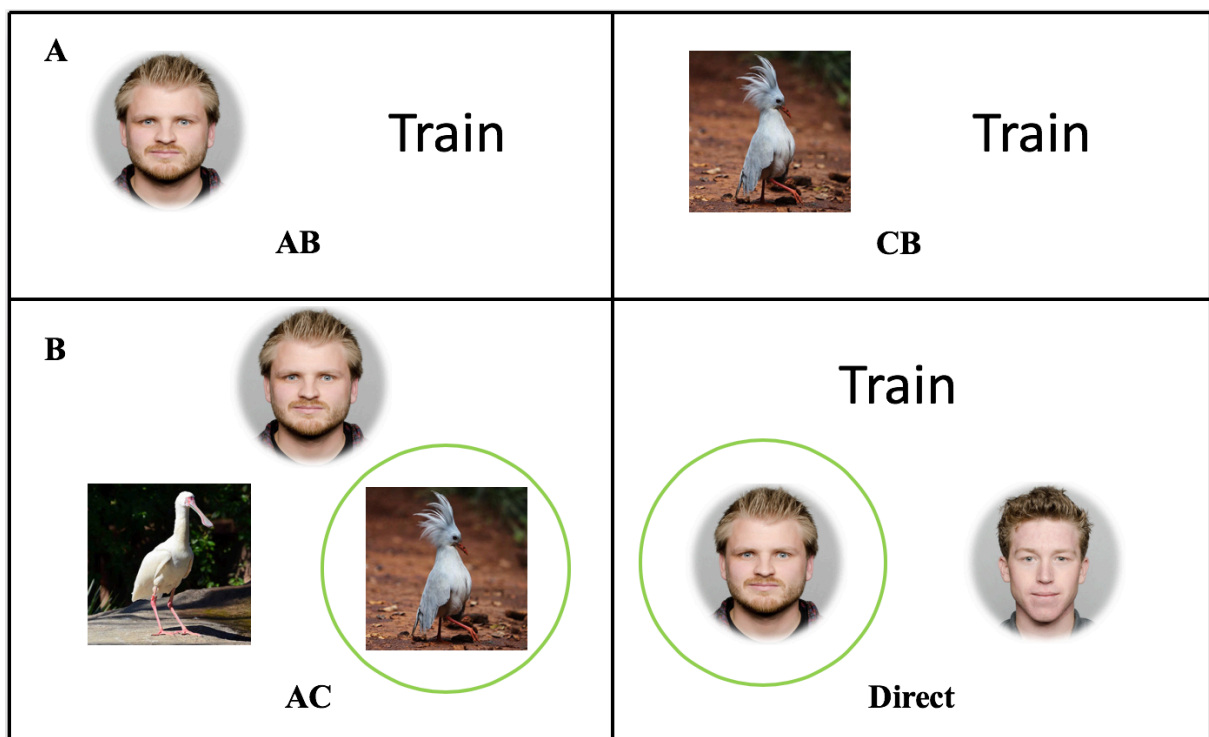


Figure 1: A standard associative memory task. *A*: Participants learn stimulus associations in the first encoding round (AB) and overlapping associations in a temporally separate second encoding round (CB). *B*: After the two encoding rounds, participants are tested for directly learned associations and, crucially, the inferred associations (AC). Participants are probed with a stimulus item (A/B), and have to choose the associated stimulus from the target item and a distractor.

One modification of this test format is to include a control condition in which participants just learn a single association, XY, over the two encoding windows (Backus, Schoffelen, Szabényi, Hanslmayr & Doeller, 2016). This allows a direct comparison in the second encoding round between the memory processes involved in storing an association pair that shares content with a previously learned encoding pair (AB/CB) and those involved in creating a new association pair with an item that has not been previously associated with another item but is equally familiar (Y/XY). The ERP exhibited by the control condition in this situation should reflect the pattern completion element of retrieving the memory for the Y stimulus. As such, any differences between the CB learning and the XY ERP could reflect the additional memory processes required for the storage of overlapping representations, and memory integration.

EEG memory effects

As the B/Y stimuli presented in the second encoding round should act as a cue for participants to recognise the stimulus from a previous experience (i.e. the first encoding round) and retrieve the memory, it was expected that the ERP correlates observed in this window would be similar of those of a cued-recall test. These ERPs are typically characterised by positive slow waves, and a widespread topographical distribution (Allan & Rugg, 1997, 1998).

Recognition ERPs have been described in the literature across three main time windows following cue presentation. First, an early (~300-500ms) frontal old/new ERP effect is said to reflect the familiarity aspect of recognition, whilst a later (~500-700ms) left parietal old/new effect is reflective of the recollection of a specific episode (Rugg & Curran, 2007), and a late (~800-1200ms) right frontal old/new ERP effect has been associated with post-retrieval operations (Wilding & Ranganath, 2011). Whilst familiarity is more of a reflection of memory strength, recollection involves the retrieval of contextual information in order to be sure that the target trace that is searched for is correct. As such, it would be expected that the retrieval involved in the memory integration process would be reflected by late positive-going ERPs.

A recent study of context reinstatement demonstrated that E-R overlap also led to more positive slow waves, which was theorised to be due to increased familiarity for the stimulus combination to be remembered due to the congruent learning conditions, and improved recollection for the specific stimulus target pairs (Bramão, Karlsson & Johansson,

2017). As such, including E-R overlap context conditions into the memory integration paradigm could lead to an increase in familiarity in the encoding rounds that, as mentioned before, may lead to a bias towards associative learning that would be reflected both by an increase in subsequent inference performance, and more positive-going ERPs for memory integration in the E-R overlap condition compared to the non-overlap condition.

Current study

The current study consisted of three experiments and had three main hypotheses. Hypothesis 1 predicted that there would be a significant difference in neural activity between the experimental condition, CB learning, and the control condition, XY learning, in the second encoding round. This hypothesis applied to all three experiments.

This hypothesis aims to uncover how the pattern completion and pattern separation mechanisms function as an integral part of the memory integration process. By including a control condition within each block as described above, this study is able to differentiate normal associative learning behaviour from behaviour that is unique to the memory integration process. Any differences discovered between CB learning and XY learning would be a novel addition to the memory integration literature, as they would reflect the additional memory processes required for successful integration to occur that have been found in previous fMRI studies (e.g. Schlichting, Zeithamova, & Preston, 2014) and, crucially, would provide a highly acute timeline for the progression of the neural activity associated with the memory integration process.

