THE NEURAL MECHANISMS OF RECOGNITION MEMORY: AN INVESTIGATION OF STUDY AND TEST BRAIN ACTIVITY AND THEIR INFLUENCE ON MEMORY OUTCOMES

by

Yun Chen

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Centre for Neuroscience
University of Alberta

Abstract

The ability to remember is fundamental to human cognition. The recognition memory paradigm has been widely used to investigate memory-related processes at both study and test phase. Two types of recognition memory are examined here, item and associative recognition memory. In an item recognition task, participants are instructed to remember a list of items (i.e., A, B, C, D . . .), then they are asked to make old-new judgments regarding the items: "probe (B), old or new?" In an associative recognition task, participants are instructed to remember a list of pairs (i.e., A-B, C-D, E-F, . . .), then they are asked to make intact-rearranged judgments regarding item-pairs: "probe (C-D), intact or rearranged". The intact probes are composed of identical pairs from study (A-B), and the rearranged probes are composed of studied items from different study pairs (A-F). With electroencephalographic (EEG) methods, one can identify brain activity related to successful encoding and retrieval. At study, encoding processes are measured by the subsequent memory effect comparing brain activity related to later-remembered and later-forgotten. At test, retrieval processes are measured by the old/new effect comparing brain activity related to correctly identified targets (hits) and correctly identified lures (correct rejections), and the retrieval success effect comparing brain activity related to correctly identified targets (hits) and misidentified targets (misses).

The objective of the four studies presented in this dissertation was to examine whether specific brain-activity features reflect recognition-memory encoding and retrieval processes, and to determine whether those features explain individual differences in memory performance. I measured event-related potentials (ERPs) and oscillatory activity during both study and test phase to explore the neural mechanisms of recognition memory. By using

an individual-difference approach, one can ask whether these brain-activity measures reflect common or distinct processes.

Using the ERP method, prior research has suggested many cognitive processes reflected in memory-related ERP features. Some of those proposed cognitive processes indexed by memory-related ERP features at study resemble other proposed cognitive processes indexed ERP features at test. In the first and the third studies, I asked whether the ERP features during study were functionally correlated with other ERP features during test, and in turn, influence memory performance. Some study ERP features were indeed correlated with test ERP features across participants; however, only a subset of those study-test ERP features explained individual differences in memory performance.

Using the oscillation method, prior research has identified changes in theta oscillations ($4 - 8\ Hz$) and alpha oscillations ($\sim 10\ Hz$) to be crucial for memory functioning. In the second and fourth studies, I investigated the function of theta and alpha oscillations during memory encoding and retrieval. The two studies examined whether these oscillations were functionally correlated with the memory-related ERP features, and in turn, influence memory performance. Theta oscillations correlated with memory performance across participants, and while alpha oscillations correlated with ERP measures across participants, but did not explain the individual difference in memory performance.

Taking an alternative approach to exploring the functions of brain activity in recognition memory tasks, the studies presented here revealed relationships between ERP features and oscillation measures and their influence on individual memory performance. Although the neural mechanisms for recognition memory are complex, the results suggest a possible unified neural mechanism encompassing both ERP features and oscillations for both item and associative recognition memory.

Preface

This thesis is an original work by Y Chen. All research projects contributing to this work received ethics approval from the University of Alberta Research Ethics Board. Project Name "Organisation and Retrieval Timecourse of Human Memory", No. Pro00009760. Chapter 2 of this thesis has been published as Chen, Y.Y., Lithgow, K., Hemmerich, J.A., & Caplan, J.B. (2014). "Is what goes in what comes out? encoding and retrieval event-related potentials together determine memory outcome", *Experimental Brain Research* (232), 3175–3190. Copyright Springer. Reprinted with permission. Kristie Lithgow was involved with conceptualization of the study and Jumjury Hemmerich assisted with the data collection. I was responsible for implementing the experimental paradigm, acquiring and analyzing the data and drafting the manuscript. Chapter 3 of this thesis is published as Chen, Y.Y. & Caplan, J.B. (2017), "Rhythmic activity and individual variability in recognition-memory: theta oscillations correlate with performance whereas alpha oscillations correlate with event-related potentials", *Journal of Cognitive Neuroscience* (29), 183–202. Jumjury Hemmerich assisted with the data collection. I was responsible for implementing the experimental paradigm, acquiring and analyzing the data and drafting the manuscript. Chapters 3 and 4 of this thesis have not been published elsewhere. Angela Wan assisted with data collection and I was responsible for implementing the experimental paradigm, acquiring and analyzing the data and drafting the manuscript. In conjunction with my supervisor Jeremy B. Caplan, I was involved in concept formation, data collection, interpretation of the data for all chapters.

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List of Abbreviations

EEG	electroencephalography
ERP	Event-related Potential
LPC	Late Positive Component
LPP	Left Parietal Positivity
RSE	Retrieval success effect
RT	Response time
SME	Subsequent Memory Effect
SW	Slow Wave

Chapter 1

General Introduction

1.1 Introduction

The ability to remember events, people and places is fundamental to human cognition. One of the major goals of studying memory is to examine encoding and retrieval processes, both cognitive and neural, that contribute to successful memory performance.

The recognition-memory paradigm has been widely used to investigate memory-related processes. Typically participants are asked to study a list of items (study phase), followed by a test phase, where the studied items are presented again along with unstudied items. Recognition memory is measured by asking the participants to make judgments on the studied (target) and unstudied (lure) items presented at test. Works in this dissertation target two types of recognition memory, item and associative recognition memory. In an item-recognition memory procedure, participants are asked to study a list of words ("CHAPTER", "ARTIST", "COMPASS"...), then asked to make old-new judgments regarding words: "'CHAPTER', *old or new*?" The studied, old items are the targets and the unstudied, new items are the lures. On the other hand, to test for association memory using an associative recognition task, participants are asked to study a list of word-pairs and learn the two items that are paired together ("CHAPTER–ARTIST", "FEATURES–COMPASS"...). They are then asked to make intact-rearranged judgments about word-pairs: "'FEATURES–ARTIST', *intact or rearranged*?" The targets are composed of identical "intact" probes ("CHAPTER–ARTIST") and the lures are "rearranged" probes made up of studied words from different

Response	Targets (old or intact)	Lures (new or rearranged)
old or intact	hit	false alarm
new or rearranged	miss	correct rejection

Table 1.1: Four categories of trials in a recognition experiment.

pairs ("FEATURES–ARTIST"). Both tasks ask participants to discriminate between target and lure probes.

Based on the response made to the recognition test, we can sort the trials into four categories (Table 1.1). Being able to correctly identify a target is as important as being able to correctly identify a lure. To measure memory outcome, hit rate alone does not tell the full story. For example, if a participant were responding "old" to every trial, we could have a 100% hit rate; however, this participant cannot differentiate targets from lures (100% false alarm rate). Together the hit and false alarm rates provide information on response bias, the tendency to respond "old" or "new" ("intact" or "rearranged"). Many studies employ "corrected recognition" scores, hit rate−false alarm rate, to account for the bias. In the following studies, I use d' as the measure for memory outcome: $d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$, where $Z(\,)$ is the z-transform. d' not only takes false alarm rate into consideration, but applies z-transformation to the hit and false alarm rate. This transformation is based on a normal distribution, which allows us to compare performance (d') across paradigms (Stanislaw & Todorov, 1999). The maximum possible value for d' is $+\infty$, reflecting a perfect memory performance, while $d' = 0$ reflects an inability to differentiate targets from lures. A participant with a higher d' value would have better discrimination of targets and lures than a participant with a lower d' value. A negative value of d' usually means participants mixed up the responses (responding "old" when intending to respond "new").

Moreover, response time (RT) is also used for measuring memory outcome. Kahana and Loftus (1999) have suggested that response time provides complementary information to accuracy. For example, faster response time has been associated with better accuracy and response confidence (Kahana, 2012). However, there are also speed-accuracy trade-offs—

faster response time at the expense of accuracy. Evaluating both accuracy and response time could give us clues about cognitive mechanisms involved or strategies used.

1.2 Theoretical perspectives on recognition memory

Murdock (1974) made the distinction between item and association memory. While the item and associative recognition procedures have many similarities, many researchers have suggested that the cognitive processes involved in remembering item and association information might be different (Clark, 1992; Clark & Burchett, 1994; Gronlund & Ratcliff, 1989; Hockley, 1992, 1994; Hockley & Cristi, 1996b; Yonelinas, 1997). Yet, it is important to note that item and association memory are highly interdependent/connected. For example, Hockley and Cristi (1996a) asked participants to make old/new judgments about items when they were instructed to study the item-item associations. They found that this group of participants performed equally well on the item recognition task compared to the group who were instructed to study the items but not the associations. In this dissertation, both item and associative recognition procedures are used to explore a more comprehensive view of processes involved in recognition memory.

1.2.1 Item recognition memory

Item recognition performance has been thought to be influenced by many factors. At study, the "Levels of Processing" framework introduced by Craik and Lockhart (1972) proposed that greater "depth" of processing eventually leads to better memory performance at test. For example, Sanquist, Rohrbaugh, Syndulko, and Lindsley (1980) examined the levels of processing at study and its latter effects on recognition memory performance. Participants studied a list of items by performing an encoding task where they were asked to determine if the two words of a pair 1) shared the same type case (orthographic), 2) rhymed with each other (phonemic), or 3) were synonyms (semantic). Afterward, participants were asked to judge if the item was from the studied list. The idea was that the semantic condition required the "deepest" level of processing, followed by the phonemic condition, and then the orthographic condition. Thus, the semantic condition should have the highest accuracy, followed by the phonemic condition, then the orthographic condition. The accuracy (hit rate) of the recognition task indeed revealed a similar pattern: semantic condition (83 %) > phonemic condition (69 %) > orthographic condition (38 %). Put simply, when participants engage in a "deep" level of processing, they will likely have a better memory outcome for the studied items compared to participants who engage in a "shallow" level of processing during study.

At test, different retrieval processes have been speculated to contribute to recognition judgments. For example, dual-process theory assumes that two distinct processes, familiarity and recollection, contribute to old/new discrimination (Yonelinas, 2002). Familiarity-based retrieval provides a sense of vaguely knowing that the item has been studied. Recollection-based retrieval provides other contextual information related to the item, apart from retrieving the item itself. To operationalize dual-process theory, the "remember/know" paradigm has been employed to study the processes. First introduced by Tulving (1985), participants are asked to make a judgment if they "know" or "remember" the item from the study list. This paradigm was then later used to estimate the contribution of the familiarity and recollection processes (Gardiner, 1988). If participants made a "know" response, it is likely that the item was retrieved using the familiarity process; whereas if participants made a "remember" response, it is likely that the item was retrieved using the recollection process. Many studies that employed this paradigm found that the old/new recognition accuracy for a "remember" response was better than accuracy for a "know" response (see Wixted & Mickes, 2010; Yonelinas, 2002, for reviews). This suggests that recollection-based retrieval could provide participants with a more accurate recognition judgment. However, it is important to note that "remember/know" responses may be driven by two distinct processes. For example, Wixted (2007) proposed that familiarity and recollection may both coexist in the brain, but that they summate to drive the old/new decision. Dunn (2008) went even further, showing that even "remember" and "know" judgments may be driven by only a single underlying decision dimension, which could be the sum of two or more sources of evidence, but they still summate to drive responses.

Single-process theory, a major alternative to dual-process theory, suggests that recognition judgment relies on a single signal-detection process based on memory strength. Each item has its own memory strength, and when an item is studied, the memory strength is increased. When participants are making a judgment, they are judging the strength of an item. Each participant sets a strength criterion and if the strength of an item is higher than this set criterion, they would respond with "old". Otherwise, they would respond with "new" (Yonelinas, 2002). To increase the memory strength of an item, one can increase the study time of an item. For example, Criss (2006) found that when participants studied items multiple times, their hit rates were better than when participants only studied items once.

1.2.2 Associative recognition memory

The dual-process theory item-recognition memory framework could also explain associative recognition. In an associative recognition task, both "intact" and "rearranged" probes are constructed from items that have been previously studied. Yonelinas (2002) argued that if familiarity reflects the strength of item-memory, it should only help to discriminate between studied and unstudied items. Given that all items presented in an associative recognition task have previously been studied, item-strength alone is not helpful for participants to discriminate between "intact" and "rearranged" probes. Recollection-based retrieval, on the other hand, would be able to provide contextual details to distinguish "intact" from "rearranged" (Rotello & Heit, 2000; Yonelinas, 2002; Yonelinas & Jacoby, 1994; Yonelinas, Kroll, Dobbins, Lazzara, & Knight, 1998). For example, Hockley and Consoli (1999) studied familiarity and recollection with an associative recognition task. Using the "remember/know" procedure, they found that significantly more "remember" responses compared to "know" responses were made to correctly identify "intact" probes. Since the "remember" responses were associated with recollection-based retrieval, it is likely that associative recognition judgments were largely based on recollection.

However, many researchers have suggested that familiarity-based retrieval could also contribute to successful associative recognition when a pair is treated as an item— this process is known as "unitization" (see Murray & Kensinger, 2013, for a review). Unitization is when the two items of a pair form a single representation for encoding (Graf & Schacter, 1989; Wollen, Webber, & Lowry, 1972). Diana, Van den Boom, Yonelinas, and Ranganath (2011) have found that pairs encoded using unitization were retrieved using familiarity-based retrieval.

In sum, the debate about processes involved in recognition memory judgments is still unresolved; however, memory-related brain-activity measures might help to gain more insights into the cognitive and neural processes related to memory functioning.

1.3 Investigating memory-related brain activity

Cognitive neuroscientists have used a number of techniques to study human cognition, including electroencephalography (EEG) which measures the summated electrical activity of a group of neurons (Kandel, Schwartz, Jessell, Siegelbaum, & Hudspeth, 2013). With a high temporal resolution on the millisecond scale, EEG is a useful tool for precisely measuring neural processes that are involved in cognition. Through the use of EEG, my intent is to continue the investigation of human recognition memory and further our basic understanding of memory functioning. A series of experiments were conducted to better understand the encoding and retrieval processes of item and association memory, in turn, providing the foundation for other basic memory research.

1.3.1 Event-Related Potentials

From a continuous recording of EEG, we can time-lock to the event of interest, then investigate the electrical activity (voltage change) after onset of the event (event-related potentials, ERPs). The positive and negative voltage changes in ERP features are often associated with various cognitive processes (Luck, 2005).

Event-related Potentials at study

During study, the **subsequent memory paradigm** has been utilized by researchers to investigate the memory-related brain activity. Pioneered by Sanquist et al. (1980), EEG activity at study was separated based on later memory performance: later-remembered and later-forgotten (see a schematic of trial-sorting in Figure 1.1). We can inspect the differences between later-remembered and later-forgotten— "subsequent memory effect", which could reflect effective encoding processes. These differences in ERP amplitude are sometimes called "Dm"— difference due to memory (Friedman & Johnson Jr., 2000; Paller, Kutas, & Mayes, 1987; Paller & Wagner, 2002; Wagner, Koutstaal, & Schacter, 1999). This approach was also later employed in fMRI studies of memory encoding (Brewer, Zhao, Desmond, Clover, & Gabrieli, 1998; Wagner et al., 1998).

Study ERPs and item memory The two most frequently reported subsequent memory effect ERP features in item memory studies, distinguished mainly by their different latencies, have been termed the **Late Positive Component** and the **Slow Wave**. Specifically, the Late Positive Component occurs around 400–700 ms after stimulus onset, has also been referred as a variant of P3 or P300 (see Polich, 2007, for a review) and is usually recorded at centro-parietal electrodes. It has been suggested to reflect shallow encoding, such as rote rehearsal (Karis, Fabiani, & Donchin, 1984). The Slow Wave is a relatively sustained voltage difference that usually starts around 800 ms after stimulus onset. It has been suggested to reflect deep levels of processing for item encoding. It is also related to the use of more complex and elaborative encoding strategies (Fabiani, Karis, & Donchin, 1986, 1990; Friedman & Trott, 2000; Karis et al., 1984; Rushby, Barry, & Johnstone, 2002; Weyerts, Tendolkar, Smid, & Heinze, 1997).

Using a levels-of-processing manipulation, Fabiani et al. (1990) recorded EEG during the study phase of an item memory task and found that participants who were instructed to use a shallow encoding strategy (repetition) elicited a larger subsequent memory effect in the Late Positive Component, whereas participants who employed deep encoding strategies (sentence generation) had a larger subsequent memory effect in the Slow Wave. The Late Positive Component and the Slow Wave subsequent memory effect have been replicated in many item memory tasks (see Lian, Goldstein, Dochin, & He, 2002, for a review), where the ERP amplitude differences between later-remembered and later-forgotten trials reflect different cognitive processes involved in successful encoding.

Study ERPs and association memory The Slow Wave has long been suggested to index possible item-item associative memory processes. Many item-memory studies employed the "deep" encoding strategies which encourage participants to make associations between items within the list. Those strategies seem to resemble the strategies that are well known to enhance verbal association-memory, for example, interactive imagery strategy asks participants to form a combined mental imagery for items of a pair. Moreover, the Slow Wave effects are usually more pronounced when participants are engaged in "deep" encoding strategies. The Slow Wave could reflect processes involved in the item–item associations. For example, Kim, Vallesi, Picton, and Tulving (2009); Kim, Binns, and Alain (2012) examined the ERPs during an item–item association memory task, and found significant subsequent-memory effects at both the Late Positive Components and the Slow Wave. More importantly, the slow-wave effect had a frontal topographic distribution. This **Frontal Slow Wave** has similarly been found in many tasks that demand item-item associative encoding (Caplan, Glaholt, & McIntosh, 2009; Kim et al., 2012; Mangels, Picton, & Craik, 2001; Wagner et al., 1999; Weyerts et al., 1997).

Event-related Potentials at test

During test, the **old/new effect** and **retrieval success effect** have been the most common means of investigating retrieval-related brain activity. The old/new effect measures memory through comparing the correct discrimination of the studied material (hits) from the unstudied material (correct rejections). Alternatively, the retrieval success effect measures memory through the successful recognition of only the studied material, comparing those remembered

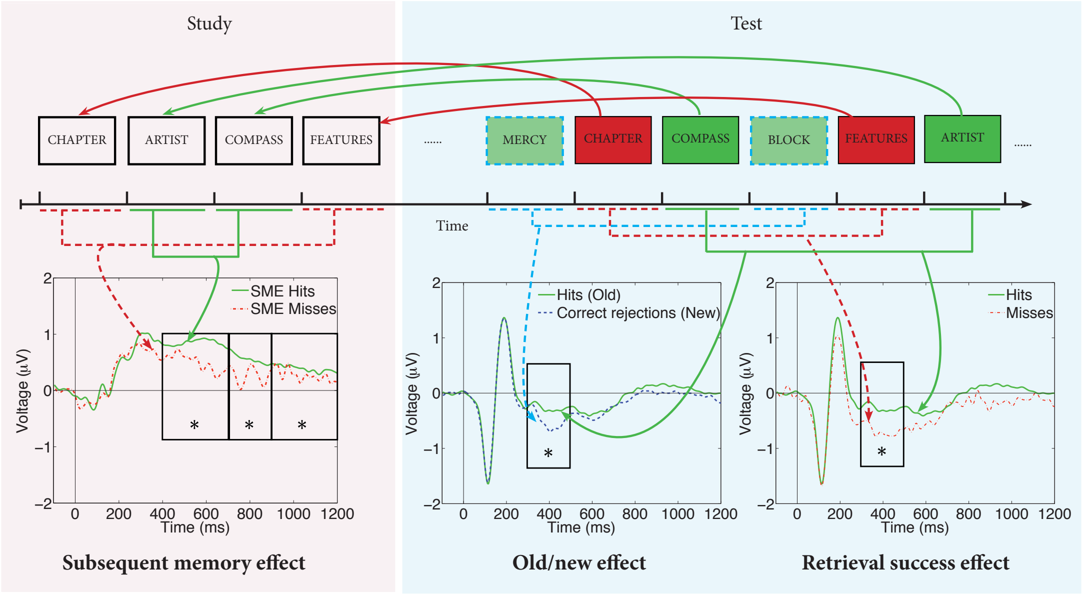

Figure 1.1: A schematic depiction of trial sorting for subsequent memory effect— at study— and old/new effect & retrieval success effect— at test. Green represents remembered/correct trials and red represents forgotten/incorrect trials. Solid box borders represent studied/old items and dashed blue box borders represented unstudied/new items. The ERP examples are take from Chapter 2, Chen et al. (2014).

(hits) and forgotten (misses, see a schematic of trial sorting in Figure 1.1). van Petten and Senkfor (1996) reported one of the few ERP studies that have taken the retrieval-success effect approach, and obtained similar findings to those reported using the old/new effect. Presumably, given the similar morphology of the resulting ERPs, this distinction has not been seen as important in many situations. However, it may hold some importance, as Chen, Lithgow, Hemmerich, and Caplan (2014) found different patterns of correlation results when we compared both effects (Chapter 2). Therefore, we take it seriously throughout this dissertation and consider both effects in analyzing test activity, which should provide us a more comprehensive view of retrieval processes.

Test ERPs and item memory Two chief features are consistently observed in old/new effects using verbal materials. First, the **FN400** appears symmetrically at frontal electrodes as a negative-going peak around 400 ms after probe onset. Second, the **Left Parietal Positivity** appears in the parietal electrodes, on the left side for verbal stimuli; it is a positive-going wave that peaks around 500–800 ms after probe onset. Sometimes, confusingly, the Left Parietal Positivity is known as the "Late Parietal Component." For clarity, LPC is reserved for "Late Positive Component" referring to the subsequent memory effect feature described above. It has been suggested that these two ERPs reflect different processes contributing to old/new recognition (see Rugg & Curran, 2007, for a review). Using the remember/know paradigm, Smith (1993) examined the ERPs for remember and know responses. The ERP amplitude of the FN400 did not differ between remember and know, whereas the amplitude of the Left Parietal Positivity differed. This suggests that the Left Parietal Positivity reflected processes involved in the remember responses, pointing towards recollection-based retrieval.

On the other hand, Finnigan, Humphreys, Dennis, and Geffen (2002) manipulated memory strength by presenting the study items once (weak-strength items) or three times (strong-strength items), and then examined the ERPs for strong-strength and weak-strength memory items during test. The ERP amplitude of FN400 and the Left Parietal Positivity were modulated by the memory strength manipulation, and showed a graded effect. This result is in line with the idea that those test ERP features index memory strength.

Test ERPs and association memory In an associative recognition task, participants are asked to discriminate "intact" from "rearranged" pairs. These two probe types are constructed using studied items. The dual-process theory could also account for associative recognition judgments. The assumption is that the familiarity-based retrieval could not support the associative recognition judgment since the rearranged pairs are constructed from the studied items. Recollection-based retrieval, on the other hand, could provide additional contextual details, which could help successfully differentiate "intact" and "rearranged" probes (Yonelinas, 2002). Since the Left Parietal Positivity has been suggested to reflect recollection-based retrieval, it is possible that associative recognition judgments rely on the recollection process which is indexed by the Left Parietal Positivity. For example, using an associative recognition procedure, Donaldson and Rugg (1998) found that the ERP amplitude of FN400 did not differ between “intact” and “rearranged” responses, whereas the ERP amplitude of Left Parietal Positivity did.

In addition to the Left Parietal Positivity, the **right frontal old/new effect** has been suggested to reflect processes that are involved in successful associative recognition judgments. The right frontal old/new effect is a positive-going peak around 400–1200 ms after probe onset that is larger over the right electrodes (Yonelinas, 2002). This effect was first reported by Wilding and Rugg (1996), whose participants studied word pairs and were later tested for their memory of those pairs. At right frontal electrode sites, remembered old pairs had a more positive waveform than the new pairs, suggesting that this effect would be essential for the retrieval of associative information that is needed for the recognition judgments (Wilding & Rugg, 1996). Many later studies using a similar procedure to test the retrieval of association memory have reported this right frontal old/new effect (Mark & Rugg, 1998; Wilding, 1999; Ranganath & Paller, 1999; Senkfor & van Petten, 1998; Trott, Friedman, Ritter, Fabiani, & Snodgrass, 1999; Weyerts et al., 1997).

1.3.2 Oscillations

Apart from ERP measures, EEG signal can also be investigated in the frequency domain. We can investigate the *rhythmic* brain activity resulting from the firing of neurons in a synchronized manner (oscillations, Buzsaki, 2006). In oscillation analysis, EEG activity is decomposed into simple sine waves with different frequencies and amplitudes. The cycle of the oscillations is qualified with Hz— cycles per second; for example a 10 Hz oscillation cycles 10 times per second. Like ERP features, oscillations, characterized by frequency and power (amplitude^2), have been associated with different aspects of cognitive processes (Buzsaki, 2006). The assumption is that when neurons are firing synchronously, there will be an increase in amplitude (power). Therefore, differences in amplitude (power) could inform us of neural activity patterns.

The power measures of oscillations usually use a windowed Fourier Transform or wavelet transform to quantify spectral power as a function of frequency. However, any signal, whether rhythmic or non-rhythmic, can produce non-zero power values (Fourier's theorem). Activity measured in this way might not necessarily be rhythmic (Klimesch, 1999). Therefore, I wanted to choose a measure that would ensure the selection of activity is rhythmic. A method for detecting oscillations, known as BOSC (Better OSCillation detection, Caplan, Madsen, Raghavachari, & Kahana, 2001; Whitten, Hughes, Dickson, & Caplan, 2011), is conservative about what is treated as rhythmic activity. When detecting oscillations, the BOSC method first models the coloured-noise background signal to determine a power threshold. In the oscillation analysis, the power threshold is set to the 95^{th} percentile of the theoretical probability distribution of the power values at a given frequency, if all the signals were produced by the coloured-noise background. In addition to the power threshold, the EEG signal is also subject to a duration threshold to ensure that the detected signal is sustained. This helps avoid labeling non-repeating signals, such as solitary evoked potentials and some artifacts, as oscillatory. The duration threshold is set at three complete cycles for each frequency. After the applications of the thresholds, one can detect when oscillations are present using $P_{episode}(f)$, derived from the BOSC method, which measures the proportion of time during which oscillations are detected at each frequency, f. $P_{episode}$, a duration measure, ensures that the results relate to sustained rhythmic activity. A $P_{episode}$ value of 0.5, for example, indicates that oscillations at the frequency of detection were deemed to be present during 50% of the recording time (see more details in Chapters 3 and 5).

As with the ERP features, memory oscillation measures can be studied using the subsequent memory effect (later-remembered versus later-forgotten) at study, and old/new effect (hits versus correct rejections) and retrieval success effect (hits versus misses) at test. The activity differences in oscillations might reflect processes that result in effective memory. The **theta ($4-8$ Hz)** and **alpha (~ 10 Hz)** oscillations in particular have been associated with memory functioning (Doppelmayr, Klimesch, Schwaiger, Auinger, & Winkler, 1998; Doppelmayr, Klimesch, Schwaiger, Stadler, & Rohm, 2000; Doppelmayr, Klimesch, Hodlmoser, Sauseng, & Gruber, 2005; Klimesch, Schimke, Ladurner, & Pfurtscheller, 1990; Klimesch, Schimke, & Pfurtscheller, 1993; Klimesch, Schimke, & Schwaiger, 1994; Klimesch, 1996, 1999; Klimesch, Schack, & Sauseng, 2005; Jensen, Gelfand, Kounios, & Lisman, 2002).

Theta oscillations

Increases in theta-oscillation activity is thought to be important for memory function. In animal research, Berry and Thompson (1978) recorded from the rabbit hippocampus while rabbits were trained on the pairing of a conditioned and unconditioned stimulus. Faster learning rates were correlated with more theta activity (Asaka et al., 2005; Griffin, Asaka, Darling, & Berry, 2004; Seager, Johnson, Chabot, Asaka, & Berry, 2002). Similarly, Landfield, McGaugh, and Tusa (1972) examined rats with footshock training. The amount of cortical theta activity was positively correlated with retention time (4–30 minutes). Results from these two studies suggested that theta oscillations were needed for learning associations between events.

With human EEG, increased theta activity is related to encoding and retrieval success of both item and association memory (See Klimesch, 1997, 1999; Kahana, Seelig, & Madsen, 2001; Nyhus & Curran, 2010, for reviews). For example, during the study phase of an item memory task, Sederberg, Kahana, Howard, Donner, and Madsen (2003) found significant increases in theta activity during successful memory encoding at both frontal and temporal sites with intracranial EEG recording. Sederberg et al. (2003) suggested that given the locations where theta activity was recorded, it was possible that theta oscillations reflected the information encoding process taking place in the hippocampus. In addition, during the test phase of an item-memory old/new recognition memory task, Osipova et al. (2006) reported that over the posterior regions, theta activity increased for correctly identified targets compared to lures. Theta oscillations have also been suggested to be involved specifically in recollection-based retrieval. Reviewed by Nyhus and Curran (2010), increased theta activity was related to better word recognition and “remember” responses in the “remember/know” procedure. It is possible that successful item recognition judgments rely on retrieval of associative and relational information, which theta oscillations facilitate. Furthermore, with item-item association memory procedures, theta oscillations at study have been shown to differ between later-remembered and later-forgotten associations (Caplan & Glaholt, 2007; Summerfield & Mangels, 2005), suggesting that theta oscillations could also facilitate successful encoding of associative information.

Alpha oscillations

Alpha oscillations have long been suggested to reflect visual inattention. When participants actively engage in cognitive tasks, alpha-band activity is reduced during the task compared to the baseline period. More importantly, less alpha activity has been suggested to index encoding processes that lead to better memory later on (see Klimesch, 1997; Klimesch, Freunberger, & Sauseng, 2010, for a review). During an item recognition task, Klimesch et al. (1993) separated the participants based on their memory performance (median-split), and found alpha activity decreased more during memory encoding for good memory performers compared to the poor performers. In addition, Klimesch, Doppelmayr, and Pachinger (1997) studied the alpha oscillations during a paired associate learning task, and found that less alpha activity during successful encoded pairs compared to the unsuccessful pairs. These results provide evidence for the suggestion that alpha is involved in memory function, but they do not completely rule out the possibility that alpha's involvement is mediated by attention.

Taken together, more theta and less alpha oscillations might be essential for both item and association memory functioning.

1.4 Summary

Using the subsequent memory effect at study, and old/new effect and retrieval success effect at test, we can measure activity associated with successful and unsuccessful memory encoding and retrieval. Individuals vary in their memory performance. Assuming that there are some basic processes, neural and cognitive, that govern how everyone remembers or forgets, if those processes are reflected in the within-subjects brain activity measures, then the observed amplitude difference in ERP features and activity-level difference in oscillations might be able to explain individual differences in memory performance.

The overarching theme of this research program is to investigate the relationship between memory-related neural activity and individual differences in memory performance. There are two main objectives. The first is to investigate which memory-related ERP features at study could affect other memory-related ERP features at test, which in turn, could explain memory performance. I ask whether the study-related ERPs are correlated with test ERPs, and whether the study and/or the test ERPs are correlated with memory performance across participants. The second objective is to investigate the functional significance of oscillations in recognition tasks. ERPs have been studied more extensively than oscillations in recognition memory. Although there are still many debates as to what cognitive processes memory-related ERPs really reflect, at least we can ask whether an oscillation corresponds to the same cognitive process as an ERP or a different process altogether. I ask if ERPs and oscillations during study might explain any common variance across participants, and similarly, the ERPs and oscillations during test.

To test these hypotheses, I correlate, across participants, 1) measures of ERPs at study to measures of ERPs at test, 2) measures of oscillations to measures of ERPs, 3) measures of ERPs and oscillations to memory outcomes. As I summarized above, many memory studies have looked at brain activity, either during study or test, but they did not directly examine the relationship of brain activity between study and test or the relationship between brain activity and memory performance. This is likely due to the insufficient power to determine correlation across participants. Many studies included a relatively small sample size ($N = 15 - 30$) compared to the works in this dissertation ($N = 55+$). The large sample size provides the statistical power that enables us to explore the between-subject differences.

It is important to note that instead of the original signal, the differences in brain activity are employed for the correlations. For example, for each participant, I calculate the subsequent memory effect by measuring the amplitude difference between later-remembered and later-forgotten ERPs. The raw amplitude of an ERP might be subject to the individual's impedance level, where the difference could reflect some processes related to memory function. Therefore, I examined whether differences in within-subject memory effects (subsequent memory effect, old/new effect, and retrieval success effect) could explain variance in memory performance across participants.

The results from the following studies expanded and refined our understanding of how memory-related brain activity at study and test affect item and associative recognition memory.

1.5 Chapter overview

The experiments in this dissertation employed both the ERP method and the oscillation method to examine the neural mechanisms of recognition memory (Table 1.2). Here I briefly outline the key aspects of the following chapters.

	Item Recognition	Associative Recognition
ERPs	Chapter 2	Chapter 4
Oscillations	Chapter 3	Chapter 5

Table 1.2: Four core experimental chapters

Using the ERP method, in Chapter 2, I test the relationship between the study and test activity for item recognition, finding that two pairs of study-test activity are correlated: the Late Positive Component at study and FN400 at test, and the Slow Wave at study and Left Parietal Positivity at test. Furthermore, only the Late Positive Component-FN400 pair explains individual differences in memory performance. In Chapter 4, I test the relationship between study and test activity for associative recognition and find that the Late Positive Component at study is correlated with the retrieval success effect at test, which explains individual differences in associative recognition memory.

Using the oscillation method, in Chapter 3, I evaluate the functions of theta and alpha oscillations in an item recognition task. I find that the theta oscillations correlate with memory performance, whereas alpha oscillations correlate with memory-related ERPs. In Chapter 5, I evaluate the functions of theta and alpha oscillations in an associative recognition task, finding the same results as in Chapter 3. These results suggest that alpha and theta oscillations might be activity present within neural networks that are essential for memory functions, regardless of verbal memory procedures.

In Chapter 6, I summarize the main findings from Chapter 2 to 5 and further discuss the significance of this research in recognition memory.

Chapter 2

Item memory: study and test event-related potentials affect memory outcome

Abstract

Understanding memory function amounts to identifying how events (cognitive and neural) at study eventually influence events at test. Many of the proposed cognitive correlates of memory-related event-related potentials (ERPs) at study resemble proposed cognitive correlates of other memory-related ERPs, recorded at test. We wondered whether a given known ERP feature at study might in fact reflect an effective-encoding process that is, in turn, tapped by another specific ERP feature, recorded at test. To achieve this, we asked which pairs of known memory-related ERP features explain common variance across a large sample of participants, while they perform a word-recognition task. Two early ERP features, the Late Positive Component (study) and the FN400 (test), covaried significantly. These features also correlated with memory success (d' and response time). Two later ERP features, the Slow Wave (study) and the Late Parietal Positivity (test), also covaried when lures were incorporated into the analysis. Interestingly, these later features were uncorrelated with memory outcome. This novel approach, exploiting naturally occurring subject-variability (in strategy and ERP amplitudes), informs our understanding of the memory functions of ERP features in several ways. Specifically, they strengthen the argument that the earlier ERP features may drive old/new recognition (but perhaps not the later features). Our findings suggest the Late Positive Component at study, in some degree, may cause the FN400 to increase at test, together producing effective recognition-memory. The Slow Wave at study appears to relate the Left Parietal Positivity at test, but these may play roles in more complex memory judgments, and may be less critical for simple old/new recognition.

2.1 Introduction

Memory experiments include two distinct phases: a study phase, during which materials are learned, and a later test phase, during which the participant is tested on their memory for the target materials. A major goal of memory research is therefore to understand how encoding processes affect processes at a later retrieval phase, in turn, to produce effective memory. In electroencephalographic (EEG) studies, encoding and retrieval phases have been studied separately, and researchers have identified event-related potentials (ERPs) associated with memory outcome during both phases. Subsequent memory effects (Brewer et al., 1998; Paller & Wagner, 2002; Wagner et al., 1998) or Differences due to Memory (Paller et al., 1987), identify brain activity during study that differentiates later-successful (remembered) versus later-unsuccessful (forgotten) items. Similarly, old/new effects identify brain activity during the memory test, that differentiates correctly responded target items (hits) from correctly responded lure items (correct rejections; Rugg, 1995). Two well studied encoding ERP features, the Late Positive Component and the Slow Wave, both show subsequent memory effects. Similarly, two well studied retrieval ERP features, the FN400 and the Late Parietal Positivity, both show old/new effects (Warren, 1980). An obvious questions is: Is there a functional relationship between those features? For example, does the Late Positive Component reflect some effective study process that results in better memory-retrieval, which in turn, is indexed by the FN400? Many studies have found that a single experimental manipulation, such as levels of processing (Fabiani et al., 1990) or recollection versus familiarity (Guo et al., 2004), can affect both an encoding and a retrieval ERP feature. However, a single variable might affect the two brain-activity measures in unrelated ways. For example, the Late Positive Component and the FN400 both show greater coupling to memory outcome when participants apply rote memorization strategies than elaborative/intentional strategies (Karis et al., 1984; Rugg & Curran, 2007). This could be because both deflections reflect conceptual priming (Kutas & Federmeier, 2011), or because one reflects conceptual priming effects whereas the other reflects familiarity (Voss & Federmeier, 2011). Indeed, these are both currently defensible interpretations of these two ERP peaks. One approach would be to continue to try to fractionate memory processes via experimental manipulations until the two peaks are dissociated. This approach has been, and should continue to be, extensively pursued. We suggest enriching this body of knowledge with a complementary approach:

asking which pairs of memory-related ERP features might be related, in the sense that they explain some common variance across participants. Prior researchers have proposed similar cognitive functions of subsequent memory effect and old/new effect ERP features, but for every example of a parallel between a proposed function of a study- and test-ERP feature, it is straight-forward to find evidence suggesting they differ. One outcome of our approach is that we may find out which memory-relevant ERP features might be promising to study together, which can in turn inform current ERP research fractionating memory function. Next, we briefly review prior evidence suggesting which study- and test-related ERP features might be functionally related.

2.1.1 ERPs at encoding and retrieval

One common approach to identifying ERPs related to successful encoding has been termed the Subsequent Memory Effect. In this approach, originally suggested by Sanquist et al. (1980) and first reported as statistically reliable by Karis et al. (1984), one isolates brain activity related to effective memory encoding by comparing ERPs during study between subsequently remembered items and subsequently forgotten items (see Friedman & Johnson Jr., 2000; Paller & Wagner, 2002; Wagner et al., 1999, for reviews). The two most frequently reported subsequent memory effect deflections are distinguished mainly by their different latencies. The Late Positive Component, a positive-going peak, occurs around 400–700 ms after stimulus onset, and is usually recorded at centro-parietal electrodes (Pz). The Slow Wave is a relatively sustained voltage difference that usually starts around 800 ms after stimulus onset, and is also typically recorded at both frontal and centro-parietal electrodes. The voltage difference between subsequently remembered items and subsequently forgotten items is thought to index cognitive processes that lead to successful memory encoding.

On the other hand, the most common means of investigating ERPs related to retrieval is by measuring the so-called old/new effect (Warren, 1980). In this approach (see Rugg & Yonelinas, 2003, for a review), ERPs are computed during the recognition-memory test, separately for target ("old") and lure ("new") items, usually confined to correct responses— hits and correct rejections, respectively— and the difference between these two ERPs is the old/new effect. Two chief features are consistently observed in old/new effects using verbal materials. First, the FN400 appears symmetrically at frontal electrodes (Fz), as a negative-going potential peaking around 400 ms after probe onset. Second, the Left Parietal Positivity appears at left parietal electrodes (P3), as a positive-going potential peaking around 500–800 ms after probe onset. For both the FN400 and the Left Parietal Positivity, old items elicit more positive waveforms than new items (hits > correct rejections). The usual inference is that this old–new difference reflects brain activity that contributes to successful memory retrieval.

One experimental manipulation that affects both subsequent memory effect and old/new effect ERPs is levels of processing. In the Levels of Processing framework, Craik and Lockhart (1972) proposed that target materials could be studied with at different levels of analysis, some of them considered "deeper" than others; the deeper-level strategies were proposed to result in better memory. Memory researchers have manipulated level of processing by instructing participants to study the material differently. With an incidental encoding procedure, Fabiani et al. (1990) found that participants who were instructed to use rote strategies (subvocal rehearsal) elicited a larger Late Positive Component for later-recalled than later-not-recalled items, whereas participants who employed elaborative strategies (combining multiple words into sentences or images) had no difference in the Late Positive Component between later-recalled and later-not-recalled items. On the other hand, the Slow Wave was more sensitive to elaborative strategies. In contrast, items studied with rote strategies produced no significant memory-related difference in the Slow Wave.

It is important to note that when one inspects subsequent memory effect ERPs, it is often not clear where the Late Positive Component ends and the Slow Wave begins (as exemplified in our ERP figures; see Figure 4.2). One could thus argue that the subsequent memory effect begins at the onset of the Late Positive Component and the Slow Wave portion of the subsequent memory effect is simply a continuation of the deflection also known as the Late Positive Component, a single deflection, which would imply that the two ERP features could reflect the same cognitive process. We shall revisit this question in the data-analysis section, when we follow up our correlation analyses with partial correlation. Researchers taking this unitary-component perspective have reported that deep encoding strategies induced a larger subsequent memory effect than shallow strategies (Donaldson & Rugg, 1998; Guo et al., 2004; Marzi & Viggiano, 2010). Guo et al. (2004) had participants perform an incidental encoding task, judging either the meaning of an item (deep encoding) or its typeface (shallow encoding). The deeply encoded items elicited a larger subsequent memory effect than the shallowly encoded items, and this effect was sustained across their 200–800 ms time window.

Thus, even if the Late Positive Component and the Slow Wave are distinct deflections, they may respond to some common cognitive processes.

The retrieval ERP waveforms also differ based on the level of processing at encoding. The participants who were instructed to use a deep strategy elicited more positive Left Parietal Positivity than the participants who were instructed to use a shallow strategy, whereas FN400 displayed no difference between the two (see Rugg & Curran, 2007, for a review). This suggests the Left Parietal Positivity reflects the results of having deeply encoded an item.

Another approach to differentiating memory ERPs at both study and test has been dual-process theory of recognition-memory. In dual-process theory, it is assumed that two distinct processes contribute to recognition-memory at time of test: familiarity and recollection (Yonelinas, 2002). The Remember/Know paradigm (Tulving, 1985) has been widely used to test dual-process theory. Participants were asked to respond “remember” if they could retrieve the item and also its context (recollection) and “know” if they could only retrieve the item (familiar). Friedman and Johnson Jr. (2000) noted that the ERP during study trials was different for subsequent remember judgements than subsequent know judgements and subsequent misses, especially after 500 ms after the onset of the stimulus, within the range of the Slow Wave.

Alternatively, Smith (1993) suggested that the posterior Late Positive Component indexes encoding processes that lead to later recollection. Supporting this, Karis et al. (1984) found that when an item was both successfully free-recalled and recognized, the Late Positive Component was even more positive than when an item was later recognized but not recalled. Paller et al. (1988) also noted that the size of the Late Positive Component predicting recognition was smaller than the Late Positive Component predicting recall. Because recollection has been suggested to resemble recall (Yonelinas, 2002), this raises the possibility that the Late Positive Component does indeed reflect encoding of some sort of contextually-laden information that can be accessed in a later recognition test.