Hypothesis 2 predicted that there would be a significant difference in neural activity during the second encoding round between CB pairs that were integrated correctly at the test phase and CB pairs that were not integrated at the test phase, as reflected by the subsequent inference performance. Differences between the pairs here would reflect the subsequent inference effect expected from successful integration, and magnitude of these EEG correlates differences would be expected to correlate positively with subsequent inference performance at the test phase. This hypothesis was investigated across all of the experiments included in this study.

Hypothesis 3 predicted that manipulating similarity through the overlap of the music context for the encoding and retrieval (E-R) stages during the encoding rounds of the integration paradigm would lead to significant differences in the EEG correlates during the second encoding round and subsequent inference performance. This hypothesis was tested across experiments 2 and 3.

To investigate this hypothesis, experiments 2 and 3 draw from context reinstatement literature, manipulating how familiar the second encoding window is to the first through the use of congruent or incongruent contexts presented across the first and second encoding phases. It could be that the increased novelty of being presented with an item that is a part of a previous pair in a different context to when it was originally encoded may lead to an increase in activity in area CA₁, triggering integration and leading to enhanced inference performance. However, the familiarity of a previously experienced context may allow the brain greater accessibility to the items that were learned previously in the same context, leading to enhanced associative memory, resulting in enhanced inference performance. Both experiments incorporate background music as the context material, to investigate if stimuli presented in a different modality than that of the task at hand will have a significant impact on the memory processes being studied.

These experiments also investigated if involving an attentional task that made the background context music task-relevant led to significant EEG correlate and behavioural differences compared to when the context was not task relevant. In experiment 2, participants completed a judgement task during the encoding phases that focused on the association being made between the stimuli, to promote deep encoding. In experiment 3, the participants instead had to attend to and keep count of a number of tones superimposed into the background context music during the encoding rounds, thus making the background context task-relevant. It was predicted that the context congruency condition would have a greater effect in experiment 3 compared to experiment 2 as a higher level of attention has been linked to an increase in the likelihood that associated items encoded at the same time will be retrieved (Le Pelley, Mitchell, Beesley, George & Wills, 2016), and so the attended-to context should result in a higher likelihood of the primary encoding being retrieved during the secondary encoding round.

The ERPs for memory retrieval and memory integration for all experiments were investigated during the second encoding round, following the presentation of the B/Y stimulus. As this time windows had an element of retrieval of contextual information associated with them, the ERPs were expected to be more positive-going late in the epoch (500msec onwards) as is often the case in recollection literature of the late left parietal old/new effect (Wilding & Ranganath, 2011). Further, for experiments 2 and 3, ERPs in the E-R overlap condition were predicted to have a more positive-going ERP, starting from an early onset (~300ms) reflecting an increase in familiarity initially, and continuing throughout the

epoch, representing an increase in memory accessibility for the target memories, and improved recollection.

Method

Participants

Experiment 1 had a sample of 26 participants (16 female), with a mean age of 24. Experiment 2 had a sample of 8 participants (5 female), with a mean age of 26. Experiment 3 had a sample of 18 participants (11 female), with a mean age of 23. Participants were obtained via convenience sampling and opportunity sampling. Participants all completed experiment 1, and either one of the two subsequent experiments. Participants were rewarded with a movie ticket worth 50 Swedish kronor upon completion of the experiments.

Stimulus materials

This study used 189 colour images of faces (95 female, 94 male) taken from the Oslo Face Database, along with 189 colour images of different birds. All images were cropped and rescaled to 500 by 500 pixels. 360 nouns were used as word stimuli, matched for length and frequency in the English language, which were obtained from the Toronto Word Pool. Stimuli material were split into triads or dyads. Each dyad (XY) consisted of a word stimulus (X) and one picture stimulus (Y). Half of the dyads had an image of a face as the picture, whilst the other dyads had an image of a bird. The triads (ABC) consisted of one face image, one bird image and a word stimulus. The triads were counterbalanced so that half of the stimulus triads had a face image for the A stimulus and a bird for the C stimulus, and half of the triads had the reverse. The B stimulus was a word in all the triads.

The stimuli were split across the two experiments. Experiment 1 used 63 face images (32 female, 31 males) and 63 bird images, whilst experiment 2 (later experiment 3) used the remaining 126 face images (63 female, 63 male). The word list was split evenly in two, and each experiment drew from one list. No stimuli appeared in both experiments.

Stimuli used for the context manipulation in experiments 2 and 3 were thirty instrumental music clips (15 of classical piano, 15 of instrumental guitar), each cut to run for exactly 101 seconds. The sound files were compressed and equalised to maintain sound quality and volume consistency. Each track was manually altered from a stereo to a mono track, to allow smoother loading and presentation in e-Prime. For experiment 3, tones of 1000Hz, each lasting .05s, were inserted pseudo-randomly into each track, so that each clip

had a different number (mean: 8, range: 4-14) of tones spaced differently across the whole of the clip. All edits to the sound stimuli were made using Audacity.

Procedure

Participants were first given a brief about what the general aims of the experiment were and were informed of the task they would be completing. All participants filled out an informed consent form before any of the experiment began. The experimenter then began fitting the EEG cap to the participant. Once the cap had been fitted, participants were seated in a sound-proof, and electrical interference-free room where the experiment would be conducted. Participants went through the instructions, that explained the procedure and the tasks required of them and were given the opportunity to ask further questions before they began the experiment.

The experimental procedure was presented and controlled by a custom program created with E-Prime (2.0) (Psychology Software Tools, 2002). Participants first completed 7 blocks of the procedure without the context manipulation, followed by 14 blocks involving the manipulation. Each block consisted of a primary encoding phase (AB encoding), a secondary encoding phase (CB encoding), a counting task, an inference test, and direct memory tests. The inference test was always presented before the direct memory test to avoid further learning that may help form the associations.

Participants were given a long break between experiment 1 and experiment 2 or 3. They could take additional breaks if needed between any of the other blocks. Once all the blocks had been completed, participants were debriefed on the aims of the study to a greater degree and were given the opportunity to ask any further questions to the experimenter before they left.

Experiment 1. Figure 2A illustrates the structure of the encoding rounds. Participants were presented with the to-be-remembered items of a pair serially, across two encoding windows. Participants were instructed to rate how easily they could make and remember the association of the presented pair after the presentation by pressing the corresponding keys (1 = Easy, 2 = Medium, 3 = Hard) to encourage deep encoding, and further ensure that participants had attended to both items presented. X items presented during primary encoding had a blank white square presented in place of the image stimulus. For the counting task, participants were presented with a random, 3-digit number on screen, and were instructed to

count backwards aloud in increments of 7. This was to clear any information in working memory before the start of the memory tests.

Figure 2B illustrates the structure of the test phase. Participants were cued with a probe stimulus (item C for the crucial AC pairs, and item B/Y for the AB/CB/XY pairs) and were tasked with picking the stimulus associated with it. A fixation point was presented in the centre of the screen for 1500ms. The cue then replaced it and was presented for 500ms. This was followed by a 2000ms blank screen, allowing participants time to retrieve the associated image. Participants were then presented with the target item and a distractor and were asked to make a binary selection of which item was associated (press “1” for an item presented on the left, press “2” for an item presented on the right). The distractor images were randomly selected from the XY pairs, with the distractors belonging to the same stimulus category as the target item (i.e. a face distractor with a face target). Participants were allowed as much time as it required for them to make their selection. An ITI was presented between each trial, with a random jitter (500-750ms).

The participants first completed the inference test, in which the probe was the C item from the ABC triad and were tasked with selecting the correct A stimulus associated with the probe. All of the possible AC associations were tested for and were presented in a random order. The distractors were pseudo-randomly paired with the targets, so that the two choices belonged to the same stimulus category. They then completed the direct tests in which the stimulus items B/Y were the probes, and the task was to retrieve the stimulus item associated with it (AB, CB or XY). During the direct tests, all possible pairs were tested (AB, CB, & XY), and these were randomly presented to the participant. The distractors were pseudo-randomly paired with the targets, so that the two choices belonged to the same stimulus category.

Experiment 2. Experiment 2 followed the same experimental structure as experiment 1, with context conditions added during the encoding rounds. During the context trials, a melody played over the presentation of the primary encoding pairs (Fig. 2C). A context familiarity period was presented either directly before or directly after the primary encoding phase, in which participants did not complete any task but were familiarised with the melody to be used as the incongruent context during the secondary encoding phase. The secondary encoding phase was split in two, so that half of the CB/XY pairs were presented with a congruent melody playing in the background (Fig. 2D), and half were presented with the incongruent context playing (Fig. 2E). The order of the presentation of the primary encoding blocks and the context familiarity block, and of the order of the presentation of the

incongruent secondary encoding pairs and the congruent secondary encoding pairs, was counterbalanced across participants. The counting task, and both tests were completed in the absence of either of the encoding contexts (i.e. in silence).

Experiment 3. Experiment 3 followed the same structure as experiment 2, but with a tone counting task included instead, to help promote the association of the stimuli with the background context. During the encoding rounds, a number of tones were inserted into the melodies acting as the learning contexts, and participants had to keep a track of how many sounded across the encoding round. Participants reported the number of tones they had heard by keying in the number at the end of the encoding rounds.

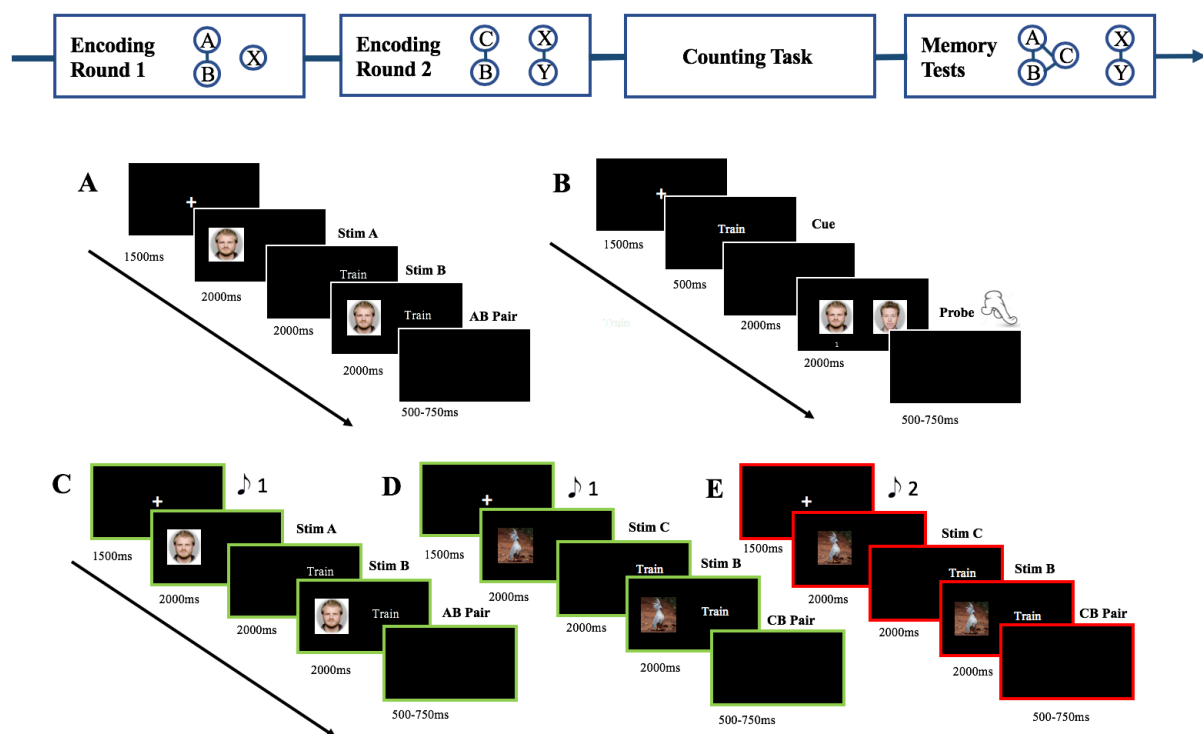


Figure 2: Experimental procedure and trial structure of the memory integration task