With the Remember/Know procedure, Curran (2004) found a significant FN400 old/new contrast at retrieval, but there was no amplitude difference between remember and know responses. In contrast, the Left Parietal Positivity significantly differentiated between remember and know responses. This result was consistent with a possible mapping of the FN400 and Left Parietal Positivity onto familiarity and recollection, respectively.

In addition to the Remember responses from the Remember/Know judgement, source memory is often thought of as a test of recollection. Source-memory judgments typically ask participants to make a second judgment about the target item (e.g., the item's color, font, location). With this procedure, the Left Parietal Positivity waveform was found to be more positive for the correctly identified old responses with source than the correctly identified old responses without source (Guo et al., 2006; Woroch & Gonsalves, 2010). These results are consistent with the proposal that the Left Parietal Positivity reflects recollection-based recognition judgments.

An alternative to dual-process theory, Signal-Detection theory, contends that recognition decisions are made based on a single memory strength of the probe item (Yonelinas, 2002; Wixted, 2007).This is consistent with evidence that the FN400 tracks participants' confidence judgments. Furthermore, Wixted (2007) also pointed out that it is possible to have a signal-detection thoery within dual-process view. For example, Woroch and Gonsalves (2010) asked participants to perform old/new judgements with confidence ratings, followed by source judgments and confidence ratings of their source responses. The FN400 was sensitive to the confidence rating of the old/new judgement, whereas the Left Parietal Positivity was sensitive to the confidence rating of the source judgement. This is in line with the idea that not only the familiarity but recollection also is in fact a graded process, that would depend on a participant's level of confidence (Wixted & Stretch, 2004). However, this pattern also suggests that the Left Parietal Positivity might not relate to the old/new judgement itself, but rather, additional recollection- or source-retrieval that can follow the primary evidence (i.e., strength of familiarity) that is used to make the old/new judgement.

A major alternative to the view that the FN400 reflects familiarity-based recognition is that the FN400 has the same source as N400 (Voss & Federmeier, 2011). The N400, mostly observed at central electrodes, is suggested to be sensitive to semantic processing (see Kutas & Federmeier, 2011, for a review). First, the N400 habituates with repetition, suggesting an effect of priming (Neville et al., 1986; Paller & Kutas, 1992; Rugg, 1990; Young & Rugg, 1992). Furthermore, with semantically related primes (semantic/conceptual priming), N400 amplitude for target is closer to baseline than with unrelated primes (Kutas & Federmeier, 2011). Voss and Federmeier (2011) demonstrated that with semantic priming without recognition, the FN400 was elicited at same latency and electrodes as to the N400, suggesting that the FN400 could be functionally identical to the N400. The Left Parietal Positivity, on the other hand, was not affected by priming, suggesting that the Left Parietal Positivity is mainly related to memory retrieval. However, the conceptual-priming interpretation of FN400 has also been challenged (see target article and commentary in Voss et al., 2012).

2.1.2 Relating ERPs at encoding to ERPs at retrieval

In considering the debate between reognition memory theories, we came to suspect that the old/new judgement itself might be as simple as the single-process theory, whereas any more complicated judgement (remember/know, source judgment, etc.) might be (quite understandably) best understood with some version of dual-process theory. We thus selected the simplest and most conventional judgement (old vs. new) to assess memory performance, to avoid inadvertently complicated the participants task. Despite the complexity of the debate about the cognitive correlates of encoding and retrieval ERP features, one can see parallels emerging: first, between the Late Positive Component and the FN400, and second, between the Slow Wave and the Left Parietal Positivity. In general, earlier deflections in ERPs seem to reflect shallower and more stimulus-driven processes (Luck, 2005), so for this completely generic reason, we might hypothesize that the earlier subsequent memory effect ERPs should have something in common with the earlier old/new effect deflections, and likewise for the later ones. In addition, the Late Positive Component and FN400 have both been linked to shallow, contextually impoverished memory, and the Left Parietal Positivity and the Slow Wave have both been linked to deep levels of processing, elaborative encoding strategies and contextually rich memory.

Our aim, therefore, was to test this set of hypotheses linking subsequent memory effect and old/new effect ERP deflections using an individual-differences approach. We measured the magnitude of the subsequent memory effect and the old/new effect for each participant (from their difference-waves), and then computed correlations between these ERP measures across participants. In addition to the old/new effect analysis, we also conducted a retrieval-success effect analysis (Dolcos et al., 2005), subtracting the retrieval ERP for hits and the retrieval ERP for misses. It is important to note that we correlated the difference waves, not the original ERPs. If we were simply correlating ERP amplitudes between study and test, one would expect, especially for the subsequent memory effect and retrieval-success analyses, that precisely the same responses would be present at study and test— namely, those that corresponded to stimulus processing. By starting with difference measures (hits–

misses or hits–correct rejections), we are in fact avoiding such ERPs and confining our analyses to deflections that at least bear some relationship to memory. We are thus not asking whether the ERP deflections at study return at test. Rather, we are assuming that the memory-related ERPs reflect different processes (encoding processes during study and retrieval processes during test), and asking whether an ERP deflection at study reflects an encoding process that results in later improved memory outcome, as indexed by a different ERP deflection at test.

We used a verbal recognition-memory procedure that is consistent with prior procedures used in subsequent memory effect and old/new effect studies, and obtained both a large number of trials per participant (225 studied words and an equal number of unstudied items as lure probes) and a large sample size (64 participants). Because we wanted there to be sufficient individual variability in study and test, we did not instruct participants to study in any specific way. In addition to the commonly adopted old/new effect analysis, we also consider a retrieval-success effect analysis, in the hope of addressing brain activity that is more closely linked to successful (versus unsuccessful) recognition-memory performance. Because the retrieval-success effect analysis compares hits vs misses at test, as does the subsequent memory effect at study, we expected the subsequent to correlate more with the retrieval success measures than with the old/new effect measures.

2.2 Methods

2.2.1 Participants

Seventy-nine (11 self-reported left-handed[1], 68 self-reported right-handed; 30 female) undergraduate students who in an introductory psychology course at the University of Alberta, aged 18–28 (mean = 20, SD = 2.29) participated for course credit. Data from 15 participants were excluded from analyses: 7 were excluded from analyses due to low rates of misses (<11 trials, < 5%), 6 due to excessive amounts of artifacts in the EEG, and 2 who presumably reversed the response-key mapping (accuracy < 50%). All participants were required to have English as their first language and had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment in accordance with the University of Alberta's ethical review board.

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[1] When we excluded these 11 participants from the analyses, the pattern of results was not affected.

2.2.2 Materials

The stimuli were nouns drawn from the Toronto Word Pool (Friendly et al., 1982) composed of 4–8 letters. Kucera-Francis frequency was between 1–712 per million. Study items and test probes were presented in the centre of the computer screen using Times New Roman 17 point font with the E–Prime presentation software version 2.0 (Psychology Software Tools).

2.2.3 Procedure

The session took place in an electrically shielded, sound-attenuated chamber. The study phase instructed participants to study each word displayed one at a time. Each study set comprised 25 words, presented one word at a time. Each word was presented for 1500 ms with jittered uniform-random intertrial interval between 300–500 ms. The end-of-list distractor task, included to reduce recency effects that can contribute nuisance variability to the memory measure, consisted of 5 equations of the form of $A(+ \ or \ -)B(+ \ or \ -)C =$, where A, B, and C were randomly selected digits between 1 and 9, and the addition and subtraction operation were randomly selected in the equation. The participant was asked to type the correct answer. Each equation remained in the centre of the screen until the participant made a response. In the recognition judgement phase, which immediately followed the distractor task, 50 words were presented, with half (25 words) from the study phase (targets, or “old” items), and half (25 words) were never presented for study (lures, or “new” items), drawn at random, without replacement from the word pool. Each probe was a single word that remained on the screen until the participant made an old/new response by pressing key 1 for old (judged to be a target) and 2 for new (judged to be a lure). Nine blocks of study/test were presented for a total of 225 study trials and 450 probe trials (Figure 5.1). For each trial, response time (RT) and accuracy were recorded.

2.2.4 Electroencephalography (EEG) Recording and Analyses

EEG was recorded using a high-density 256-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, OR), amplified at a gain of 1000 and sampled at 250 Hz. Impedances were kept below 50 kΩ and EEG was initially referenced to the vertex electrode (Cz). Data were analyzed by custom MATLAB scripts in conjunction with the open-source EEGLAB toolbox (Delorme & Makeig, 2004, `http://sccn.ucsd.edu/eeglab`). Signal was average

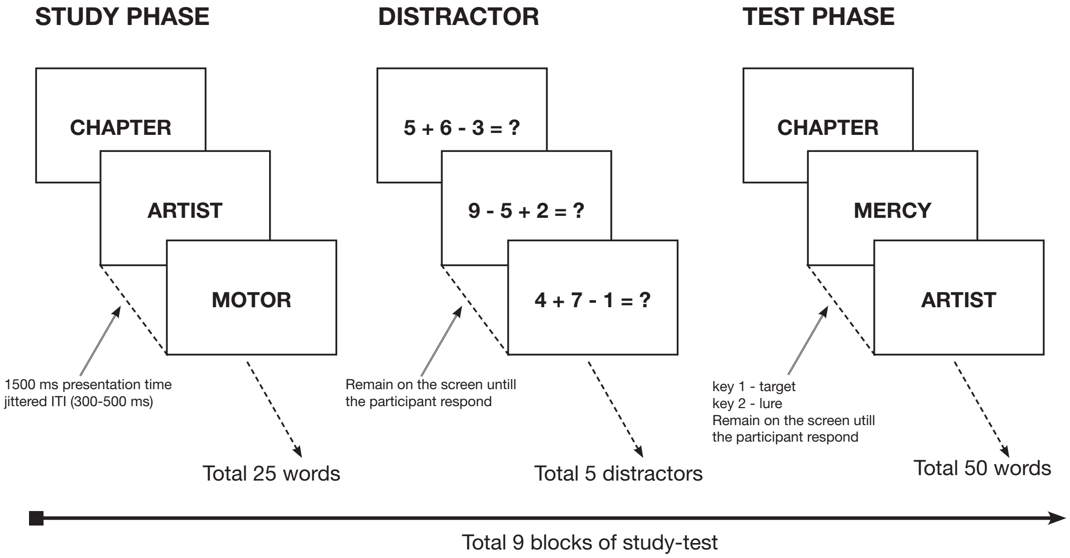


Figure 2.1: The procedure of the experiment. Each box illustrates the computer screen at a particular stage in the task (text has been enlarged relative to the screen size to improve clarity of the figure). There were 9 blocks of study–distractor–test.

re-referenced, and digitally bandpass filtered between 0.5–30 Hz. Artifacts were corrected via Independent Component Analysis, implemented in EEGLAB. Trials for which voltage deviated 300 μV from baseline were rejected. As a result, a mean of 19 (range 0–53 per subject) trials out of a total of 225 during the study phase were rejected and a mean of 34 (range 1–81 per subject) trials out of a total of 450 during the recognition-test phase were rejected. Trials were referenced to a 100 ms pre-stimulus baseline. Based on the participants' responses during the test phase, trials were separated into subsequently remembered items (subsequent memory effect hits) and subsequently forgotten items (subsequent memory effect misses). The two subsequent memory effect components were analyzed at electrode Pz in the time window of 400–700 ms latency post–stimulus for the Late Positive Component. Due to the longer time window of the Slow Wave (700–1200 ms) and variability in time windows in which the Slow Wave has been reported in the literature, we separated the Slow Wave into 700–900 ms (Slow Wave-Early) and 900–1200 ms (Slow Wave-Late) post–stimulus. The two old/new effect components were analyzed in the time window of 300–500 ms post–stimulus for the FN400 at electrode Fz, and 500–800 ms post–stimulus for the Left Parietal Positivity at electrode P3. The same time windows and electrodes were used for the retrieval-success effect analyses. The selection of analysis electrodes and time window were based on previous ERP studies. Additionally statistical analyses were carried out using PASW Statistics 18 for Mac, Release Version 18.0.0 (SPSS, Inc., 2009, Chicago, IL, `www.spss.com`) on the mean voltage differences at the corresponding electrodes and time windows.

2.3 Results

2.3.1 Behavior

Accuracy and RT are summarized in Table 5.1. Reassuringly, accuracy was not near ceiling or floor, which would have made our analyses difficult. Standard deviations of both accuracies and RTs are large; thus, there is good reason to expect that there is meaningful variability across participants that could support our planned correlation analyses.

2.3.2 ERPs

We first analyzed ERPs during study and test separately to check whether we could replicate the classic ERP components of interest.

Condition	Accuracy [%]	Response time [ms]
hits (old)	79.9 (10.6)	971 (195)
misses (old)	20.1 (10.6)	1369 (440)
correct rejections (new)	87.0 (11.6)	1095 (269)
false alarms (new)	13.0 (11.6)	1537 (554)

Table 2.1: Accuracy (percentage) and response time (ms) values, reported along with their standard deviations across subjects in parentheses.

Encoding stage

Three subsequent memory effect components, the Late Positive Component, the Slow Wave-Early and the Slow Wave-Late, were analyzed at electrode Pz (Figure 4.2). Paired-samples, two-tailed t-tests comparing mean voltage between SME-hits and SME-misses were significant at all time intervals of interest at Pz [Late Positive Component: $t(63) = 2.63$, $p < 0.05$; Slow Wave-Early: $t(63) = 2.98$, $p < 0.05$; Slow Wave-Late: $t(63) = 2.24$, $p < 0.05$], where SME-hits were more positive than SME-misses. Thus, we replicated these classic subsequent memory effect components (Paller & Wagner, 2002).

Retrieval stage

We first analyzed the retrieval ERPs in the usual manner, taking the old/new-effect approach. We compared the ERP for correct old trials (hits) with the ERP for correct new trials (CRs). Two components can be seen: the FN400 (Figure 2.3a) and the Left Parietal Positivity (Figure 2.3b). Paired-samples t-tests on mean voltage confirmed both old/new effect components [FN400 at electrode Fz: $t(63) = 4.52$, $p < 0.01$; Left Parietal Positivity at electrode P3: $t(63) = 5.76$, $p < 0.01$], consistent with prior findings (Rugg & Curran, 2007).

In addition to the old/new effect analysis, we conducted a retrieval-success effect analysis, comparing the ERP for hits to the ERP for misses. Figure 2.3 shows that the FN400 (c) and Left Parietal Positivity (d) were also readily observable in the retrieval-success effect analysis, and were significant [FN400 at electrode Fz: $t(63) = 5.08$, $p < 0.01$; Left Parietal Positivity electrode P3 [$t(63) = 3.88$, $p < 0.01$]. To foreshadow the correlation analyses, note that our sensitivity was greater for the FN400 in the retrieval-success effect analysis, but was greater for the Left Parietal Positivity in the old/new effect analysis. One can see a high degree of resemblance between the timecourses and topographies of the retrieval-success

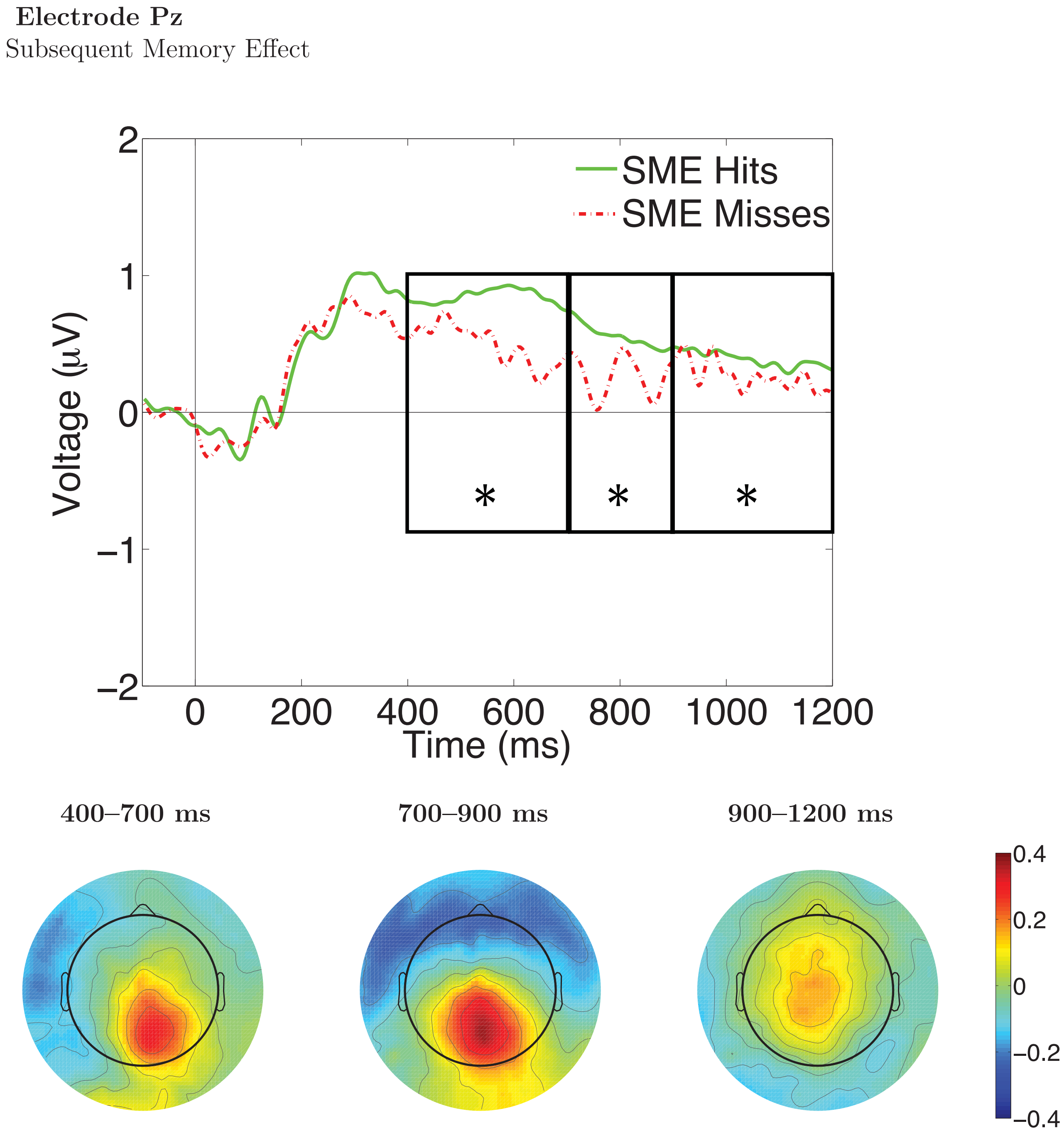


Figure 2.2: Grand-average Subsequent Memory Effect ERPs at Pz. Encoding ERPs for subsequently remembered trials (SME hits) are contrasted with subsequently forgotten (SME misses) trials. Topographic maps are spline plots, where color reflects mean voltage $[\mu V]$ over the corresponding time window.

effect and old/new effects in Figure 2.3; as we suggested in the Introduction, this may be part of the reason previous researchers have not drawn a large distinction between these two approaches.

In sum, the two encoding-related ERP deflections and the two retrieval-related ERP deflections (in both the old/new effect and retrieval-success effect analyses) were present and statistically robust, setting the stage for the correlation analyses comparing them to one another.

2.3.3 Relationship between encoding and retrieval ERPs

We now turn to our main hypotheses regarding the relationship amongst these study- and test-phase deflections. For each participant, the subsequent memory effect measure was the average ERP voltage difference between hits and misses during study at Pz, during the respective time windows. Likewise, the old/new effect measures were the voltage difference between hits and CRs during retrieval at the corresponding electrodes and time windows of interest and the retrieval-success effect measures were the same as the old/new effect measures, but computed as hits–misses during test.

Correlations between ERP components within-phase

In order to understand the relationship between ERP components during encoding and retrieval, we first need to evaluate the relationship between two components from the same memory stage. If the components in the same memory stage are highly correlated, it will be more difficult to make interpretations from the across–phase correlation than if the components are independent. During encoding, the Late Positive Component was positively correlated with Slow Wave-Early [$r(62) = 0.74$, $p < 0.05$], as well as with Slow Wave-Late [$r(62) = 0.55$, $p < 0.05$]; Slow Wave-Early and Slow Wave-Late were correlated as well [$r(62) = 0.72$, $p < 0.05$]. Therefore, if two subsequent memory effect components correlate with a given retrieval ERP component, additional follow-up analyses (partial correlation) will be carried out to clarify the findings. During retrieval, on the other hand, the FN400 old/new effect was not significantly correlated with the Left Parietal Positivity old/new effect [$p > 0.1$] and likewise for the retrieval-success effect analysis [$p > 0.1$].