Top: across 7 blocks for experiment 1 and 14 blocks for experiment 2, participants learned dyad (YX) and triad (ABC) associations between colour images of faces and birds, and concrete word stimuli. Bottom: *A*: The encoding rounds of experiment 1 saw each item of a stimulus pair presented serially for 2000ms each, followed by a simultaneous presentation of the pair for 2000ms. Participants were presented with the AB pairs during the first encoding round, and CB pairs during the second encoding round. *B*: At the test phase participants were presented with a cue (item A for the inference test, items B/Y for the direct associations tests) for 500ms. They were given 2000ms to retrieve the associated image before being presented with a forced choice between the target image and a distractor. *C*: For the first encoding round of experiments 2 and 3, the stimuli were presented with a music context playing throughout the window. *D*: In the congruent context condition, the music from the first encoding round was played whilst participants completed the second encoding round. *E*: In the incongruent context condition, a second music context, that had been previously familiarised with the participant, was played whilst participants completed the second encoding round. The test phases for experiments 2 and 3 were completed as in experiment 1 (B), with the absence of background music.

EEG Recording

The electroencephalogram (EEG) was recorded continuously using a Neuroscan (Compumedics, El Paso, TX, USA) NuAmps amplifier (1000hz sampling rate; left mastoid reference) from 62 Ag/AgCl scalp electrodes mounted in an elastic cap. The montage included eight midline electrode sites (FPz, Fz, FCz, Cz, CPz, Pz, POz, and Oz) and 28 sites over each hemisphere (FP1/FP2, AF3/AF4, AF7/AF8, F1/F2, F3/F4, F5/F6, FT7/FT8, FT9/FT10, FC1/FC2, FC3/FC4, FC5/FC6, C1/C2, C3/C4, C5/C6, T7/T8, CP1/CP2, CP3/CP4, CP5/CP6, TP7/TP8, TP9/TP10, P1/P2, P3/P4, P5/P6, P7/P8, PO3/PO4, PO7/PO8, and O1/O2). Additional electrodes were used as ground (AFz), reference sites, and for recording the electrooculogram (EOG). The EOG electrode was placed below the left eye.

Behavioural Data Analysis

Experiment 1. Cued-recall accuracy was calculated for each participant as the percentage of correct responses for each condition. One sample t-tests were run to investigate if performance was above chance for each of the memory tests (AC/AB/CB/XY). Additionally, an ANOVA was run between the direct association pairs to check for significant differences between performance.

Experiments 2 and 3. Cued-recall accuracy was calculated for each participant as the percentage of correct responses for each test type in each of the congruency conditions. To decide how to conduct the analysis of the behavioural data between the two experiments that utilised context with slightly different methodologies, a three-way ANOVA with the factors experiment number (2 vs 3), congruency condition (E-R overlap vs non-overlap), and memory type (AB recall, CB recall, XY recall, and AC inference) was performed on the cued-recall accuracy. The analysis revealed that no effect involving the factor experiment number. As such, for the remainder of the behavioural analysis, the two data sets were concatenated and treated as one continuous data set.

As before, for each of the context conditions, one sample t-tests were run to investigate each of the memory test performances against chance. Next, two-way ANOVAs with the factors memory test type and context condition was performed on the cued-recall accuracy both for all of the stimuli pairs (i.e. including AC inference), and just for the direct associations.

EEG Data Analysis.

The EEG data were analysed using FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). Offline, the EEG data were high-pass filtered at .1Hz, downsampled to 500Hz,

transformed to a linked-mastoid reference and a baseline correction of 200ms was applied based on the whole trial. The continuously recorded data were divided into epochs of 6 seconds, ranging from 1000ms before stimulus onset to 5000ms after onset. Trials were inspected manually, and those containing artefacts not related to blinks and horizontal eye movements were removed. Independent component analysis was computed, and components representing oculomotor artefacts (such as blinks) that could be clearly distinguished from the EEG were removed. If any channels were bad, these were interpolated. The data were physically examined following this, and trials that contained residual artefacts were removed. Two participants were removed from all experimental analyses due to an insufficient number of trials remaining following this process, and one participant was removed from experiment 3, having not finished the entire procedure. This left data for 25 participants for the final analysis of experiment 1, 8 participants for experiment 2, and 16 participants for experiment 3.

For the second encoding round an average of 38 CB trials (range 29-42) and 38 XY trials (range 28-42) remained for the final analysis of experiment 1. An average of 34 CB trials (congruent= 35 trials, range 25-43, incongruent= 34 trials, range 23-41) and 34 XY trials (congruent= 34, range 28-38, incongruent =34, range 27-42) remained for the final analysis of experiment 2. An average of 35 CB trials (congruent =35, range 21-42, incongruent =35, range 22-41) and 34 XY trials (congruent = 34, range 23-42, incongruent =34, range 21-42) were remained for the final analysis of experiment 3.

Experiment 1. To investigate the neurological differences between the mechanisms for encoding a new associative pair of stimuli and the encoding of a pair of stimuli to be integrated into a previous association, the analysis focused on the second encoding round of the study. It looked at the contrast between the reactions to the onset of the B item, which had become part of a related association in the first encoding phase, and the Y item, which had been encoded alone in the first encoding phase. The epoch to be investigated began at the onset of the stimulus and continued for 2 seconds following onset. The data was investigated across three separate time windows, based on a visual inspection of the ERP: 1) 250-500msec, 2) 500-800msec, and 3) 800-1500msec. The data was investigated across nine distinct electrode regions, with scalp position (frontal, central, and posterior) and hemisphere (left, central, right) as factors included in the analyses.

For each time window, a three-way ANOVA with the factors stimuli pair type (CB vs XY), scalp position, and hemisphere (both calculated based on the amplitudes of electrodes:

F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4) were performed. Significant interaction effects involving the factor pair type were analysed further using a simple main effect analysis, whilst main effects of pair type that occurred in the absence of interaction effects analysed through one-way ANOVAs. Before the analyses were conducted, the data were checked to make sure that they met all assumptions, including the levels of data, significant outliers, dependant variable distribution, and tests of sphericity.