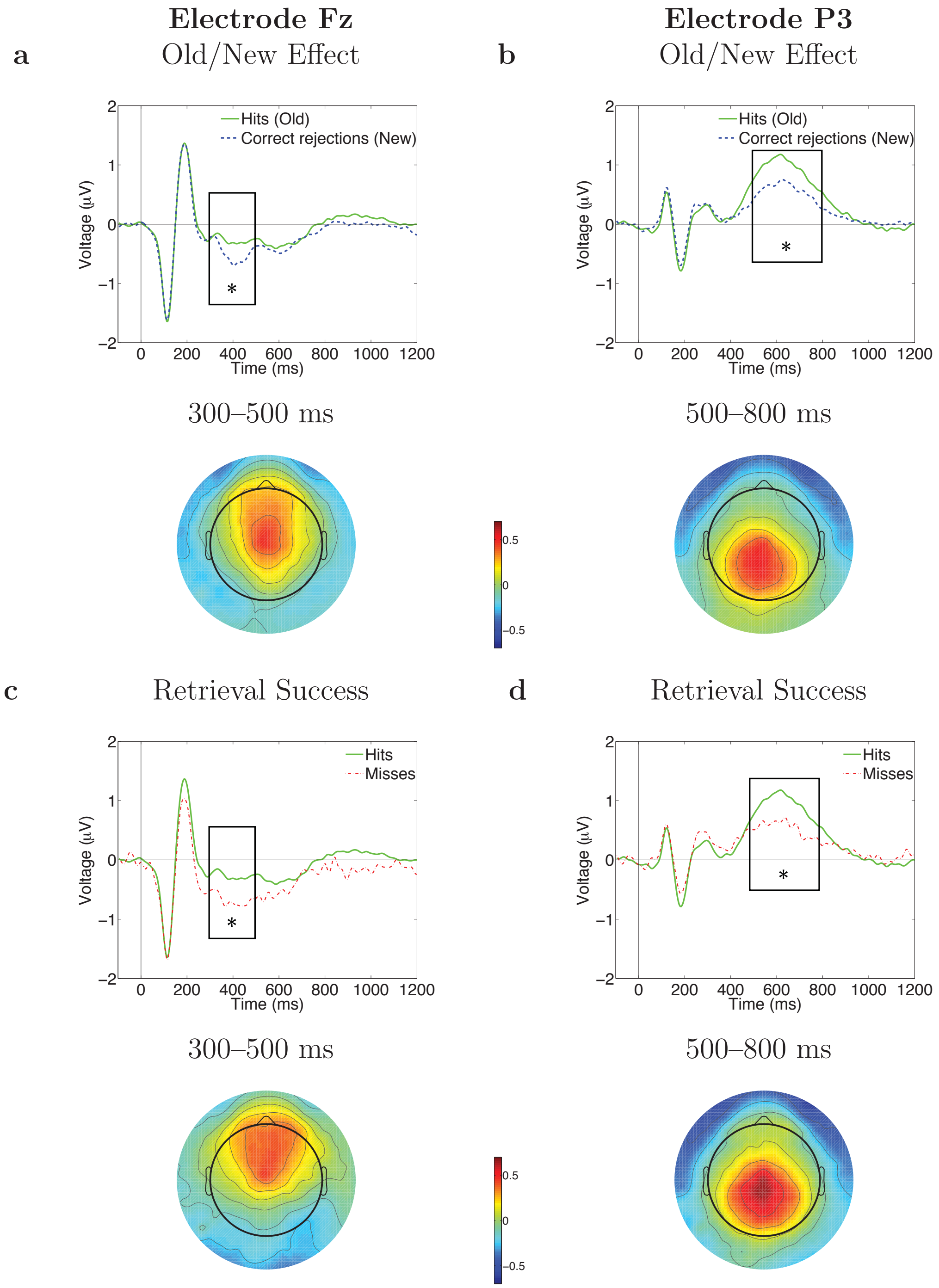


Figure 2.3: Grand-average ERPs and topographic distribution across participants during the test phase, applying the Old/new effect approach (a,b) and the Retrieval Success approach (c,d). The Old/new effect contrasts ERPs for correctly identified old items (hits) with ERPs for correctly identified new items (correct rejections), at Electrode Fz (a), showing the FN400 and at Electrode P3 (b), showing the Left Parietal Positivity. Retrieval Success contrasts ERPs for correctly identified old items (hits) with ERPs for incorrectly identified old items (misses), again shown at both Electrode Fz (c) for the FN400 and at Electrode P3 (d) for the Left Parietal Positivity. Topographic maps are spline plots, where color reflects mean voltage $[\mu V]$ over the corresponding time window.

	LPC	SW-Early	SW-Late
FN400	0.10	–0.01	-0.27^*
Left Parietal Positivity	$[0.25^*]$	0.35^*	0.06

Table 2.2: Pearson correlation ($df = 62$) between encoding ERPs (subsequent memory effect) and retrieval ERPs (old/new effect) across participants. * $p < 0.05$. [ ] indicates that this significant correlation become non-significant after the partial correlation analysis.

Correlations between ERP components across-phase

To directly test our hypotheses, we correlated each component-measure (from the corresponding difference wave) of the subsequent memory effect with each component-measure from the old/new effect across participants and reported in Table 5.3. Contradicting our prediction, the FN400 was not correlated with Late Positive Component; neither was it correlated with the Slow Wave-Early. The FN400 was significantly, but negatively, correlated with the Slow Wave-Late, consistent with the notion that the FN400 and the Slow Wave-Late reflect distinct, mildly mutually exclusive memory strategies.

Consistent with our prediction, the Left Parietal Positivity was positively correlated with the Slow Wave-Early, but was also unexpectedly correlated with the Late Positive Component. Because the subsequent memory effect components are not independent, follow-up analysis is needed for further clarification. Partial correlation, controlling for the Late Positive Component, indicated a positive correlation between the Slow Wave-Early and the Left Parietal Positivity (old/new effect), $r(61) = 0.26, p < 0.05$; in contrast, partial correlation, controlling for the Slow Wave-Early, found no significant correlation between the Late Positive Component and the Left Parietal Positivity (old/new effect), $r(61) = -0.02, p > 0.1$. This suggests that the positive correlation between the Late Positive Component and the Left Parietal Positivity (old/new effect) was mediated by Slow Wave-Early.

As a complementary, but arguably more direct comparison of encoding and retrieval ERPs, we next correlated the subsequent memory effect measures with the retrieval-success effect measures, which we report in Table 2.3. The FN400 was significantly positively correlated with the Late Positive Component, matching our prediction, as well as with the Slow Wave-Early, which was unexpected. The Left Parietal Positivity was not correlated with either the Late Positive Component or the Slow Wave-Early, and, surprisingly, trended toward negatively correlating with the Slow Wave-Late. As before, due to the dependence of the

	LPC	SW-Early	SW-Late
FN400	0.51^*	$[0.43^*]$	0.13
Left Parietal Positivity	0.14	0.15	$-0.22^\dagger$

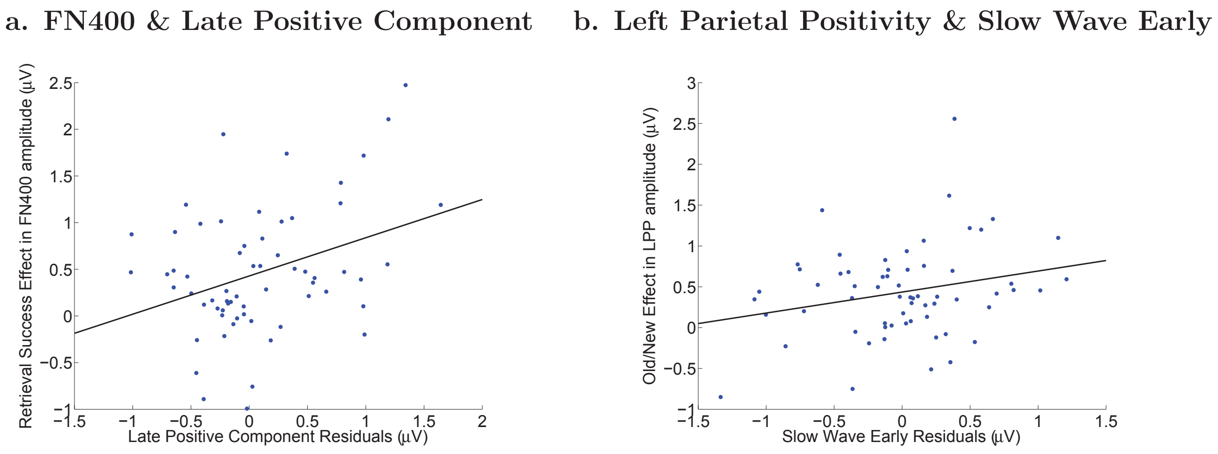
Table 2.3: Pearson correlation ($df = 62$) between encoding ERPs (subsequent memory effect) and retrieval ERPs (retrieval-success effect) across participants. * $p < 0.05$; † $p < 0.1$; [ ] indicates that this significant correlation become non-significant after the partial correlation analysis.

subsequent-memory measures, follow-up analyses are required. Again, a partial correlation analysis was applied to explain the relationship between the FN400 (retrieval-success effect), and two subsequent memory effect components. Partial correlation, controlling for the Slow Wave-Early, indicated a positive correlation between the Late Positive Component and the FN400 (retrieval-success effect), $r(61) = 0.35, p < 0.05$; in contrast, partial correlation, controlling for the Late Positive Component, found no significant correlation between the Slow Wave-Early and the FN400 (retrieval-success effect), $r(61) = 0.08, p > 0.1$. This suggests that the positive correlation between the Slow Wave-Early and the FN400 (retrieval-success effect) was mediated by the Late Positive Component. In addition, to ensure our selection of time of those ERP features, we included a timepoint-by-timepoint correlation analysis on Appendix and ploted in figure4.4. In sum, the timepoint-by-timepoint correlation analysis confirmed our selection of time winddow for ERPs.

In sum, our predicted correlation pattern was found, but only when using the retrieval-success effect measure of the FN400 and the old/new effect measure of the Left Parietal Positivity 2.4.

2.3.4 Relationship between memory-related ERPs and behavioral measures

Because EEG measures are observational, one can always ask whether a given ERP feature is relevant for memory performance or not. In the case of memory-related ERPs, we examine the differences between remembered and not remembered trials (subsequent memory effect at encoding, and retrieval-success effect at retrieval). The assumption is that these ERP-differences could reflect some processes related to memory function. However, if ERP measures could also be shown to explain variance in memory performance across subjects, that would provides additional convergent evidence that would strengthen the argument for



a. FN400 & Late Positive Component **b. Left Parietal Positivity & Slow Wave Early**

Figure 2.4: Across–subject scatter plots illustrating relationships between pairs of ERPs across memory stages (a) showing FN400 Retrieval Success Effect (difference wave of hits-misses) at test positively correlating with the residual of the Late Posivity Component (difference wave of hits-misses) after controlling for Slow Wave Early at study; (b) showing the Left Parietal Positivity Old/New effect (difference wave of hits-correct rejections) at test correlating with Slow Wave Early (difference wave of hits-misses) controlling for Late Posivity Component at study.

behavioral relevance. To test this possible behavioral relevance, we correlated, across subjects, each difference-wave measure of the subsequent memory effect, old/new effect, and retrieval-success effect each with d' and response time of hits. Of the encoding ERPs, the Late Positive Component correlated positively with d' [$r(62) = 0.29$, $p < 0.05$] and negatively with response time [$r(62) = -0.28$, $p < 0.05$]. The correlations between the Slow Wave and both d' and response time were not significant. Of the retrieval ERPs, we found no significant correlations using the old/new effect measure; however, with the retrieval-success effect measure, FN400 correlated positively with d' [$r(62) = 0.34$, $p < 0.05$] and negatively with response time [$r(62) = -0.26$, $p < 0.05$] (Figure 2.5). The Left Parietal Positivity was not correlated with either behavioral measure.

As reported in the previous section, we found a significant correlation between the Late Positive Component, and the FN400 (retrieval-success effect). To further understand the relationship between the ERPs and behavior, we carried out partial correlations. While controlling for d', the Late Positive Component and the FN400 remained significantly correlated [$r(62) = 0.47$, $p < 0.05$]. However, when controlling for either the Late Positive Component or the FN400, the correlations between d' and the other ERP measure were

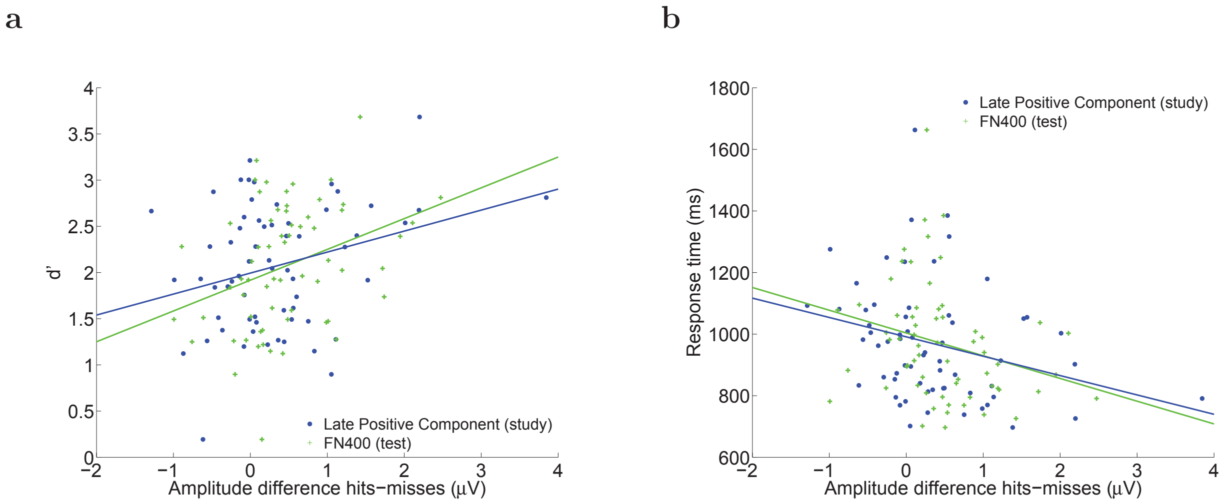


Figure 2.5: Across–subejcts scatter plots illustrating relationships between ERPs and behavioral measures (a) showing a positive correlation of d' with the Late Positive Component amplitude difference between hits and misses at study (blue “•”), and also with FN400 amplitude difference between hits and misses at test (green “+”); (b) showing a negative correlation of response time with the Late Positive Component amplitude difference between hits and misses at study (blue “•”), and FN400 amplitude difference between hits and misses at test (green “+”).

no longer significant. The same pattern emerged with a partial correlation controlling for response time. The Late Positive Component remained significantly correlated with the FN400 [$r(62) = 0.48$, $p < 0.05$], but the correlation with response time no longer stayed significant when controlling for either ERP measure. This correlation pattern suggests that some of the shared variance between the ERP components drives memory outcome, but the two ERP components also share variance that is untapped by the old/new memory test.

2.4 Discussion

Introducing an alternative approach to memory ERP research, we exploited individual variability by correlating memory-related ERPs at study with those at test, across participants. This analysis provides a new way of testing hypotheses about the cognitive significance of memory-related ERP deflections: namely, one can ask whether two ERP deflections reflect common or distinct processes (i.e., explain common or independent portions of the variance) and can ask whether a given ERP deflection explains individual variability in memory performance. This approach provides new insights that can inform previous interpretations of memory-related ERP deflections, as we elaborate below.

Our chief goal was to test whether a commonly reported pair of study-related ERP deflections mapped onto a commonly reported pair of test-related ERP deflections, as might be inferred from the current literature. At first blush, we found support for this pattern; the Late Positive Component and the FN400 were positively correlated (using the retrieval-success effect analysis) and the Slow Wave and the Left Parietal Positivity were positively correlated (using the old/new effect analysis), after partial correlation analyses took into account the statistical dependence of the subsequent memory effect components. This pattern of results echoes prior findings that the Late Positive Component and the FN400 correspond to “shallow” encoding processes, whereas the Slow Wave and the Left Parietal Positivity correspond to “deep” encoding processes (Fabiani et al., 1990; Rugg & Curran, 2007). The Late Positive Component and the FN400 (retrieval-success effect) correlated with d’ and response time, which strengthens the notion that these two early ERP features are relevant to memory performance. However, the Slow Wave and Left Parietal Positivity correlated only when the old/new analysis (not retrieval success, which takes memory outcome into account); this, and their non-significant correlation with behavioral measures weakens the evidence for these late ERP feature contributing directly to old/new recognition-memory.

Although some researchers have functionally distinguished the Late Positive Component from the Slow Wave, measures of these subsequent memory effect components are highly correlated. This is evident in many published subsequent memory effect ERP figures: it is often not clear when the Late Positive Component ends and the Slow Wave begins (Figure 4.2), leading one to wonder whether at least some of the variance in the Slow Wave should really be viewed as a continuation of the voltage shift due to the Late Positive Component. However, the fact that the retrieval ERPs correlated differentially with the Late Positive Component and the Slow Wave suggests that, although they may overlap, they are at least partly functionally distinct.

When we correlated the Left Parietal Positivity (retrieval-success effect) with the two Slow Wave windows, we only found a trend toward a negative correlation between Left Parietal Positivity and Slow Wave-Late. It is not clear why Left Parietal Positivity and Slow Wave-Late were negatively correlated; however, it may be that although Slow Wave-Late and Left Parietal Positivity were both suggested to reflect “deeper” processing, they could have different neural sources, possibly reflecting slightly mutually exclusive, deep strategies. Finally, the dependence of the Slow Wave-Early correlation with the Left Parietal Positivity on the old/new analysis suggests that the cognitive process tapped by the Slow Wave-Early affects how, at test, lure items will be processed, which we discuss below.

At retrieval, we applied both the old/new effect approach (comparing hits with correct rejections) and the retrieval-success effect approach (comparing hits with misses). Both approaches have been used to investigate ERP signals related to memory retrieval, but they could be quite different. The old/new effect discriminates old from new items (which were, by definition, never presented during study), whereas the retrieval-success effect discriminates remembered from not-remembered items (all having been presented during study). The conventional ERPs and topographies look similar using these two approaches (Figure 2.3), which may explain why there has not been much debate about the relative merits of each method. However, correlations are sensitive not to mean values, but to variability around the means, and our correlation results suggest that the subtle difference between old/new effect and retrieval-success effect may be cognitively relevant.

The FN400 correlated with the Late Positive Component only when the retrieval-success effect measure was used, suggesting that it is tightly linked to effective judgments of studied items (namely, study processes tapped by the Late Positive Component), but reflects little about how the response to lure items is influenced by what happens at study. We found support in our dataset that the FN400 correlated with memory performance measures, d' and response time. Moreover, this FN400–memory performance measure correlation was significant only using the retrieval success contrast of FN400. This is in line with the view that the FN400 reflects the strength of the probe item in the signal-detection model or the familiarity-strength in a dual-process model of recognition memory. Our findings are compatible with the view that the FN400 and the N400 are related, in that they both reflect semantic processing, because of evidence that the Late Positive Component reflects some semantic processing (Kutas & Federmeier, 2011). Our findings are also compatible with the view that the FN400 indexes the memory strength or confidence (Finnigan et al., 2002; Woroch & Gonsalves, 2010). The coupling of the Late Positive Component to the FN400, however, means that whatever interpretation is ultimately favored for the FN400 may also apply to the Late Positive Component.

In contrast, our Left Parietal Positivity correlated positively with the Slow Wave-Early (when controlling for the Late Positive Component) when the old/new effect analysis was used, but no significant correlation was found using the retrieval-success effect measure. This suggests that the Left Parietal Positivity does not reflect recognition success as a consequence of encoding processes *per se* (as measured by our subsequent memory effect components). This finding is reminiscent of numerous sources of evidence that parietal-lobe contributions to memory retrieval are more closely linked to metamemory processes, such as judgments of recollection, than to veridical recognition itself (Ally et al., 2008; Cabeza et al., 2008; Wagner et al., 2005; Woroch & Gonsalves, 2010). Our findings thus suggests that the Left Parietal Positivity could be used to discriminate old from new items (targets from lures), based on what happened during study (as indexed by the Slow Wave-Early). This at first seems paradoxical, because new items were not available to the participant during study. However, there are precedents for this kind of result. The latency of the Left Parietal Positivity increased with increasing hit rate but also increased with increasing correct rejection rate across participants (Johnson Jr. et al., 1985). We did not find any significant correlation between behavioral measures with the amplitude of the Left Parietal Positivity; however, it is possible that latency carries different information than amplitude.

Finnigan et al. (2002) argued that the Left Parietal Positivity facilitates the discrimination of old and new items. There is in fact a class of models of recognition memory that embody the assumption that strengths of new items could be influenced by study processes; a prominent and well tested model, Retrieving Effectively from Memory (REM; Shiffrin & Steyvers, 1997), is an example. In REM, when an item is studied, episodic traces are formed and test items are later compared to those memory traces to determine the old/new judgment. In addition, in REM, the more target items are studied, the more unstudied items, when presented as lure probes, will have *less* similarity to memory for the list. This prediction of a strength-based mirror effect was then observed in behavioural data (Criss, 2006, 2009), and further supported by neuroimaging evidence (Criss et al., 2013). The Slow Wave-Early during encoding might thus contribute to memory in a manner that reduces the memory match for unstudied items. Likewise, the Left Parietal Positivity may reflect a portion of recognition-test activity that is sensitive to the reduced memory match for unstudied items.

There has been an ongoing debate about whether old/new recognition judgments are based on one continuous-valued source of information or two qualitatively different sources, familiarity and recollection, termed single-process theory and dual-process theory, respectively (see Yonelinas, 2002, for a review). ERPs have been rallied in support of both models (Rugg & Curran, 2007; Rugg & Yonelinas, 2003). In the old/new effect, the FN400 and Left Parietal Positivity have been thought to index familiarity and recollection, respectively. Paller and Kutas (1992) first suggested that the Left Parietal Positivity could index recollection, followed up by Allan et al. (1998); Wilding et al. (1995) who suggested that the Left Parietal Positivity would also index a recall-like process. Our results cannot select between single- and dual-process theory. That said, we did replicate those Left Parietal Positivity, retrieval ERP feature that has been linked to recollection and source judgment. The standard dual-process theory argument would be that the Left Parietal Positivity reflects recollection, and recollection drives the old/new recognition judgement. However, if the Left Parietal Positivity truly reflected information derived from study that led to better recognition memory, then one would expect the retrieval-success effect-measured Left Parietal Positivity to correlate with one of the later ERP components of the subsequent memory effect (Slow Wave) and also with behaviour memory outcomes.