Finally, to see if the amplitude differences in this encoding round had a functional effect on inference performance, two analyses were performed. First, the mnemonic benefit was calculated by subtracting each participant's XY pattern completion performance from their AC inference performance and was correlated with any significant EEG amplitude difference of the two stimuli pair types. Second, to test the subsequent inference effect of learning at this stage, CB pairs that were subsequently inferred correctly were contrasted against CB pairs that were not inferred correctly at test, and this EEG difference was correlated with the mnemonic performance in the same manner as described above. For this analysis, a subset of participants who had missed a minimum of 15 inference trials across experiment 1 was created (N=6).

Experiments 2 and 3. To build on the results of experiment 1, the analysis for the context experiments looked into the second encoding phase round. For experiments 2 and 3, along with the factors mentioned above, this analysis also investigated the effects of the E-R overlap during learning, and how this was represented in the brain wave data. Once again, the epoch began at the onset of the B/Y item on screen and continued for 2 seconds. The data were investigated across the same time windows and the scalp and hemisphere locations of the electrodes of interest remained consistent with the previous analyses.

First, to decide how to proceed with the analysis of the two context experiments with slightly different distractor tasks, a five-way ANOVA with experiment (2 vs 3), stimulus pair type (CB vs XY), context condition (E-R overlap vs non-overlap), scalp position, and hemisphere was calculated for each time window. In this analysis, the experiment factor did not have a significant main effect or any significant interaction effects across any of the time windows, showing no significant differences between the two sets of data (all $p > .73$). As such, the data was concatenated for the remainder of the analysis.

A three-way ANOVA with stimulus pair type (CB vs XY), scalp position, and hemisphere as factors was performed for context condition, in each time window. Significant interaction effects involving the factor pair type were analysed further using a simple main

effect analysis, whilst main effects that were significant in the absence of an interaction effect were analysed through one-way ANOVAs.

Next, to elucidate if there were any differences between the EEG correlates of CB learning that was correctly inferred into an AC representation at test and a CB pair that was not inferred into an AC representation at test, a subset of 15 subjects that had reached the threshold of a minimum of 15 inference trials missed was created and their data was analysed across the predefined time windows. For the trials to be valid, the participant had to have correctly recalled the CB pair at test in both conditions, thus ensuring that learning had taken place over this phase, and that any differences were present as a result of different mechanisms. One-way ANOVAs with subsequent inference performance (AC hit vs AC miss) as the factor were conducted for each of the time windows.

Results

Experiment 1

Behavioural results. On average, participants correctly inferred 77% of the AC pairs, and remembered an average of 91.9% of the AB pairs, 92.8% of the CB pairs, and 88.6% of the XY pairs. The analysis revealed that all of these scores were significantly above chance (all $p < .001$). The analysis showed no significant differences between direct association pairs ($p > .20$).

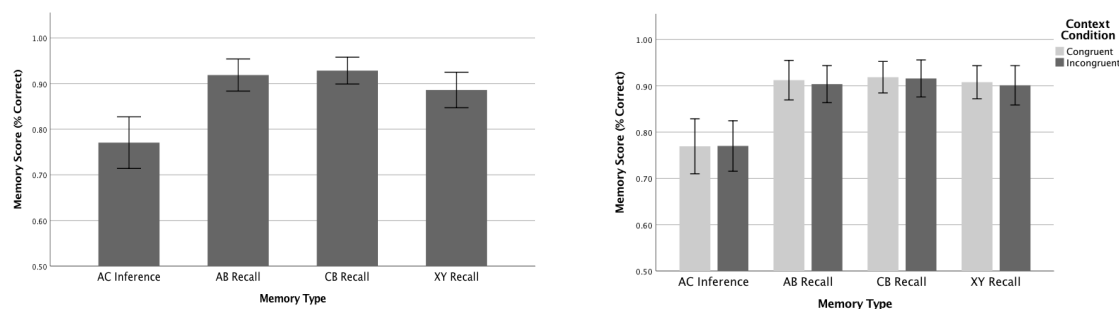


Figure 2: Behavioural performance. Across the different association memory types, performance for directly learned association pairs was better than for inferred pairs. This was true for both experiment 1 (left), and for each context condition of the concatenated data of experiments 2 and 3 (right).

Electrophysiological results. Figure 3A shows that CB learning was associated with slightly more negative-going amplitudes when compared with the pattern completion of the XY learning. The difference seemed to begin at around 250msec after stimulus onset and continued throughout the epoch. As opposed to familiarity or recognition components often seen in memory-based ERP studies, the ERP here is characterised by slow waves with

widespread topographical distributions, which is typical of the results observed in cued-recall tests (Wilding & Raganath, 2011). In the late window, there appears to be a tendency for a right-lateralised negative-going slow wave.

The three-way analysis revealed no significant interaction effects or main effects of the factor stimulus pair (all $p > .283$) across the time windows, signifying that the amplitude differences between the conditions were negligible. As such, no further analyses were performed across this factor.

The analysis of the subsequent inference effect (Fig 4A) revealed no significant main effects or interaction effects of the factor subsequent performance (hit vs miss). No further analyses were performed on this data.