Many memory ERP papers have looked at both ERPs at encoding and ERPs at retrieval (e.g., Cycowicz & Friedman, 1999; Evans & Federmeier, 2007; Friedman, 1990a, 1990b; Friedman & Trott, 2000; Guo et al., 2006; Smith, 1993; Weyerts et al., 1997), but they did not directly test for relationships of ERPs across phases. This is very likely due to insufficient power for the correlation analysis. Many ERP studies have relatively smaller sample size (typically 15–30 participants) than our sample (N=64 included participants) which delivered us sufficient power to support the between-subject, across-phase correlations. Our findings show that across-phase correlations can add precision to our understanding of the cognitive processes tapped by study- and test-related ERPs, in the spirit of memory research, by following memory from encoding to retrieval. By directly relating ERPs between encoding and retrieval, we obtained a more nuanced understanding of the electrophysiological mechanisms of memory. We deliberately took a heavily *a priori* approach to focus our current work on clarifying the four most highly replicated memory ERP components related to recognition-memory at study and test. Clearly, there are numerous other ERP components that have been reported during study and test phases of memory tasks, and similar approach could be useful in elucidating the cognitive processes tapped by them as well. The proportion of variance accounted for by our correlation results, while significant, is not large, which suggests (not surprisingly) multiple processes are involved in both encoding and retrieval stages. Even where positive correlations were observed, the correspondence between encoding and retrieval ERPs is certainly not complete.

2.5 Conclusion: Implications for interpretating the cognitive meaning of memory-related ERPs

As we expressed in the introduction, our approach is complementary to other published approaches. Far from replacing standard, within-phase ERP analyses, our approach leads to findings that provide new constraints on how we can understand the cognitive significance of ERP features. For example, in the introduction, we described the ongoing debate about whether the FN400 reflects familiarity or conceptual priming (Voss & Federmeier, 2011). Our findings cannot resolve that debate, but they do suggest that the cognitive function of the FN400 is linked to that of the Late Positive Component, and should be investigated together. If definitive evidence were found that the FN400 reflected conceptual priming, that would suggest that the Late Positive Component also reflects encoding processes that lead to conceptual priming. If the FN400 reflects a combination of conceptual priming and familiarity effects, then the Late Positive Component may also reflect this same combination. Furthermore, the coupling of the FN400 with the Late Positive Component suggests that one might even be able to pinpoint the cognitive function of the FN400 by studying the functions of the Late Positive Component.

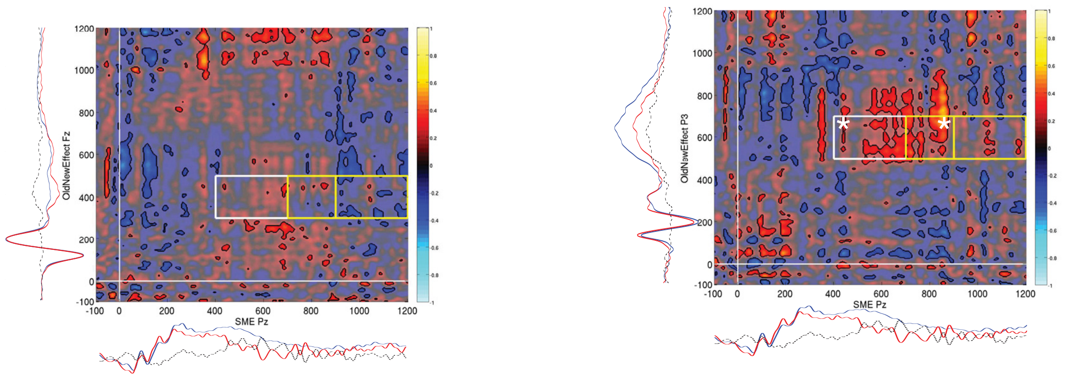
As for the late ERP features, our findings suggest that they may be less instrumental in driving old/new recognition than previously thought. Rather, the coupling of the Slow Wave and the Late Parietal Positivity might jointly drive more complex memory judgments, such as remember/know, source judgments or association-memory.

2.6 Robustness to the selection of time windows

One of the trickiest challenges in ERP research is the selection of time windows of analysis. We wanted to test our hypotheses in a manner that would speak directly to the ERP components that have reported previously, and thus designed our time windows in a way that would minimize our visual-inspection bias by referring to time windows during which the ERP components of interest have been previously reported. However, one can still worry that our results were sensitive to the precise choice of time window, particularly because the time windows used in previous research has varied. To assess the robustness of the correlation results, we plotted the full, timepoint-by-timepoint correlation value in Figure 4.4. Although there are patches of significance outside the windows of interest, the general impression one gets from these figures is that the pattern of results we obtained are relatively robust to the selection of time windows. This applies both to the old/new effect analysis (panels a and b) and the retrieval-success effect analysis (panels c and d).

Correlation across participants at different memory stages and electrodes

a SME (Pz) & old/new effect (Fz) **b** SME (Pz) & old/new effect (P3)



c SME (Pz) & RSE (Fz) **d** SME (Pz) & RSE (P3)

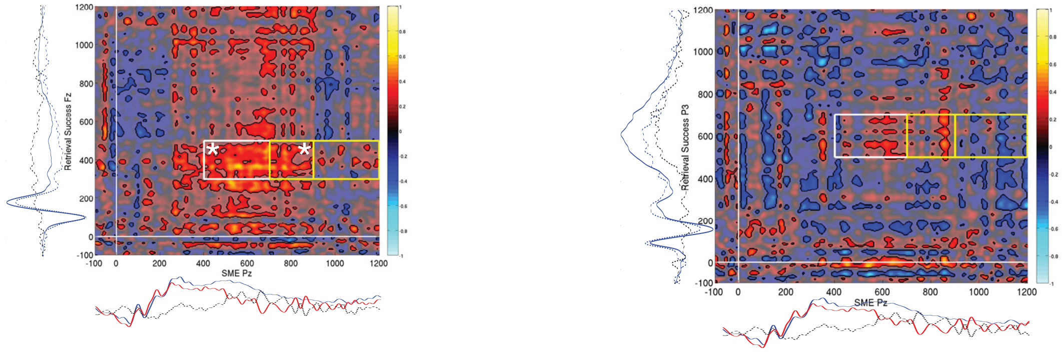


Figure 2.6: Correlation between encoding and retrieval ERPs across all participants, for all combinations of encoding and retrieval times. The horizontal axis represents the time course at electrode Pz during the encoding stage (subsequent memory effect). The vertical axis represents the time course at electrode Fz (FN400) or P3 (Left Parietal Positivity) during the retrieval stage (old/new effect or retrieval-success effect), with the 100 ms pre-stimulus baseline, and 1200 ms post-stimulus time. The subsequent memory effect (encoding hits–misses) is correlated with the old/new effect (hits–correct rejections; panels a and b), or retrieval-success effect (hits–misses; panels c and d) at every pair of time samples. The white line marks the onset of the stimulus and the semi-transparent white screen masks out any non–significant points ($p > 0.05$, pointwise). The boxes on the figure indicate the time windows selected for the main correlation analyses, where the white box marks the time window selected for Late Positive Component and yellow boxes mark the time window selected for Slow Wave-Early and Slow Wave-Late. "*" denotes significance ($p < 0.05$) when the corresponding time windows were averaged across. The insets are the corresponding ERPs of interest, with the black, dashed plot being the ERP difference wave from which were derived the voltage values that went into the correlation calculations.

Chapter 3

Rhythmic activity and individual variability in item recognition memory

Abstract

During study trials of a recognition-memory task, alpha ($\sim 10\ Hz$) oscillations decrease, and concurrently, theta ($4-8\ Hz$) oscillations increase when later memory is successful versus unsuccessful (subsequent-memory effect). Likewise, at test, reduced alpha and increased theta activity are associated with successful memory (retrieval-success effect). Here we take an individual-differences approach to test three hypotheses about theta and alpha oscillations in verbal, old/new recognition, measuring the difference in oscillations between hit-trials and miss-trials. First, we test the hypothesis that theta and alpha oscillations have a moderately mutually exclusive relationship; but no support for this hypothesis was found. Second, we test the hypothesis that theta oscillations explain not only memory effects within subjects, but also individual differences. Supporting this prediction, the duration of theta (but not alpha) oscillations at study and at test correlated significantly with d' across participants. Third, we test the hypothesis that theta and alpha oscillations reflect familiarity and recollection processes, by comparing oscillation measures to event-related potentials (ERPs) that are implicated in familiarity and recollection. The alpha-oscillation effects correlated with some ERP measures, but inversely, suggesting that the action of alpha oscillations on memory processes are distinct from the role of familiarity- and recollection-linked ERP signals. The theta-oscillation measures, despite differentiating hits from misses, did not correlate with any ERP measure; thus, theta oscillations may reflect elaborative processes not tapped by recollection-related ERPs. Our findings are consistent with alpha oscillations reflecting visual inattention, which can modulate memory, and with theta oscillations supporting recognition-memory in ways that complement the most commonly studied ERPs.

3.1 Introduction

Electroencephalographic (EEG) oscillations are rhythmic brain activity, some of which are thought to play important roles in memory function. Broadly speaking, better memory is associated with more theta ($4-8\ Hz$) activity but less alpha ($\sim 10\ Hz$) activity (Doppelmayr et al., 1998, 2000, 2005; Klimesch, 1996, 1999; Klimesch et al., 2005, 1990, 1993, 1994; Jensen et al., 2002). To understand the specific roles of rhythmic activity in recognition memory, we ask three questions about how theta and alpha oscillations might contribute to memory in a verbal episodic, recognition task. Taking an individual-differences approach, we seek evidence complementary to within-subject effects, about 1) how alpha and theta oscillations relate to one another, 2) how alpha and theta oscillations relate to memory-performance and 3) how alpha and theta oscillations relate to event-related potentials whose functions in recognition-memory have been well characterized.

Theme 1: the relationship between alpha and theta oscillations As just described, theta and alpha activity have seemed to relate in opposite ways to successful memory during study and test in contrast to some experimental manipulations. This raises the question: is there always a push-and-pull relationship between these two rhythms? Because often, when theta oscillations increase, alpha oscillations decrease across a given manipulation, it is possible that alpha and theta rhythms are strictly mutually exclusive. Two specific ideas have been proposed, that might lead one to this prediction. Klimesch (1999) speculated that theta and alpha might be two dynamic modes of a single network that supports memory function, where the theta mode facilitates encoding of new information and the alpha mode facilitates retrieval of memory. In this sense, these measures of oscillations would reflect a switch in operating frequency of the network. What follows is that theta and alpha duration and power should have a strict opponent-relationship with one another.

Alternatively, Klimesch et al. (2010) suggested alpha and theta oscillations each reflect numerous, but different, cognitive processes relevant to memory. For example, alpha activity differentiates stimulus types (concrete vs. abstract words, Schack, Weiss, & Rappelsberger, 2003), and attentional demands (see Klimesch, 1999, for a review); on the other hand, theta activity is associated with rehearsal, retention, and working memory (see Klimesch, 1997, 1999; Kahana et al., 2001, for a review). Even if theta and alpha activity originate from different networks, if they reflect cognitive processes that tend to be even somewhat mutually exclusive, alpha oscillations would tend to decrease when theta oscillations increased, and vice-versa. We adapted this logic to individual differences: If theta-oscillation measures are greater for a given participant, alpha-oscillation measures should be relatively smaller for that same participant; conversely, if alpha-oscillation measures are greater for a given participant, theta-oscillation measures should be relatively smaller for that same participant. Thus, we tested the mutual-exclusivity hypothesis, which predicts a negative correlation across participants between measures of alpha and theta oscillations. Specifically, our approach was to measure the subsequent memory effect (remembered – not-remembered items) at study and the retrieval-success effect (remembered – not-remembered items) at test in both alpha and theta activity for each participant, and to compute the correlation between those oscillation measures across participants. By starting with the difference in activity between remembered and not-remembered items, we restrict the analysis to activity that already distinguishes memory outcome within-subjects.

There are reasons one might not expect a negative correlation between duration or power of theta and alpha oscillations across participants. Instead of an inevitable opponent relationship between the two rhythms, it could be that many experimental manipulations happen to have opposite effects on alpha than on theta. Alpha and theta oscillations may just happen to respond in complementary ways to many experimental factors that have been studied. In this case, individual variability may not affect alpha and theta activity in opposite ways. The alternative prediction, then, is no significant correlation between theta and alpha measures across participants.

Yet other evidence leads one even to expect a positive correlation. Some studies have found that theta showed the same subsequent-memory effect as alpha activity: remembered trials had less alpha activity and less theta activity than forgotten trials (Burke et al., 2013; Depue et al., 2013; Fell et al., 2011; Lega, Jacobs, & Kahana, 2012). Lisman and Jensen (2013) and Hanslmayr and Staudigl (2014) argued that the proximity of theta and alpha frequencies might have contributed to their similar activity pattern, with alpha activity "bleeding in" to the theta band. Alternatively, Bonnefond and Jensen (2012) showed that increased alpha activity could enhance later memory performance by inhibiting external visual distracters. Further, it has long been known that visual imagery is an effective strategy for word memory (Paivio, 1969; Roediger, 1980). Theta activity, in turn, has been linked to mental imagery tasks (Bhattacharya, 2009; Li et al., 2009; Kawasaki & Watanabe, 2007). Moreover, alpha oscillations may also become more prevalent during visual imagery (Bartsch, Hamuni, Miskovic, Lang, & Keil, 2015), since alpha oscillations often synchronize during internally directed attention (as reviewed by Klimesch, Sauseng, & Hanslmayr, 2007). It is possible that when a participant employs an imagery-based strategy, both alpha and theta oscillations might increase to inhibit external stimuli, and to engage in mental imagery, respectively. In this case, the third prediction is a significant positive correlation between measures of theta and alpha activity across participants.

Theme 2: Convergent evidence for relevance to memory performance The logic of the subsequent-memory effect and retrieval-success effect is that these differences in brain activity could reflect some processes related to memory function, because they identify activity that differs between successful (remembered) and unsuccessful (not remembered) memory outcomes. But, because oscillation measures, like all brain-activity measures, are observational and correlational, it is always possible that theta and alpha oscillations are not necessary for memory performance, and could be epiphenomenal; additional convergent evidence is desirable.

Phase-coding and phase-coherence of theta oscillations was proposed to be the neural mechanism for encoding of episodic memory (Fell et al., 2001, 2003; Summerfield & Mangels, 2005; Weiss & Rappelsberger, 2000). Put simply, theta oscillations are thought to play a crucial role in successful encoding, and the difference in theta activity should produce a behavioral difference— a difference in memory performance. Some previous researchers have taken within-subjects effects further by splitting their participants into two groups based on their memory performance. Klimesch (1997) summarized numerous studies that found participants in a good-memory group had a greater decrease in alpha power, during both study and test, than participants in a poor-memory group. Complementing this, Doppelmayr et al. (1998) found parallel effects for theta power during test; participants in the good-memory group had a larger increase in theta activity than participants in the poor-memory group. Those results show that both alpha and theta oscillations can differentiate groups of participants based on their memory performance; if alpha and theta oscillation measures could also be shown to explain variance in memory performance (d' or response times of hits) across subjects in a continuous manner, that would provide additional convergent evidence that would strengthen the argument for their behavioral relevance. If not, that would weaken the argument, and suggest that we might be looking at a spectator process, or a process that is simply not relevant to the memory test we use. We expect to see a positive correlation between measures of theta activity and memory performance (d'), and a negative correlation for measures of alpha activity.

However, it is important to note that a large body of research has also suggested that an increase in alpha activity could also be beneficial to memory performance. When participants were asked to retain information in their mind, there were increased alpha activity during retention (synchronization), and alpha desynchronizes after the retention (Busch & Herrmann, 2003; Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003; Herrman, Senkowski, & Rottger, 2004; Jensen et al., 2002; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999; Sauseng et al., 2005; Schack & Klimesch, 2002). This active retention would lead to better memory performance later on. Thus, we might expect to see a positive correlation between measures of alpha activity and memory performance (d').

Theme 3: Using prior knowledge about event-related potentials to query the possible cognitive roles of alpha and theta oscillations Much of recognition-memory research has centered around a specific ongoing cognitive-process debate between single-process theory and dual-process theory. The dual-process position assumes that participants use two separable sources of information to make old versus new decisions: familiarity and recollection. Familiarity is supposed to be a relatively simple strength signal, whereas recollection is supposed to reflect additional, detailed contextual retrieval. In oscillation studies of recognition-memory, it has been proposed that theta activity is involved specifically in recollection. Reviewed by Nyhus and Curran (2010), increased theta power is related to better recognition, but more so when participants respond correctly to source judgements or make correct "remember" responses (compared to "know" responses), two ways researchers have attempted to operationalize recollection (e.g., Guderian & Düzel, 2005; Guderian, Schott, Rochardson-Klavehn, & Düzel, 2009; Gruber, Tsivilis, Giabbiconi, & Müller, 2008; Osipova et al., 2006). Other studies have implicated theta activity in familiarity-based retrieval. For example, Klimesch, Doppelmayr, Yonelinas, et al. (2001) found more theta power for "know" than "remember" responses. Moreover, Caplan and Glaholt (2007) measured oscillations during the study phase of a relational memory task (cued recall or word-pairs and triples), which is part of some definitions of recollection (Yonelinas, 2002). They found that anterior theta oscillations had greater duration for more accurate and faster participants. In short, theta oscillations are related to recognition memory, but it is not clear how this oscillation contributes to memory function and whether it is related to familiarity or recollection or both, or would be more consistent with single-process theory, which we consider in the Discussion.

In contrast to oscillations, recognition memory has been studied extensively using event related potentials (ERPs). Thus, if a particular oscillation were found to correlate with a particular ERP feature across participants, that would suggest a possible functional link between them. Then, what we know about the corresponding ERP (its cognitive or behavioral role) might also apply to the corresponding oscillation; and if not, then we could infer they do not relate to common cognitive demands of the task. The amplitude of the FN400 (frontal old/new effect) is sensitive to manipulations thought to affect familiarity, and the Left Parietal Positivity (parietal old/new effect) amplitude is sensitive to manipulations thought to affect recollection (see Rugg & Curran, 2007, for a review). Interestingly, Jacobs, Hwang, Curran, and J. (2006) noted that the timing of two bursts of theta activity coincided with the latencies of both the FN400 and the Left Parietal Positivity. They speculated that the earlier theta-activity signals were related to familiarity, and the later, to recollection. This interpretation would lead one to predict that measures of theta oscillations should correlate with both the FN400 and the Late Parietal Positivity, which we test as well.

Although there is still debate about what cognitive processes memory-related ERPs really reflect, at least we can ask whether an oscillation might correspond to the same cognitive process as a given ERP measure or a different process. Chen et al. (2014) took a similar individual-differences approach, to ask if ERPs during study and ERPs during test might explain any common variance across participants, and found that earlier ERPs (the Late Positive Component at study and FN400 at test) were correlated. The later ERPs (the Slow Wave at study and the Left Parietal Positivity) were also correlated. Using the same logic and approach, we correlated, across participants, measures of trial-averaged oscillations related to memory-success, to measures of ERPs related to memory-success. If, indeed, the same cognitive process is contributing to both an ERP feature and an oscillation measure, we should see a strong correlation between the two.

Quantifying oscillatory activity We wanted to choose a measure that would be relatively selective for rhythmic activity and minimally influenced by non-repeating signals. Most studies of memory-related oscillations have used windowed Fourier Transform or wavelet transforms to quantify spectral power as a function of frequency. Measured this way, activity need not necessarily be rhythmic (Klimesch, 1999). Any signal, whether rhythmic or non-rhythmic, can produce non-zero power values (Fourier's theorem). Transient artifacts or (non-repeating) event-related potentials may contribute to an increase in measured oscillatory power. Importantly, EEG signal, like most natural signals, has a coloured-noise form, meaning that power decreases with an approximate relationship of $1/f^{\alpha}$, where the lower frequency signals have a larger amplitude than the higher frequency signals. The coloured-noise form is present even when oscillatory activity is not present. This means the power not only measures the sum of power due to rhythmic genuine oscillations but also the non-rhythmic background signal that has energy in the corresponding frequency.

A method for detecting oscillations, known as BOSC (Better OSCillation detection, Caplan et al., 2001; Whitten et al., 2011), is conservative about what is treated as rhythmic activity, ensuring that, relative to conventional power measures, the results are more specific to oscillations, and relatively less influenced by non-repeating signals. Specifically, the BOSC method models the coloured-noise background signal to determine thresholds that enable one to detect when oscillations are present, so-called "oscillatory-episode detection." In addition to the power threshold, the EEG signal is also subject to a duration threshold to ensure that the detected signal is sustained (see Methods). Thus, the most popular measure derived from the BOSC method is termed $P_{episode}(f)$, a measure of the proportion of time during which oscillations were detected at each frequency, f. $P_{episode}$, a duration measure, ensures that the results relate to sustained rhythmic activity, and cannot be explained away by non-repeating signals. A measure of duration rather than size, $P_{episode}$ values are immediately interpretable: a $P_{episode}$ value of 0.5, for example, indicates that oscillations at the frequency of detection were deemed to be present during 50% of the recording.