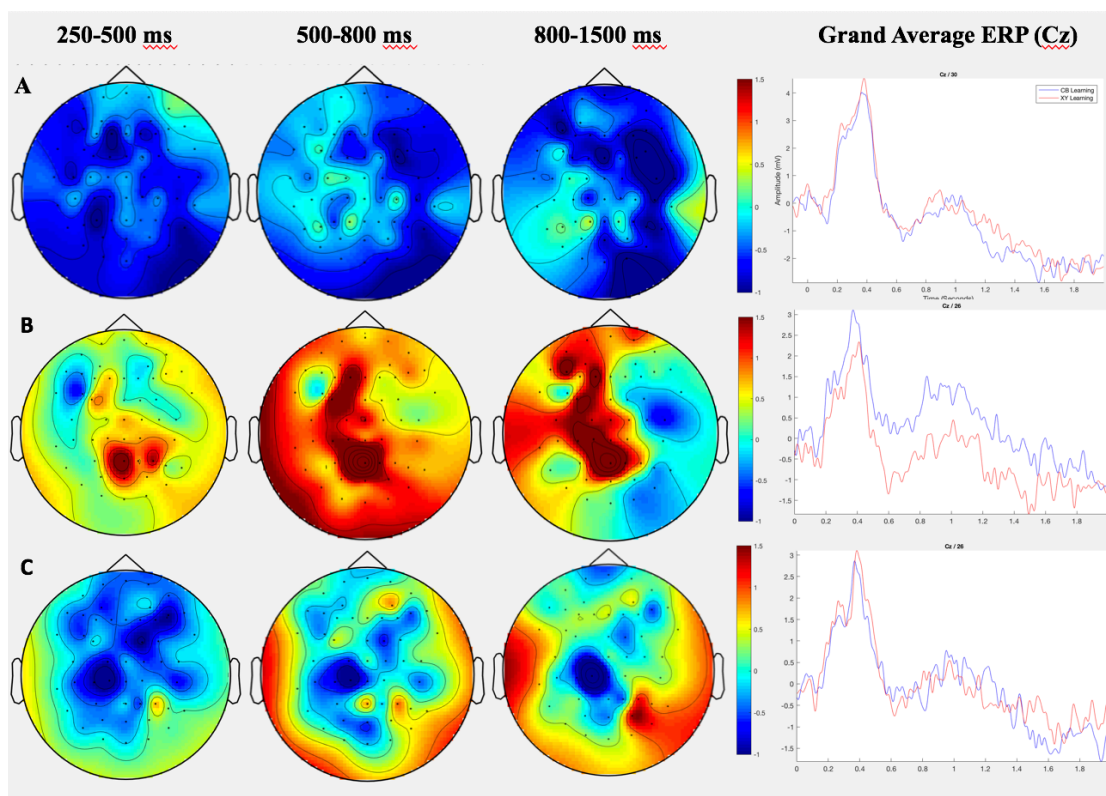


Figure 3: Topographic distributions and average waveforms from a representative electrode (Cz) of the memory recall and memory integration effects exhibited in the second encoding round of: A) experiment 1; B) the congruent condition of the concatenated experiments 2 and 3; and C) the incongruent condition of the concatenated experiments 2 and 3. The distributions were calculated as the difference between CB learning and XY learning.

Experiments 2 and 3

Behavioural results. In the congruent context condition, participants successfully inferred 77.92% of AC pairs, and remembered 91.7% of AB pairs, 92.6% of CB pairs, and 91.5% of XY pairs. In the incongruent context condition, participants successfully inferred 78% of AC pairs, and remembered 90.8% of AB pairs, 92.1% of CB pairs, and 90.8% of XY pairs. The analysis revealed that all of these scores were above chance (all $p < .001$). The two-way ANOVA revealed no effects of the factor context condition. The two-way ANOVA with

factors direct association pairs and congruency condition revealed no significant effects of association pair, signifying that there were no significant differences between performance.

Electrophysiological Results. Figure 3B shows that in the E-R overlap condition, CB learning was characterised by more positive-going amplitudes throughout the epoch compared to XY learning. The topographical plots show that these positive amplitudes began based at the central-posterior region in the 250-500msec window and become lateralised on the left hemisphere as the epoch progressed. Figure 3C shows that, in the non-overlap condition, the amplitudes between the CB and XY conditions were more similar, particularly in the late time window of the epoch, with the CB learning exhibiting more negative-going amplitudes at the initial stages of the epoch. The topographical plots show that, whilst the negative amplitudes were widespread across the 250-500msec time window, they became more centralised as the epoch progressed.

In the context congruent condition, the analysis revealed a significant main effect of stimulus type across the 500-800ms time window, with the correlates of the CB pairs exhibiting significantly more positive-going amplitudes [$F(1,414) = 5.801, p = 0.16$]. To clarify the functional relationship between the EEG differences exhibited in this time window, and the mnemonic benefit to subsequent inference, a bivariate correlation was performed on the data; it was not significant ($p > .80$). There were no effects interaction or main effects of the factor stimulus pairs across the 250-500ms and 800-1500ms time windows.

To investigate the subsequent inference effect in the second encoding round, a subset of participants who hit the threshold for minimum number of missed trials had their data analysed across the key fact, subsequent inference performance. The analysis revealed no effects across this factor (Figure 5B). As such, no additional analyses were performed.

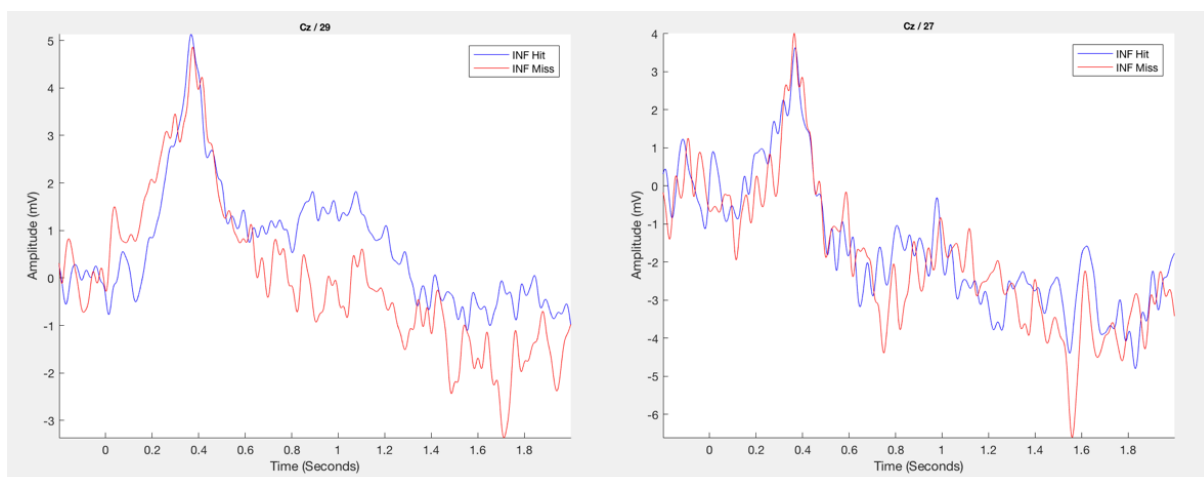


Figure 5: Representative ERPs of the subsequent memory effect (SIE) subsets of experiment 1 (A) and the concatenated data of experiments 2 and 3 (B).