This kind of measure of duration deviates from most approaches to quantifying oscillations, which measure power (amplitude squared). $P_{episode}$, therefore, is (by design) relatively insensitive to how large a rhythm is, measuring, instead, how long it lasts. That said, the BOSC method allows one to measure the power within oscillatory episodes, given that they were detected. Although duration of detected oscillations and average-power measures may be related, there is evidence that they can be sensitive to quite different sources of brain activity (Caplan, Bottomley, Kang, & Dixon, 2015). Rather than quantify power within detected oscillations, we simply conducted parallel sets of analyses using the more conventional power measure, log-transformed power as measured with the Morlet wavelet transform. When the conventional power measure agreed with the $P_{episode}$ measure derived from the BOSC method (which they nearly always did), that suggests either that the effects may be driven by duration rather than power, or that power increases approximately along with duration. Where they differ, that may indicate either that the $P_{episode}$ method missed an effect on power that does not influence the duration of occurrence of oscillations, or that the conventional power measure is picking up some non-rhythmic signal or short-duration signal that we wish not to confidently call rhythmic (recall that the BOSC criteria are designed to minimize Type I error; signal that fails to meet the strict criteria should therefore be viewed as indeterminate as to whether they reflect rhythmic or non-rhythmic activity).

Design of the current study We used a verbal recognition-memory procedure that was consistent with prior procedures and obtained both a large number of trials per participant (225 studied words and an equal number of unstudied items as lure probes) and a large sample size (66 participants). Because we wanted there to be sufficient individual variability in study and test, we did not instruct participants to study in any specific way. Yonelinas (2002) reviewed evidence that when participants are given Remember/Know, source or confidence judgements in addition to old/new judgements, that could change the way they make the old/new response itself. Because our aim at this stage was to understand the contributions of oscillations to old/new recognition, not Remember/Know, nor source, nor confidence judgements, we stick to the standard, simple old/new judgement response procedure.

3.2 Methods

3.2.1 Participants

Eighty-six (12 self-reported left-handed[1], 69 self-reported right-handed; 32 female) undergraduate students from an introductory psychology course at the University of Alberta, aged 17–28 years (mean = 20, SD = 2.29) participated for course credit. Data from 20 partici-

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[1] When we excluded these 12 participants from the analyses, the pattern of results was not affected.

pants were excluded from analyses: 7 were excluded from analyses due to low rates of misses (<11 trials, $< 5\%$), 11 due to excessive artifacts in the EEG, and 2 who presumably reversed the response-key mapping (accuracy $< 50\%$), for a total of 66 participants included. Of the final sample, 59 were part of the 64 participants included in Chen et al. (2014), but the broader filter (0.1–50 Hz) used here resulted in more participants being excluded due to uncorrectable artifacts. Therefore, to more closely equate the sample size with that of Chen et al. (2014), we ran an additional 8 participants, all but one of whom (due to excessive artifacts) could be included in the present analyses. All participants were required to have English as their first language and had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment, and the procedures were approved by a University of Alberta ethical review board.

3.2.2 Materials

The stimuli were nouns drawn from the Toronto Word Pool (Friendly et al., 1982) composed of 4–8 letters. Kucera-Francis frequency was between 1–712 per million. Study items and test probes were presented in the centre of the computer screen using Times New Roman 17 point font with the E–Prime presentation software version 2.0 (Psychology Software Tools).

3.2.3 Procedure

The methods are the same as in (Chen et al., 2014). The session took place in an electrically shielded, sound-attenuated chamber. Each study set comprised 25 words, displayed one at a time for intentional study. Each word was presented for 1500 ms with jittered uniform-pseudo-random intertrial interval between 300–500 ms. The end-of-list distractor task, included to reduce recency effects that can contribute nuisance variability to the memory measure, consisted of 5 equations of the form of $A(+\ or\ -)B(+\ or\ -)C =$, where A, B, and C were randomly selected digits from 1 to 9, and the addition and subtraction operation were randomly selected in the equation. The participant was asked to type the correct answer. Each equation remained in the centre of the screen until the participant made a response. In the test phase, which immediately followed the distractor task, 50 words were presented, half (25 words) from the study phase (targets, or “old” items), and half (25 words) not previously presented (lures, or “new” items), drawn at random, without replacement, from the word pool. Each probe was a single word that remained on the screen until the

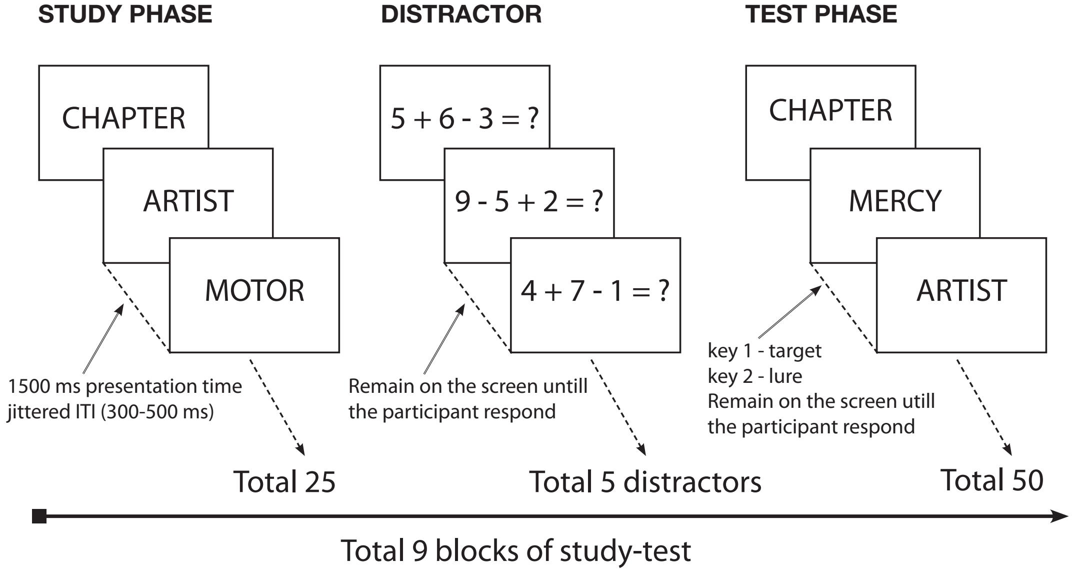


Figure 3.1: The experimental procedure. Each box illustrates the computer screen at a particular stage in the task (text has been enlarged relative to the screen size to improve clarity of the figure). There were 9 blocks of study–distractor–test.

participant made an old/new response by pressing key 1 for old (judged to be a target) and 2 for new (judged to be a lure). Nine blocks of study/test were presented for a total of 225 study trials and 450 probe trials (Figure 5.1). For each trial, response time (RT) and accuracy were recorded.

3.2.4 Electroencephalography (EEG) Recording and Preprocessing

EEG was recorded using a high-density 256-channel Geodesic Sensor Net (EGI, Electrical Geodesics Inc., Eugene, OR), amplified at a gain of 1000 and sampled at 250 Hz. Impedances were kept below 50 kΩ and EEG was initially referenced to the vertex electrode (Cz). Data were analyzed by custom MATLAB scripts in conjunction with the open-source EEGLAB toolbox (Delorme & Makeig, 2004, `http://sccn.ucsd.edu/eeglab`). Signal was bandpass filtered between 0.1–50 Hz and average re-referenced to a common average. Artifacts were corrected via Independent Component Analysis, implemented in EEGLAB (Jung et al., 2000). The selection of components was based on visual inspection of the spatial topographies, time courses, and power spectral characteristics of all components. The components accounting for stereotyped artifacts including eye blinks, eye movements, and muscle movements were removed from the data. Event latencies were corrected with a time lag correction due to a known hardware calibration problem identified by EGI. Study trials were separated into subsequently remembered items (subsequent memory effect hits) and subsequently forgotten items (subsequent memory effect misses) based on the participants' responses during the test phase, and likewise for activity during test trials.

3.2.5 ERP analysis

ERPs were analyzed as in Chen et al. (2014). ERP trials were time-locked to the onset of stimulus and referenced to a 100 ms pre-stimulus baseline. Electrodes and time windows were selected to be consistent with previous measurements of our ERP features of interest. The two subsequent memory effect components were analyzed at electrode Pz in the time window of 400–700 ms latency post–stimulus for the Late Positive Component. Due to the longer time window of the Slow Wave (700–1200 ms) and variability in time windows in which the Slow Wave has been reported in the literature, we separated the Slow Wave into 700–900 ms (Slow Wave-Early) and 900–1200 ms (Slow Wave-Late) post–stimulus. For test activity, the two retrieval-success effect (hits–misses) components were analyzed in the time window of 300–500 ms post–stimulus for the FN400 at electrode Fz, and 500–800 ms post–stimulus for the Left Parietal Positivity at electrode P3.

3.2.6 Oscillation analysis

Oscillations were analyzed over the entire continuous EEG recording (without epoching to avoid edge effects) in both power and BOSC analysis. Oscillations occurring at all frequencies for each trial was calculated by averaging $P_{episode}$ and power over the time window of 0–1200 ms post-stimulus (which encompasses the timing of all the ERP measures of interest) for each trial. The frequency bands of interest comprised the following central frequencies: theta, 4.00 Hz, 4.78 Hz, 5.66 Hz and 6.72 Hz; and alpha, 8.00 Hz, 9.51 Hz and 11.31 Hz. For band-specific analyses, $P_{episode}$ and log-power were averaged across the frequencies sampled within the band. Analysis was confined to the frontal and parietal midline electrodes, Fz, and Pz, with an emphasis on Fz for theta oscillations and Pz for alpha oscillations.

Conventional power analysis The entire continuous EEG recording (without epoching to avoid edge effects) was analyzed with a Morlet wavelet transform, with a width of 6 cycles and sampled 24 frequencies logarithmically over the 1–45 Hz range. Wavelet power values were than log-transformed, and normalized by dividing the given log-power by the sum of log-power across all frequencies. Frequencies within a band were collapsed by averaging the log-power within that particular band. Analysis was also confined to the same electrodes as in the BOSC analyses. For each participant, one power value was obtained at each frequency, at each electrode, averaging over all trials of a given condition.

BOSC analysis The BOSC method is based on the same wavelet transform as the power analysis. In applying this method (Caplan et al., 2001; Whitten et al., 2011), signals were only classified as rhythmic if they exceeded a particular power threshold for a given frequency for a minimum length of time (duration threshold). Briefly, the power threshold was set to the 95$^{\text{th}}$ percentile of the probability distribution of power values (the $\chi^2(2)$ distribution expected based on the fit mean-power value, after fitting the power spectrum, estimated from the entire continuous record, with a linear regression in log-log coordinates) at a given frequency. The duration threshold was set at each frequency to three cycles. Activity was labeled rhythmic when both the power threshold and the duration threshold were exceeded. The proportion of time oscillations were detected within a time segment, denoted $P_{episode}(f)$ was calculated for each frequency, f. With the power threshold, this method is not sensitive to changes in the amplitude of oscillations above the threshold; however, it is thus more selective for rhythmic (repeating) activity than other methods (Caplan et al., 2001; van Vugt, Sederberg, & Kahana, 2007; Whitten et al., 2011).

Finally, consider that the limits of frequency bands, like theta and alpha, have varied considerably across studies. This makes it important to examine each sampled frequency individually. To check the robustness of our frequency bands, we also examined our correlation analyses at all frequencies sampled over the 1–45 Hz range.

All statistical analyses were carried out using MATLAB and Statistic Toolbox Release 2008b (The MathWorks, Inc., Natick, Massachusetts, United States) and IBM SPSS Statistics for Mac, Version 21.0. (IBM Corp., Armonk, NY).

Condition	[%]	Response time [ms]
hits (old)	76.7 (14.1)	953 (222)
misses (old)	23.3 (10.2)	1313 (435)
correct rejections (new)	85.3 (15.9)	1074 (299)
false alarms (new)	13.7 (11.4)	1507 (573)

Table 3.1: Accuracy (percentage) and response time (ms) values, along with their standard deviations across subjects in parentheses.

3.3 Results

Average accuracy was approximately mid-way between ceiling (100%) and floor (50%) levels (Table 5.1). This feature, combined with sizeable standard deviations for both accuracy and RT suggests that there is meaningful variability across participants that might be explained in our analyses. First, we checked whether we could replicate the standard within-subject memory effects, analyzing the subsequent-memory effects and retrieval-success effects at both alpha and theta frequencies. Then we tested the hypothesis that there is a trade-off relationship between the two frequency bands, which in turn, facilitate both encoding and retrieval (theme 1). Next, we tested the behavioral relevance of alpha and theta oscillations by correlating memory-outcome measures with the oscillation measures (theme 2). Finally, we interrogated the possible cognitive functions of alpha and theta oscillations by correlating memory-related ERPs with the oscillation measures (theme 3).

3.3.1 Replication of subsequent memory and retrieval-success effects

The subsequent memory effect was analyzed at electrodes Fz and Pz (Figure 5.2a,b). Paired-samples, two-tailed t tests comparing the duration of oscillatory activity ($P_{episode}$) between subsequent hits and subsequent misses. Subsequent hits had theta oscillations at electrode Fz more of the time than subsequent misses, and subsequent hits had alpha oscillations at electrode Pz less of the time than subsequent misses in the alpha band (Table 5.2). A similar pattern was found at test when we conducted a retrieval-success effect analysis, comparing theta and alpha activity for the hits to misses (Figure 5.2c,d). Paired-sample, two-tailed t tests comparing mean $P_{episode}$ values confirmed the retrieval-success effect in both the theta (at Fz) and alpha (at Pz) bands (Table 5.2).

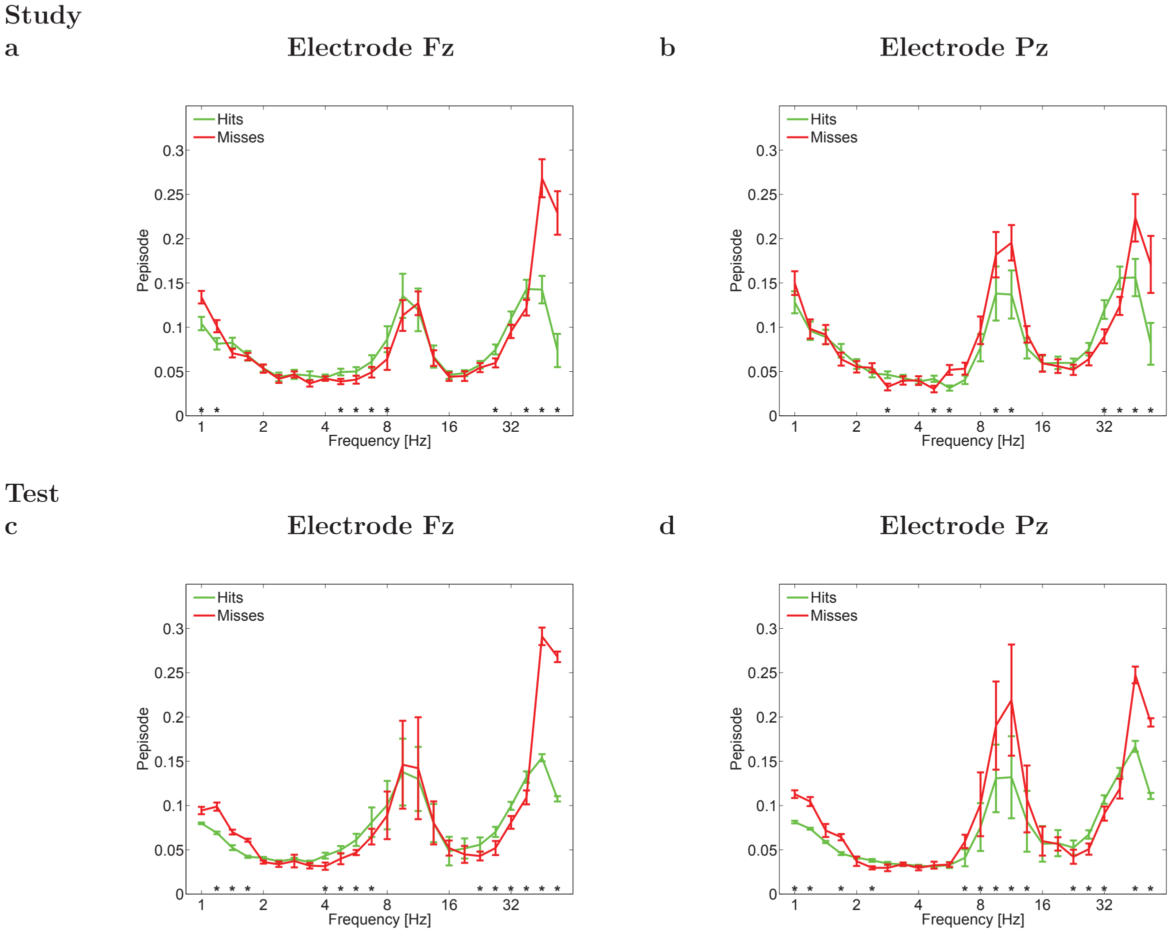


Figure 3.2: Average proportion of oscillatory activity ($P_{episode}$) is plotted as functions of frequency between hits (green) and misses (red) during study and test. Error bars represent 95% confidence intervals * denotes significant ($p < 0.05$) differences between hits and misses.

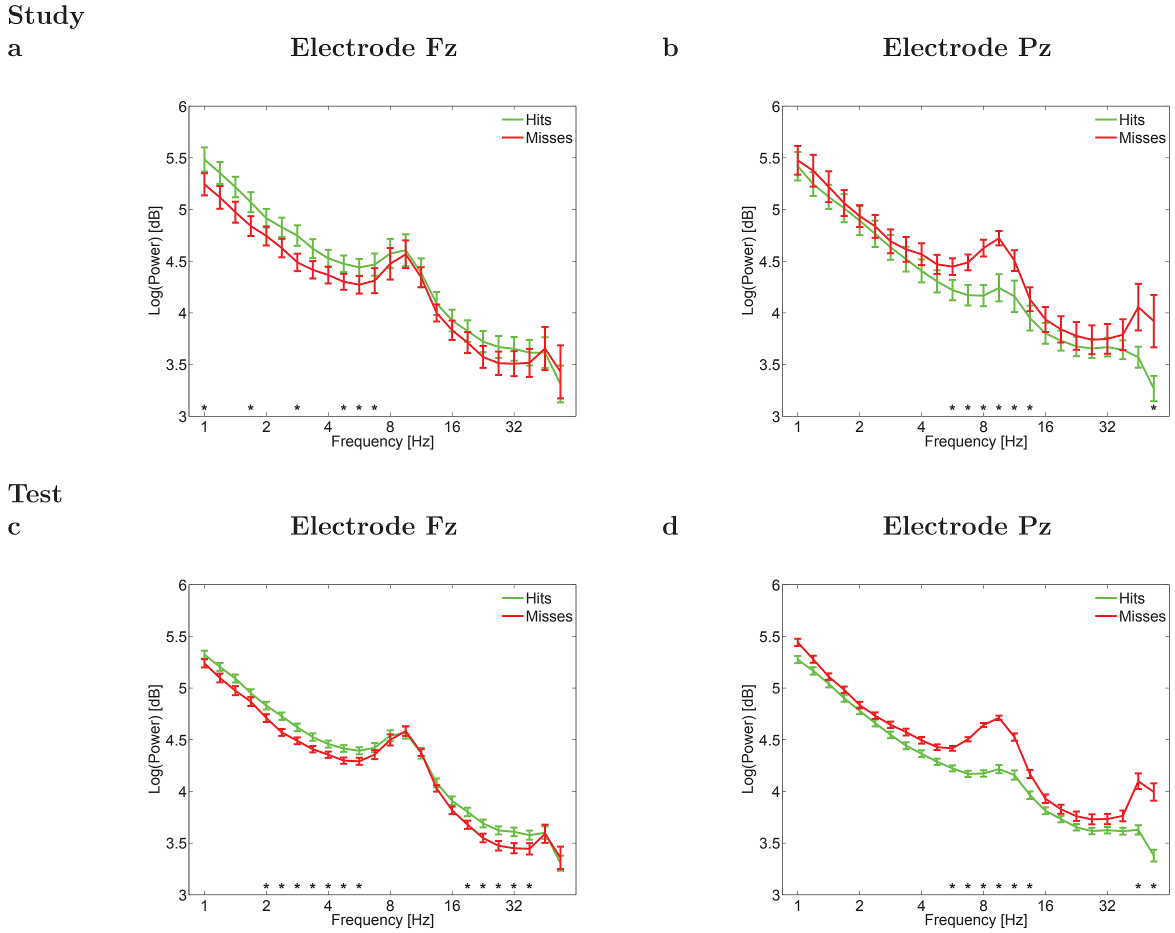


Figure 3.3: Average wavelet power (log-transformed) is plotted as functions of frequency between hits (green) and misses (red) during study and test. Error bars represent 95% confidence intervals * denotes significant ($p < 0.05$) differences between hits and misses.

The mean-power analysis produced the same pattern of results in the theta and alpha band at both study ($\alpha : t(65) = -5.60$; $\theta : t(65) = 3.08$, $p < 0.05$) and test ($\alpha : t(65) = -5.39$; $\theta : t(65) = 3.08$, $p < 0.05$; Figure 3.3). In sum, both the duration of oscillatory activity ($P_{episode}$) and mean-power analyses replicated previous within-subjects findings of alpha activity decrease and theta activity increase during hits versus misses, at both study and test (Fell et al., 2011; Klimesch, 1999; Klimesch, Doppelmayr, Pachinger, & Ripper, 1997; Klimesch et al., 2010). This lays the groundwork for the individual-differences analyses that are the main focus of the study.

Finally, note that there were differences in the gamma band between hits and misses (Figure 5.2). This is in line with prior findings suggesting gamma activity is related to

	Study		Test	
Electrodes	α	θ	α	θ
Fz	-0.89	**3.37***	0.19	**2.72***
Pz	**-2.73***	-1.34	**-5.23***	-0.21

Table 3.2: t-values from paired-samples, two-tailed t-tests ($df = 65$) comparing mean $P_{episode}$ between subsequent hits & subsequent misses during study, and between hits & misses during test for alpha and theta oscillations at electrodes of interests. $*$ denotes $p < 0.05$.

memory function (Jensen, Kaiser, & Lachaux, 2007), although beyond the scope of our hypotheses.

3.3.2 Theme 1: Possible inverse relationship between theta and alpha oscillation

We now turn to our first question, regarding the relationship between alpha and theta at both study and the test. First, ignoring memory outcome, we evaluate the possibility that participants who generally have more alpha activity, correspondingly, have less theta activity. We correlated, across participants, the $P_{episode}$ values in the alpha band (measured at Pz) with the $P_{episode}$ in the theta band (measured at Fz), at both study and test, averaged over trials, regardless of memory outcome. We found no significant correlation between alpha and theta oscillation durations at study ($r(64) = 0.16,\ p > 0.1,\ 95\%\ CI\ [-0.09, 0.40]$), nor at test ($r(64) = 0.11,\ p > 0.1,\ 95\%\ CI\ [-0.07, 0.37]$). Although the confidence intervals cannot exclude negative correlation values, they suggest that if the underlying correlation is negative, it must be quite small in magnitude. Next, by incorporating memory outcome into the analysis, we correlated the subsequent-memory effect and the retrieval-success effect ($P_{episode}$ difference measure of hits–misses, for study and test activity, respectively) across participants. Again, no significant correlation was found at study ($r(64) = 0.18,\ p > 0.1,\ 95\%\ CI\ [-0.07, 0.42]$), nor at test ($r(64) = 0.19, p > 0.1,\ 95\%\ CI\ [-0.04, 0.39]$).

To assess the robustness of the correlation results to the choice of frequency limits of the theta and alpha bands, and to address the possible bleed-in effect between alpha and theta measures mentioned in the Introduction (Lisman & Jensen, 2013; Hanslmayr & Staudigl, 2014), we plotted the full matrix, frequency-by-frequency, of correlation values between electrode Fz and Pz at both study and test in Figure 3.4. Frequencies nearby one another were correlated positively (see the bright color diagonal effect), as expected. There were significant correlations in other regions of the figure, beyond the frequencies of interests, which might be worth looking into for further follow-up studies; for example, delta- and gamma-frequency $P_{episode}$ measures appeared to be correlated, as well as posterior gamma- with anterior theta-frequency oscillations, which might reflect a theta/gamma multiplexing process that has been suggested to support memory (Bragin et al., 1995; Belluscio, Mizuseki, Schmidt, Kempter, & Buzsáki, 2012; Lisman & Jensen, 2013; Mormann et al., 2005; Sederberg et al., 2003). More importantly, the frequencies in the alpha and theta bands (outlined in the black box) showed no strong negative correlations, suggesting that averaging across frequencies within each band did not misrepresent the underlying pattern.

The mean-power measure also produced a non-significant (p ¿ 0.1) correlation between alpha and theta power at study (r(64) = 0.16) and at test (r(64) = 0.20) regardless of memory outcome. Moreover, by incorporating memory outcome into the analysis (subsequent-memory effect and the retrieval-success effect), no significant (p ¿ 0.1) correlation was found at study (r(64) = 0.18) and at test (r(64) = 0.11). Thus, a trade-off relationship between alpha and theta activity did not appear to be present in our task.

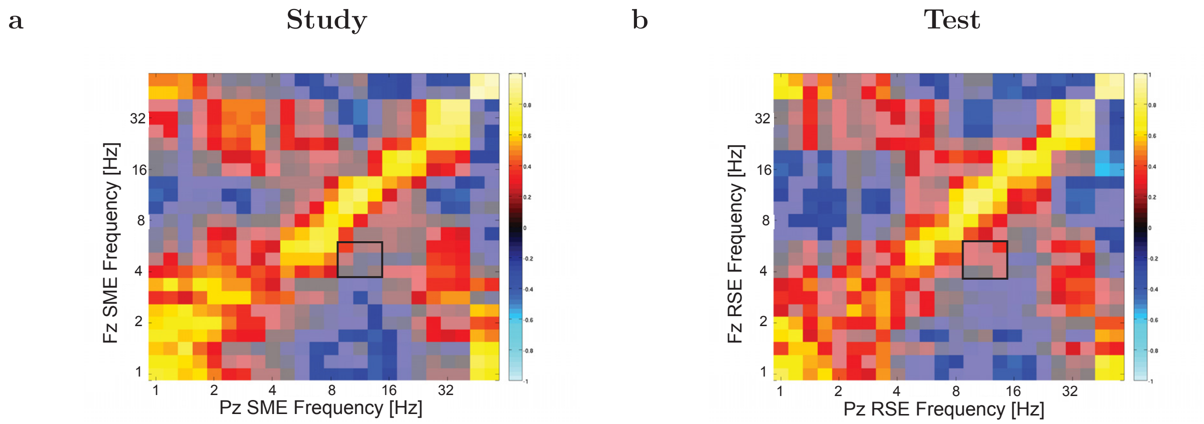


Figure 3.4: Pearson correlation ($df = 64$) plotted for all $P_{episode}$ frequencies between electrode Fz and Pz at study and test. The semi-transparent while screen masks out any non-significant points ($p > 0.05$). The black boxes on the figure indicate the frequencies selected for the main correlation analysis: theta (at Fz) and alpha (at Pz).

3.3.3 Theme 2: Relationship between oscillations and individual variability in memory-outcome

We next examined the behavioral relevance of these memory-related oscillations. If oscillation measures could be shown to explain variance in memory performance across participants, that would corroborate the within-subjects results, and strengthen the role of theta and alpha oscillations in this recognition task. We first correlated the theta and alpha ($P_{episode}$) subsequent memory effects with the behavioral measures (d' and mean response time for hits) across participants, and likewise for the retrieval-success effects (Table 5.3). There was a significant correlation between d' and theta-oscillation durations at study (Figure 3.5) but not at test. Although speculative, it may be that theta oscillations are just more short-lived and thus harder to measure at test. Note that at least at the higher range of the theta band, the correlations were positive, just not significant.

The mean-power measure produced the same pattern of results: a significant correlation between d' and theta power at study ($r(64) = 0.30, p < 0.05$) but not at test, and non-significant ($p > 0.1$) correlations between alpha power and response time ($study : r(64) = -0.1$; $test : r(64) = -0.03$), or d' ($study : r(64) = -0.05$; $test : r(64) = 0.02$). Thus, more theta activity (measured by both $P_{episode}$ and mean-power measures) during study may lead to better recognition memory performance later on. On the other hand, there was no support for our prediction that alpha oscillations would inversely correlate with either behavioral measure Although alpha oscillations (both measures) showed significant subsequent-memory and retrieval-success effects within subjects, the individual differences in alpha oscillations ($P_{episode}$ and mean-power measures) may not reflect individual differences in performance.

Again, to assess the robustness of these results, we conducted a broadband version of this analysis and plotted correlation values as functions of all frequencies at electrodes Fz and Pz (Figure 5.3). In general, the broadband analyses confirmed the results of the band-averaged analyses. Although there was no significant correlation between RT and band-averaged retrieval oscillation measures, 4.7 Hz oscillations at electrode Fz correlated negatively with RT (significantly, uncorrected). This appeared to be washed out by other frequencies when averaged across frequencies within the theta band (Figure 5.3,d).

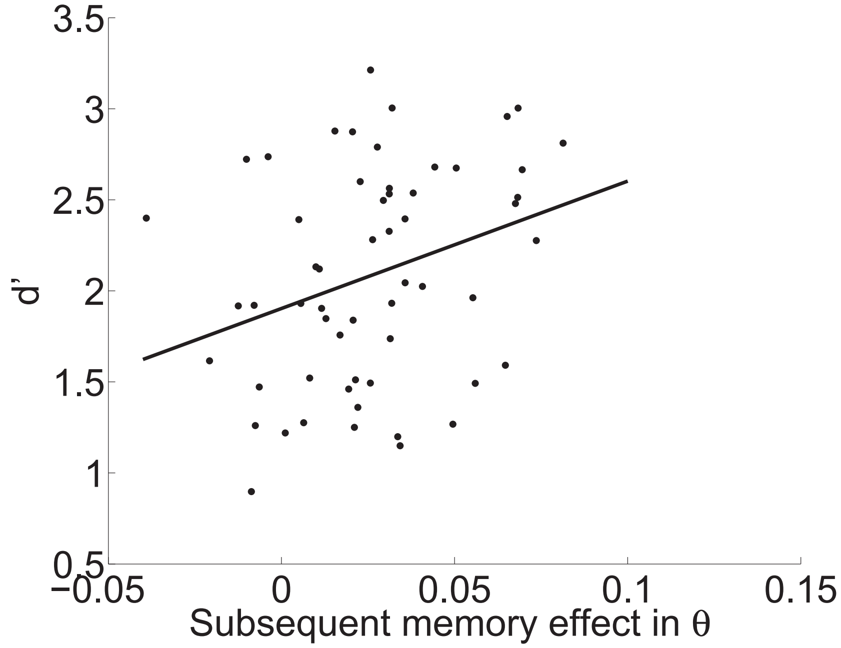


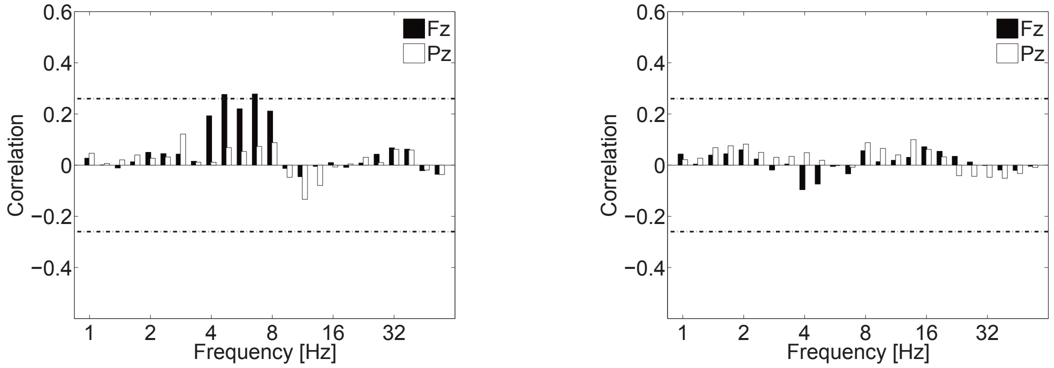
Figure 3.5: Relationship between d' and the size of the subsequent-memory effect in the theta band ($r(64) = 0.30$). Each point represents a single participant. The subsequent-memory measure is the proportion of oscillations ($P_{episode}$) for hits minus misses.

	Study		Test	
	α	θ	α	θ
d'	-0.06 (-0.31, 0.2)	**0.30*** (0.04, 0.52)	-0.12 (-0.36, 0.14)	0.09 (-0.17, 0.34)
RT	0.08 (-0.19, 0.33)	-0.07 (-0.31, 0.20)	0.03 (-0.23, 0.28)	-0.21 (-0.45, 0.05)
Late Positive Component	[0.33* (0.08, 0.54)]	-0.12 (-0.36, 0.14)	–	–
Slow Wave-Early	[0.31* (0.07, 0.54)]	-0.08 (-0.33, 0.18)	–	–
Slow Wave-Late	**0.46*** (0.23, 0.64)	0.07 (-0.18, 0.32)	–	–
FN400	–	–	**0.29*** (0.04, 0.51)	0.02 (-0.24, 0.27)
Left Parietal Positivity	–	–	-0.15 (-0.39, 0.11)	0.06 (-0.20, 0.32)

Table 3.3: Pearson correlation ($df = 64$) between 1) mean $P_{episode}$ alpha (recorded at Pz) and theta (recorded at Fz) oscillations with behavioral measures (d' and response time, RT); 2) study mean $P_{episode}$ alpha and theta oscillations with study ERPs (the Subsequent Memory Effect); 3) retrieval mean $P_{episode}$ alpha and theta oscillations with retrieval ERPs (retrieval success effect). Reported along with 95% confidence interval, $*$ denotes $p < 0.05$; [ ] indicates that this significant correlation become non-significant after the multiple regression model (see main text).

Study

a **d’** **b** **Response Time**



Test

c **d’** **d** **Response Time**

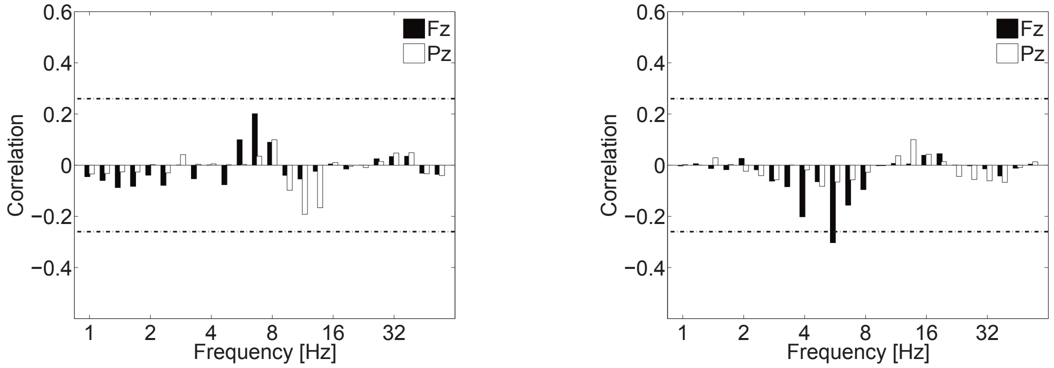


Figure 3.6: Pearson correlation ($df = 64$) plotted for all $P_{episode}$ frequencies at study (a,b) and test (c,d)correlating with d’ (a,c) and response time (b,d). Oscillations were recorded at electrode Fz and Pz. The dashed lines denote the significance thresholds ($p < 0.05$, two-tailed).

3.3.4 Theme 3: Relationship between oscillations and memory-related ERPs

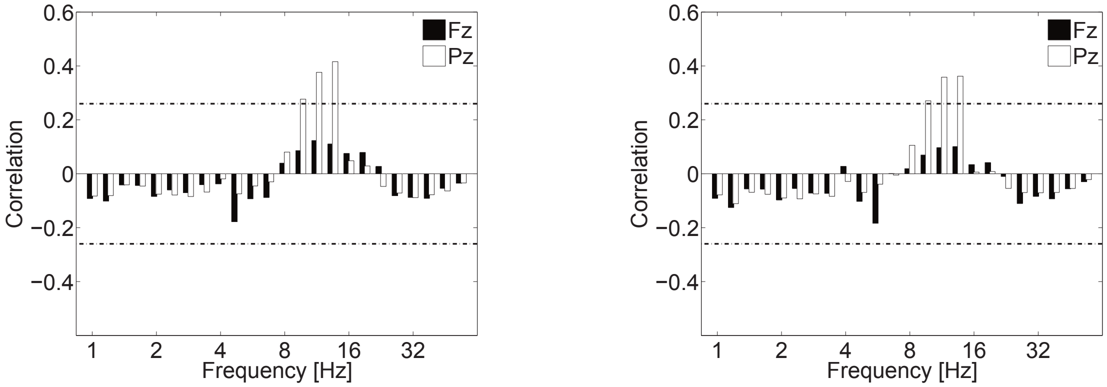
We aimed to inform our understanding of the possible functions of the alpha and theta oscillations to recognition-memory by seeking possible relationships between well studied memory-related ERPs and oscillation measures. Using the $P_{episode}$ measure, we thus correlated, across subjects, each oscillation measure with mean-voltage measures of the most commonly reported ERPs implicated in recognition-memory, as laid out in the Introduction. Surprisingly, the theta-band subsequent-memory effect was not correlated with any of the three ERP subsequent-memory effects. However, the alpha-band subsequent-memory effect was correlated with all three: the Late Positive Component, the Slow Wave-Early, and the Slow Wave-Late time windows (Table 5.3). The broadband analysis at study confirmed this; alpha-band oscillation durations (subsequent-memory effect) were correlated with the Late Positive, Slow Wave-Early and Slow Wave-Late (Figure 5.4).

The mean-power analyses produced the same pattern of results: significant ($p < 0.05$) correlation between subsequent memory effect alpha power with the Late Positive Component ($r(64) = 0.34$), the Slow Wave-Early ($r(64) = 0.36$), and the Slow Wave-Late ($r(64) = 0.52$).

It is important to note that Chen et al. (2014) found the subsequent-memory effect ERPs in all three time windows to be mutually correlated with one another. To resolve this ambiguity, multiple regression was run with $P_{episode}$(alpha) as the measure and the Late Positive Component, the Slow Wave-Early, and the Slow Wave-Late as the three predictors. This model explained 18% of the variance. The only significant predictor was the Slow Wave-Late, $\beta = 0.38,\ t = 2.63,\ p < 0.05$ (Figure 3.8a). The Late Positive Component, $\beta = 0.14,\ t = 0.79,\ p > 0.1$, and the Slow Wave-Early, $\beta = 0.01,\ t = 0.08,\ p > 0.1$, were not significant predictors. These results suggested that the Slow Wave-Late was the main predictor for $P_{episode}$(alpha); the positive correlation between alpha duration and the Late Positive Component, and the Slow Wave Early might be due to the positive correlation with the Slow Wave-Late.

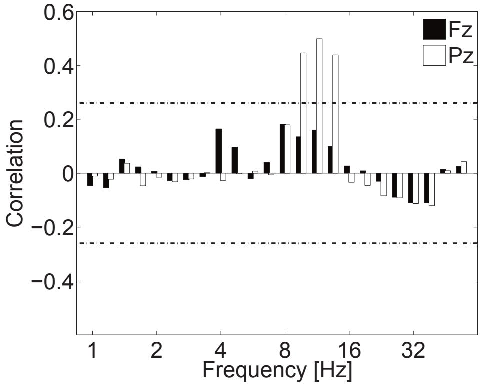
This same multiple regression was run with alpha-band mean-power as the measure, and the Late Positive Component, the Slow Wave-Early, and the Slow Wave-Late as the three predictors. As above, we found the Slow Wave-Late $\beta = 0.41,\ t = 3.13,\ p < 0.05$ was the only significant predictor.

It may seem logically backwards that later activity could explain away earlier activity. Quite likely, activity is already ramping up at the times of the two earlier ERPs signals, but this early activity is only coupled with alpha activity if it either is sustained throughout the entire window of analysis, or appears during the time frame of the Slow Wave-Late. Initially, we predicted that increase in alpha activity might correlate with memory-related ERP negatively. Rather, the positive correlation between alpha oscillation measures and Slow Wave-Late indicates that if a participant has more alpha-suppression (less alpha activity), the amplitude difference is smaller for the Slow Wave-Late. Researchers have functionally distinguished the Late Positive Component from the Slow Wave, where the former is thought to index the encoding of item information or "shallower" processing, and the latter is thought to index "deeper" levels of processing (Fabiani et al., 1990; Karis et al., 1984). It would follow that when participants use deeper strategies (such as visual imagery) to learn new information, we should expect to see a bigger subsequent memory effect during the Slow Wave. Another line of research also found that when participants turned their attention inward, or engaged in mental imagery, increased alpha power was observed (Bartsch et al., 2015). Taken together, we speculate that our participants were employing strategies that tapped into the deeper processes indexed by the Slow Wave, this was also reflected in increased alpha oscillations (both measures).



a **LPC**

b **Slow Wave - Early**



c **Slow Wave - Late**

Figure 3.7: Pearson correlation ($df = 64$) plotted for all $P_{episode}$ frequencies at study correlating with subsequent memory effect ERPs (a, LPC, b, Slow Wave Early, c, Slow Wave Late). Oscillations were recorded at electrode Fz and Pz. The dashed lines denote the significance thresholds ($p < 0.05$, two-tailed).

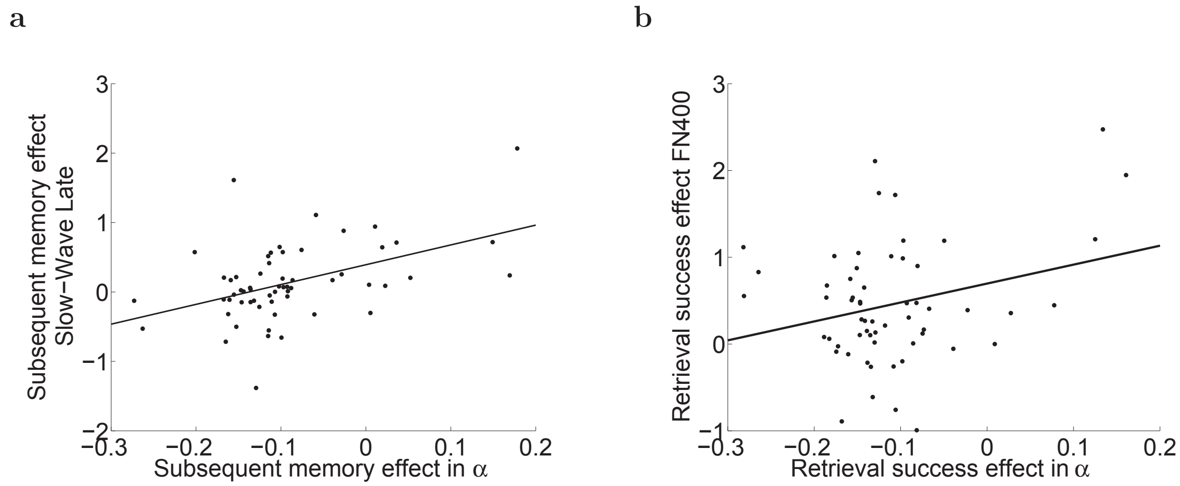


Figure 3.8: Relationship between a) Slow Wave-Late and the size of the subsequent-memory effect in the alpha band (r(64) = 0.46), and b) FN400 and the size of the retrieval-success effect in the alpha band (r(64) = 0.29). Each point represents a single participant. The subsequent-memory measure is the proportion of oscillations ($P_{episode}$) for hits minus misses at study, and the retrieval-success measure is the proportion of oscillations ($P_{episode}$) for hits minus misses at test.