Discussion

This study extended the previous memory integration literature by investigating the temporal progression of the mechanisms involved with the memory integration process by modifying a standard associative inference task (Zeithamova & Preston, 2010) to be used with EEG. Following this, it investigated if memory integration could be enhanced or hindered, as reflected by subsequent inference performance, through the manipulation of the context in which two temporally separate events were experienced. Experiments 1, 2 and 3 provide some of the first accounts of the memory integration process that are high in temporal resolution, whilst experiments 2 and 3 provide the first accounts of the effects of context reinstatement on the memory integration process, and the first use of background music during encoding during a memory integration procedure.

Until now, studies of memory integration have mainly consisted of fMRI studies that focus primarily on the encoding phase of the experiment, wherein the participant encodes an overlapping representation. Whilst this technique has great spatial resolution, and these studies are able to investigate where activations or reactivations of certain cortical areas lead to subsequent integration (Zeithamova & Eichenbaun, 2013; Schlichting, Zeithamova & Preston, 2012; Zeithamova, Schlichting & Preston, 2012), it is somewhat lacking in the ability to track exactly when in time these activations are being made. The current study capitalised on the high temporal resolution of EEG to track how and when brain activity significantly differed between recollection and integration.

Contrary to previous fMRI and MEG work, that has focused on the importance in the differences in activity during the encoding of overlapping content to subsequent inference performance (e.g. Backus et al., 2016; Schlichting, Zeithamova & Preston, 2014; Zeithamova, Schlichting & Preston, 2012) the current study only found a significant main effect of stimulus type during the second encoding round of the context experiments, and only for the context-congruent condition. Otherwise, the ERPs between CB and XY learning were remarkably similar.

Addressing first the significant result, the CB encoding in the context congruent condition of experiments 2 and 3 were characterised by significantly more positive-going slow waves in the 500-800ms time window. In the second encoding round, it was expected that the ERP would reflect the retrieval of the AB/Y memory trace from the first encoding window once the Y/B item was presented. As such, the current ERPs here are not reflective of

the E-R overlap effect that has been shown to reflect increased memory accessibility to the target episode and be characterised by more positive-going amplitudes across the 600-900ms post-probe-onset time window (Bramão, Karlsson & Johansson, 2017), but are consistent with the positive-going slow waves that are associated with episodic retrieval (Allan & Rugg, 1997).

That this EEG difference, nor the difference between the subsequent inference effect CB pairs, did not correlate significantly with inference performance was a surprising outcome, but some explanations can be offered to help understand the outcomes. First, participant performance for the encoding and retrieval of the direct association pairs was at the ceiling, with only one direct association pair being retrieved less than 90% of the time on average (XY pairs, experiment 1). As integration in this paradigm was reliant on the encoding of the direct association pairs, the consistently high performance across these tests leaves little room for improvement, which may explain why inference scores also remained consistent across experiments and congruency conditions. Secondly, as will be probed further below, it could be that the crucial time period for integration was not during the second encoding round, but rather at the test phase, where integration became task-relevant. As the test phase was completed in the absence of the congruent background music, it could be that the increased memory accessibility associated with context reinstatement (Bramão, Karlsson & Johansson, 2017) was not present during the critical time period for integration, and so context manipulation had no significant influence on inference performance.

In experiment 1, and the incongruent context condition of experiments 2 and 3, the EEG correlates of CB encoding and XY encoding during the second encoding phase in these experiments were remarkably, and unexpectedly, similar. In the context of this experimental procedure, there may be an explanation for these findings. Memory integration is based on the theory that events that share content are stored as overlapping memory traces in a relational memory network (Eichenbaum, 1999; Larkin, Lykken, Tye, Wickelgren & Frank, 2014), and that these memories are reactivated to extract behaviourally-relevant information between a previously stored memory, and a temporally separate experience (Schlichting & Preston, 2012). It could be suggested that the memory integration process does not just rely on the reactivation of a single memory representation, but rather that many previous experiences that share content with the current experience could be reactivated in order to best inform behaviour. Moreover, as memory integration can occur without conscious experience (Mullen & Dymond, 2014; Shohamy & Wagner, 2008; Wimmer & Shohamy, 2012), these separate experiences may be stored as overlapping representations even when there is no need

to integrate them together. It could be that it is not until the inference needs to be made that the overlapping representations that were stored separately are reactivated and bound into a single representation through memory integration.

The surprising lack of difference in the ERPs during the second encoding round leaves the question of whether novelty or familiarity act as the triggers for memory integration somewhat up for debate. However, when this is viewed in terms of the experimental context, an assumption can be suggested of this (non-)result. Reggev, Sharoni, & Maril (2018) showed that when the novelty of the stimuli is based on real-life experience rather than the experimental context, there is no effect of memory potentiation – it is irregularity within the experimental context that is of key importance. Applying this experimental context logic slightly differently, it could be speculated that there was no situational novelty during the encoding phases of the current study, as participants were not only aware that they would not view stimulus pairs, but also that certain stimuli would appear twice, and that it would not be behaviourally relevant until later in the experiment. As the task (encoding stimuli pairs) remained consistent across the two encoding rounds, it could be that the novelty of viewing a previously seen stimulus in a new association pair was not enough to trigger integration. Rather, it was only when the probe stimulus was presented in a situation where the task violated the expectations of the previous experience- attempting to infer a relationship at the test phase- that area CA₁ detection novelty and triggered the memory integration process. With this speculation, then, it would be during the test phase, not the encoding rounds, that the effect of memory integration could be reflected in the EEG correlates in this paradigm.

Further, in fMRI literature, the task-relevant characteristic of memory integration has been linked to activation of the mPFC, which is said to bias memory reactivation towards memory traces that are currently task-relevant (Preston & Eichenbaum, 2013). It could be that integrating the related association was not task-relevant during the encoding rounds- rather the encoding of the singular memory traces into the relational memory network (Eichenbaum, 1999) was sufficient to allow for subsequent inference at a later time period (i.e. at test phase). It could be that it is only when area CA₁ compared the current experience of the probe stimulus with the expected experience that had come before that the hippocampus and mPFC began to interact, the mPFC biasing memory towards task-relevant memories (Preston & Eichenbaum, 2013), CA₃ pattern completing the relevant memories, CA₁ comparing the experiences (Larkin, Lykken, Tye, Wickelgren & Frank, 2014), mPFC selecting the appropriate response (Kroes & Fernández, 2012), and area CA₃ storing the new, overlapping

representation (Rolls, 2013). As such, it would be expected that the EEG correlates between inference and direct retrieval would differ most during the test phase.

To further elucidate the effect of novelty and similarity on memory integration, experiments 2 and 3 investigated neural correlates of memory integration and the consequence of the E-R overlap effect through reinstating the context of the first encoding window, or a different, equally familiar context during the second encoding window. In contrast to previous research on context reinstatement, the current study failed to find any significant mnemonic benefit usually resulting from reinstating the congruent context (Smith & Vela, 2001) or increased novelty through the incongruent condition to activate area CA₁ and trigger integration (Schlichting, Zeithamova, & Preston, 2014). Further, the current study failed to find significantly more positive-going amplitudes that are a regularly observed characteristic of E-R overlap, when compared to non-overlap (Bramão, Karlsson & Johansson, 2017). This suggests that context manipulation here did not have any effect on the accessibility towards the target event in memory. Based on the set-up of the current study, a number of reasons for this outcome can be suggested.

First, this was one of the first studies to employ a cross-modality context reinstatement in a memory integration paradigm. Whilst the context that was being reinstated was presented in the auditory modality, the integration task was conducted solely within the visual modality. In experiment 2, participants simply had to complete the visual memory integration task, whilst completing a judgement task on the associations made as an attentional measure, and to clear working memory; as such, the auditory context in this experiment was not task relevant. That this was reflected by a lack of difference between the E-R overlap and non-overlap conditions is consistent with the study of Kou et al. (2018), in which the authors found that students could inhibit background noise and music that was not task-relevant, resulting in comparable learning between environments with noisy backgrounds and silent environments.

Experiment 3 aimed to rectify this, by replacing the judgement task of experiment 2 with an attentional task that made the background music relevant to the task during the encoding windows; counting a series of tones that were superimposed into the background music tracks. By having to attend to the background music, it was expected that the context manipulation would produce significant differences in both behaviour and the electrophysiological data. However, this was again not the case. The reason for this could be that the context manipulation was only employed during the encoding phases, and not the test phase, which has been shown to be the critical period for integration in this experimental procedure. With context manipulation being employed whilst participants were storing the

stimuli pairs as separate representations, the effects of the may not have been clear, as the recall scores for each of the different stimuli pair types were consistently at the ceiling level across the experiment.

Lastly, it may be more likely that the cross-modality approach failed simply because the auditory context was not effective enough as a retrieval cue to influence the behavioural or neurological results in a meaningful way. Research has shown that context reinstatement only facilitates memory performance when the context being reinstated is diagnostic of the target episode (Bramão & Johansson, 2017; Nairne, 2002, 2006). In the current study the E-R overlap context was presented in the background of 18 different stimuli pairs, 12 of which were in the first encoding window, and it could be that this severely reduced the effectiveness of the context as a retrieval cue which, instead of increasing accessibility to the target event, had a negligible impact on memory performance.

Future Research

Based on the findings of the current study, a few recommendations could be made for future researchers to improve and expand upon the findings presented here. Primarily, future research using a paradigm similar to that presented here should look into analysing the test phase of the procedure in order to investigate the EEG correlates that may relate to memory integration in that time window. Whilst fMRI studies have been concerned with the cortical reactivation in this phase of the experiment, and its functional benefit to subsequent inference ability, the current study suggests that this may not be the critical time period for memory integration in all situations. EEG research revealing neural correlates that are functionally significant to subsequent inference would vastly improve the current knowledge of memory integration, and the key to these findings may lie in the test phase, where integration is behaviourally relevant.

With regards to when integration occurs, future research could further investigate the interaction between integration processes and task-relevance. One way that this could be achieved could be by having participants visualise the integration stimuli triad together as a single representation during the second encoding phase, compared to attempting to integrate the items at the test phase, as in this study. Not only could this reveal more about the nature temporal progression of memory integration, it could also illuminate the neural correlates of retrieving a pair of inferred stimuli from an already-integrated triad, and if this differs from regular stimulus pair recollection.

With regards to context, future research could investigate how making context stimuli truly task-relevant can influence the memory integration mechanisms. One way of doing this would be to employ the use of visual contexts, such as background images with the stimuli pairs superimposed on top of them. By keeping the context in the same modality as the main experimental task, congruent context conditions may lead to enhanced memory performance, in line with previous research (Smith & Vela, 2001). Another way to make context more task-relevant, this time keeping the multimodal approach that was employed in this study, could be to have participants report not only the correct inference at test, but also the context that the stimuli were presented in. In this way, participants would need to associate the background music with the association being formed of the stimuli, and this may well be easier to achieve if the context remains congruent, rather than changing across learning episodes. Finally, researchers could consider including background congruent or incongruent background music during the test phase, as here it would be more relevant to the task at hand, as it would have been presented along with each of the pattern separated episodes to be integrated.

Finally, to further investigate the functional relevance of the neural correlates, researchers could analyse the EEG output using more advanced statistical techniques, such as multivoxel pattern analysis (MVPA). This technique would allow researchers to investigate whether information is reactivated during subsequent learning windows (e.g. Zeithamova, Dominick & Preston, 2012)- in this case, whether there is evidence that memory for the AB stimulus pair is present during the second encoding window train. A computer could then be trained based on the neural pattern produced by the brain to predict subsequent memory performance. It could be that through MVPA, the key neural patterns for successful inference could be uncovered, further expanding the understanding of the mechanisms involved in the phenomena.

Conclusion

This study aimed to provide a temporal account of how EEG correlates during the learning of overlapping stimulus pairs reflected the memory integration process, as measured through subsequent inference performance. Across three experiments, in each of which inference performance was significantly above chance, this study found only one time window that demonstrated any significant neural correlates relating to memory integration, signifying that the memory integration may have taken place in a different time window of the paradigm used here- most likely during the test phase. Across two experiments, this study demonstrated that background music was not effective as a context in influencing memory

accessibility by increasing familiarity across encoding rounds. Taken together, these experiments demonstrate the robust nature of memory integration across a variety of situations, with behavioural performance reproduced reliably across each, and provide insight of how to go ahead with subsequent research looking to investigate this memory process.

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