During test, we found a positive correlation between $P_{episode}$(alpha) and the FN400, but not with the Late Parietal Positivity. $P_{episode}$(theta), again, did not correlate with any retrieval ERP measure (Table 5.3). We also conducted the broadband analysis to assess the robustness of the correlation results. No frequencies showed any significant relationships with the FN400 except within the alpha band. Moreover, we found no significant correlations between any frequencies and the Left Parietal Positivity (Figure 5.5).

Using the mean-power measure, the correlation between the alpha-band retrieval-success effect and the FN400 was not significant, although it was in the same direction as found for $P_{episode}$ (mean-power: $r(64) = 0.18, p > 0.1$).

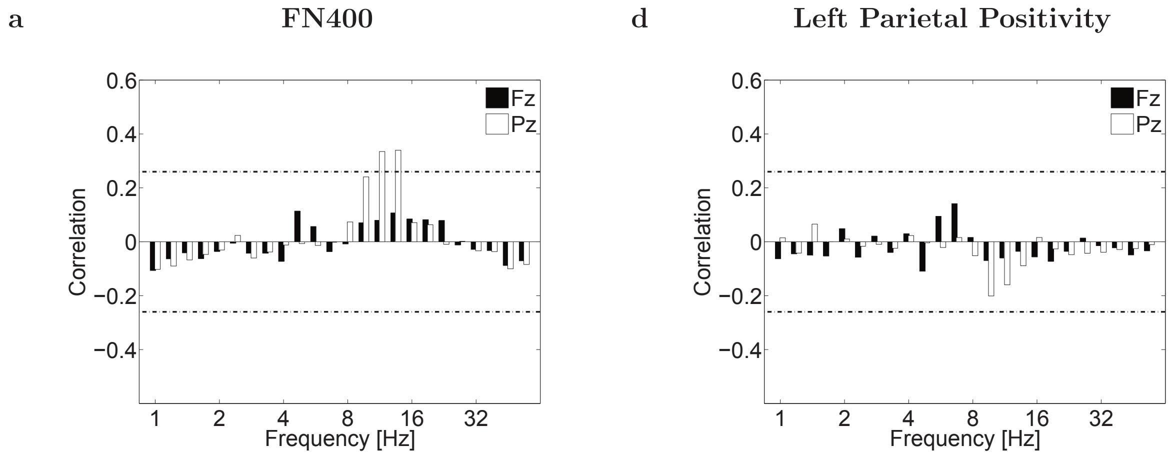


Figure 3.9: Pearson correlation ($df = 64$) plotted for frequencies showing retrieval success effect at retrieval correlating with retrieval success effect ERPs (a, FN400, b, LPP). Oscillations were recorded at electrode Fz and Pz. The dashed lines denote the significance thresholds ($p < 0.05$, two-tailed).

The old/new effect versus the retrieval-success effect

We have argued (Chen et al., 2014), that it makes most sense to compare study activity and test activity using the subsequent memory effect and retrieval-success effect measures, since they both take into account memory success versus failure. However, the bulk of published research regarding ERPs during recognition test has measured the so-called "old/new effect," contrasting correct-old versus correct-new items (hits – correct rejections). Indeed, Chen et al. (2014) found that, for ERPs, although the within-subjects effects appeared similar for retrieval-success effect and old/new effect comparisons, the individual-differences effects were quite different. We thus asked if our results would be different if we substituted the old/new effect for the retrieval-success effect. The paired-samples, two-tailed t-test, comparing mean $P_{episode}$ between hits and correct rejections during test, was significant for the theta band at electrode Fz ($t(65) = 2.73$, $p < 0.05$), with theta oscillations more of the time during hits than correct rejections, but not was significant for the alpha band ($t(65) = -0.68, p > 0.1$) at electrode Pz, replicating prior results (Klimesch, 1999; Klimesch, Doppelmayr, Stadler, et al., 2001).

In addition, we tested the possible relationship between the $P_{episode}$(theta) old/new effect and the ERP old/new effects (FN400 and Left Parietal Positivity) across participants (Table 3.4). There was a significant correlation between the theta-band old/new effect and

	d'	RT	FN400	Left Parietal Positivity
θ	**0.29*** (-0.08, 0.51)	-0.17 (-0.28, 0.41)	-0.03 (-0.29, 0.22)	0.11 (-0.14, 0.36)

Table 3.4: Pearson correlation ($df = 64$) between retrieval theta oscillations (Old/New effect: hits - correct rejections) with behavioral measures (d' and RT) and with retrieval ERPs (Old/New effect); theta recorded at electrode Fz. $*$ denotes $p < 0.05$.

d' (Figure 3.11) but not RT. The theta-band old/new effect was not significantly correlated with the FN400, nor with the Left Parietal Positivity. Checking the robustness of correlation, in the broadband analysis, one can also see a strong correlation with d' of the old/new effect at several frequencies within the theta-band (Figure 3.10).

Checking the key findings with the mean-power measure, the old/new effect was also significant in the theta-band at electrode Fz ($t(65) = 2.53,\ p < 0.05$). The correlation between the theta-band old/new effect and d' did not reach significance using the mean-power measure, although it was still nominally positive ($r(64) = 0.16,\ p > 0.1$).

In sum, the results concerning alpha oscillations ($P_{episode}$ and mean-power measures) are consistent with alpha oscillations reflecting attention. In the old/new effect, hits are contrasted with correct rejections; because a correct rejection is a correct response, it is plausible that visual attention is as elevated during correct rejections as during hits (in contrast to during misses, which might, sometimes, reflect lapses in visual attention). The positive correlation between d' and theta oscillations ($P_{episode}$ but not mean-power measure) also strengthens the behavioral relevance of theta oscillations for old/new recognition. This raised the question whether theta oscillations might be related to differentiation effects in recognition (Shiffrin & Steyvers, 1997), which motivated the following additional analyses.

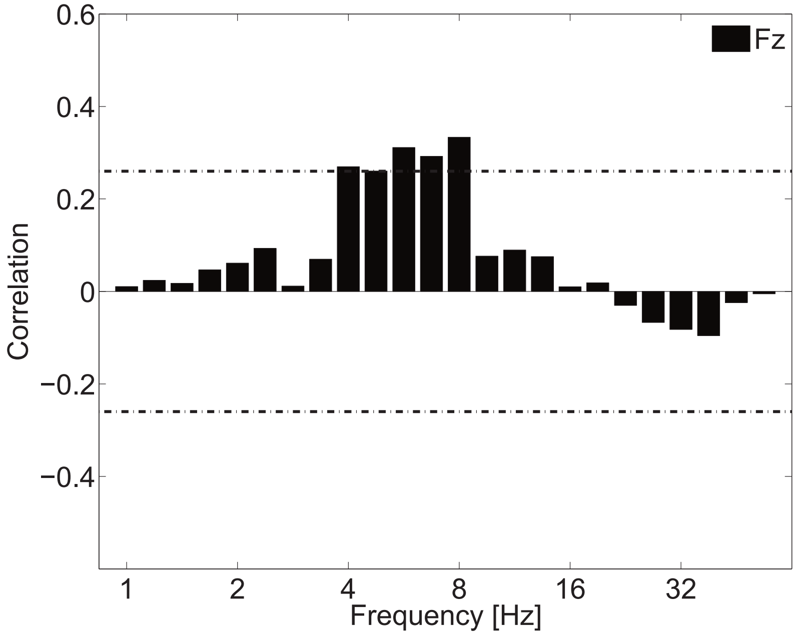


Figure 3.10: Pearson correlation ($df = 64$) plotted for frequencies showing old/new effect at retrieval correlating with the d'. Oscillations were recorded at electrode Fz. The dashed lines denote the significance thresholds ($p < 0.05$, two-tailed).

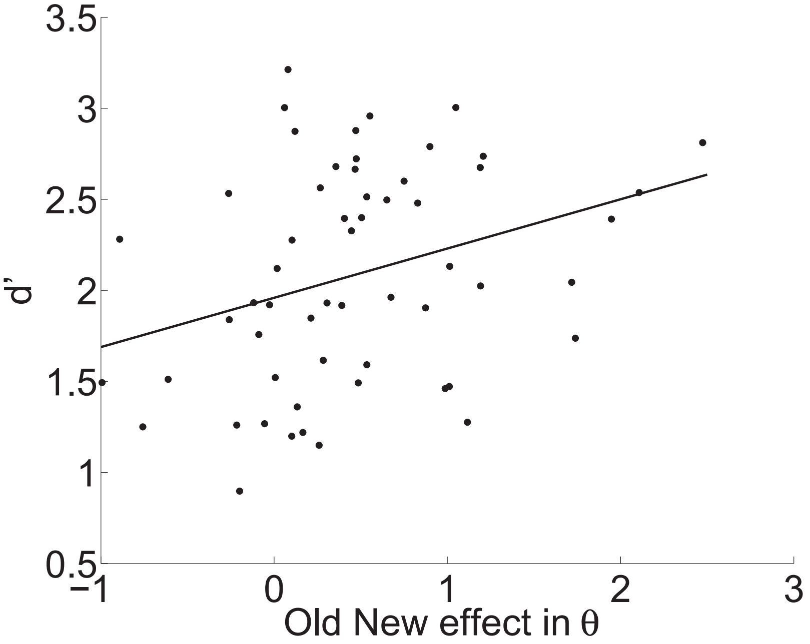


Figure 3.11: Relationship between d' and the size of the old/new effect in the theta band (r(64) = 0.29). Each point represents a single participant. The theta old/new effect measure is the proportion of oscillations ($P_{episode}$) for hits minus correct rejection, recorded at electrode Fz.

3.3.5 Follow-up analysis of theta oscillations and memory outcome

The finding that theta oscillation duration covaried with d' during test, only when we contrasted hits with correct rejections (old/new effect), but not hits–misses, led us to move beyond the difference measures. A multiple regression was run with d' as the measure and $P_{episode}$(theta) during study for later-hits, during study for later-misses, during hits at test, during misses at test and during correct rejections at test as the five predictors[2] (Table 5.4). The model explained 17% of the variance. The significant predictors were theta-oscillation durations during study for later-hits, during hits at test, and during correct rejections at test. The theta oscillations during study for later-misses, and misses at test, were not significant. Thus, theta-oscillation durations associated with successful memory (hits at both study and test) were the main predictors of d', along with theta oscillations during correct rejections, with a negative β. This suggests that theta oscillations help to encode items well,

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[2] We could not include false alarms due to low trial counts.

predictors	beta	t
θ Hits (study)	0.61	2.36*
θ Misses (study)	0.21	0.42
θ Hits (test)	0.88	2.21*
θ Misses (test)	0.09	0.35
θ Correct Rejection (test)	-0.62	-2.61*

Table 3.5: Regression model for theta activity predicting d'. The theta activity measure is the proportion of oscillations ($P_{episode}$) for hits and misses during study, and hits, misses and correct rejections during test, recorded at electrode Fz. $*$ denotes $p < 0.05$.

but also support the discrimination of old from new items. In differentiation models, such as Retrieving Effectively from Memory (Shiffrin & Steyvers, 1997), when an item is studied, a memory trace is formed; later a test item is compared to those formed memory traces to make an old/new decision. The better list-items are studied, not only will studied items match better, but unstudied items will match memory of the list worse, leading to strength-based mirror effect. Theta oscillations at study might index the formation of memory traces which, later on, lead to reduction of the degree to which new items match memory. Likewise, theta oscillations at test may reflect the strength of the match of the probe item to memory. Studied items that are correctly identified (hits) may thereby be more likely to evoke theta oscillations, matching memory better, than lure items that are correctly identified (correct rejections), matching memory less.

Note that the correlation between the theta-band old/new effect and d' did not reach significance using the mean-power measure. Thus, it was not warranted to conduct the multiple regression analysis with mean-power.

3.3.6 Robustness to the selection of time windows

To assess the robustness of the correlation results to the choice of time-windows of analysis, we re-ran our analyses for the theta and alpha bands, using the $P_{episode}$ measures, varying the time window following stimulus onset, in 200-ms segments. The full 1200-ms window, therefore, was broken down into six segments. Importantly, the BOSC analysis had been run over the continuous recording, and was only then calculated by averaging the $P_{episode}$ values during each of the time windows: 1–200 ms, 201–400 ms, 401–600 ms, 601–800 ms, 801–1000 ms and 1001–1200 ms. It is important to note that $P_{episode}$, just as with any measure of power, integrates over signal before and after the 200-ms window of interest. Thus, the final 200-ms windows of analysis should not be taken as instantaneous estimates of oscillatory activity; rather, our objective here was to test whether our effects might depend critically on the selection of the time window. In general, the smaller time-window results were similar to the full 1–1200 ms window. Across all six time windows, the pattern of significance (and sign) that were the same as the full-window analysis, for alpha oscillations, were: the non-significant correlation between the alpha subsequent-memory effect and both d' and RT, the significant correlation with Late Positive Component and Slow Waves, the non-significant correlation between the alpha retrieval-success effect and behavioral measures and the Left Parietal Positivity. For theta oscillations, the unchanged findings were: the non-significant correlation between the theta subsequent-memory effect and RT, as well as all subsequent-memory effect ERP measures, the non-significant correlation between the theta retrieval-success effect and behavioral measures, FN400, and the Left Parietal Positivity, the significant correlation between theta old/new effect and d', the non-significant correlation between the theta old/new effect and FN400, and the Left Parietal Positivity. There were three results that were significant within 1–1200 ms time window analyses but non-significant (although the correlations were unchanged in sign) at some of the shorter time-windows: 1) the theta subsequent-memory effect significantly correlated with d' at the first four time windows but was non-significant at 801–1000 ms ($r(64) = 0.19, p > 0.1$) and 1001–1200 ms ($r(64) = 0.19, p > 0.1$); 2) the theta old/new effect significantly correlated with d' at the first four time windows but was non-significant at 801–1000 ms ($r(64) = 0.19, p > 0.1$) and 1001–1200 ms ($r(64) = 0.18, p > 0.1$); and 3) the alpha retrieval-success effect significantly correlated with FN400 across all except the 601–800 ms window ($r(64) = 0.21, p > 0.1$). Still, the signs of the effects were all unchanged from the full window to all sub-windows. Using the mean-power measure, the pattern of significance were the same as the mean-power full-window analysis. Thus, overall, the pattern of results appears robust to choice of time window.

3.4 Discussion

Exploiting individual variability, we correlated measures of alpha and theta oscillations with each other, with behavioral memory outcomes, and with memory related ERPs. This approach revealed new evidence regarding the possible functions of alpha and theta oscillations in recognition memory, as we elaborate next.

3.4.1 Theme 1: A possible trade-off relationship between alpha and theta oscillations

Our first goal was to test whether alpha and theta oscillations are inversely correlated across participants, in a simple recognition task. We did observe the subsequent-memory and retrieval-success effects in both alpha and theta oscillations as reported by Klimesch (1997); Klimesch et al. (1990, 1993, 1994); Klimesch, Doppelmayr, Pachinger, and Ripper (1997); Klimesch et al. (2010); Rugg and Dickens (1982). However, our correlation results offer no support for any trade-off relationship. Alpha and theta oscillations may play different roles in memory encoding and retrieval, but these cognitive functions appear independent, and in this experiment, do not display a straight-forward trade-off relationship with one another, at least with respect to individual variability and old/new recognition memory. It is likely that the individual variability in our study may not affect alpha and theta activity in opposite ways. Thus, prior findings of alpha and theta oscillations changing in opposite directions may be specific to those experimental manipulations, rather than reflecting an inevitable push-and-pull relationship between the two rhythms.

3.4.2 Theme 2: Relevance of alpha and theta oscillations to recognition-memory outcome

Measures of alpha oscillations did not correlate with either d' or RT, suggesting alpha oscillations are not major drivers of old/new recognition. Prior research has suggested that the amount of theta activity at test can index memory performance (Doppelmayr et al., 1998, 2000). In our data set, theta activity at study was correlated with d', and theta activity at test was only correlated with d' using the old/new effect contrast (but not with retrieval-success effect). Caplan and Glaholt (2007) found that theta-oscillation duration was correlated, across individuals, with accuracy and response time of a relational memory task. Theta oscillations might thus support item-memory encoding and retrieval via relational memory strategies, such as formation of interactive imagery or sentences.

3.4.3 Theme 3: Memory-related oscillations and memory-related ERPs

ERPs have been studied more extensively in relation to recognition-memory than oscillations. Prior research has suggested many possible functional roles those ERP features could reflect. Although this is still under debate, at least we can ask whether an oscillation might correspond to the same cognitive process as an ERP or a different process. At study, measures of alpha-band oscillations were correlated with features of the ERP subsequent-memory effect, most robustly, with the Slow Wave-Late. In contrast, measures of theta-band oscillations at study did not correlate with any ERP measure. The Slow Wave has been thought to index elaborative memorization strategies (Fabiani et al., 1990), which could include "deep" levels of processing as well as relational or imagery-based strategies. Interestingly, reviewing a large body of research, Nyhus and Curran (2010) thought it likely that theta oscillations are engaged in relational and association-memory encoding, in item- as well as relational memory tasks. This suggested a clear hypothesis: theta oscillations and the Slow Wave reflect a common, relational process, in which case they should correlate with one another during study. This correlation, however, was not significant. This raises the possibility that if theta oscillations are involved in associative or relational encoding, they do so in a very different way than the Slow Wave.

There was a strong correlation between measures of alpha oscillations and the Slow Wave-Late. It is plausible that one's level of visual attention during study could influence the quality of later memory. Klimesch et al. (1993) asked if attention was the only relevant factor for the suppression of the alpha during successful memory encoding. Klimesch et al. (1993) presented participants with a list of characters to remember, after a short delay participants were presented with a target and lure to select which one was from the study list. Importantly, the study lists were manipulated in two ways: varying list length and varied versus consistent mapping. In the "varied mapping" condition where the characters comprising each list were randomly drawn from a larger stimulus pool. In the "consistent mapping" condition, the set of characters in each list within a block was identical, thus demanding less attention than the varied mapping condition. Alpha power decreased more in the varied mapping condition than the consistent mapping condition, suggesting that alpha (decrease) indexed attention. More importantly, within each mapping condition, the later-remembered encoding trials also had less alpha power. In line with these results, Gevins, Smith, McEvoy, and Yu (1997) found that alpha power decreased during an N-back task, but more so for the more challenging condition than a simpler control condition (3-back versus 1-back). This result suggested that as memory load increased, alpha activity decreased. Our results were consistent with these findings that alpha activity decrease more during remembered trials than the forgotten trials (at both study and test). In other words, it is possible that decreased alpha activity might not only index attention, but perhaps memory-relevant cognitive processes.

Furthermore, alpha activity has also been suggested to index inward attention; when a participant focuses more on their internal thoughts, the alpha activity may increase. The positive correlation between measures of alpha oscillations and the Slow Wave-Late is also consistent with that idea, presuming that the Slow Wave reflects such deep levels of processing. It is possible that the increase in alpha duration and power captured the inward attention required for making mental visual representations of items during encoding, which may also be indexed by the Slow Wave-Late.

At test, the FN400 and the Left Parietal Positivity have been suggested to index familiarity-based and recollection-based retrieval, respectively (Rugg & Curran, 2007). There are several reasons to expect theta oscillations support recollection-based recognition judgements (Nyhus & Curran, 2010), which leads one to predict a positive correlation between theta oscillations and the Late Parietal Positivity. However, we did not see a straight-forward mapping of the theta activity onto the Left Parietal Positivity, nor even the FN400. Instead, the retrieval-success measure of alpha oscillations correlated with the FN400. These correlations remained non-significant when measured with the old/new effect contrast (although, recall that the theta-band old/new effect did correlate significantly with d'). In other words, theta oscillations may be important for recognition-memory at test, perhaps in distinguishing old from new items, but not in the same way as the Late Parietal Positivity. We did see a significant correlation between alpha activity and the FN400, adding to other evidence that alpha activity is important for memory-retrieval (Klimesch et al., 1990), and may contribute to a common retrieval process as the FN400, perhaps familiarity or conceptual or semantic priming (Rugg & Curran, 2007; Voss & Federmeier, 2011).

Yet other alternative accounts to dual-process theory remain viable. For example, Wixted (2007) proposed that familiarity and recollection may both coexist in the brain, but that they summate to drive the old/new decision. Dunn (2008) went even further, showing that even remember and know judgements may be driven by only a single underlying decision dimension (which could be the sum of two or more sources of evidence, but they still summate to drive responses). Thus, it is also possible that theta (as well as alpha) oscillations reflect memory quality, or strength, but do not map clearly onto recollection and familiarity.

Our results added more evidence that alpha activity might index visual attention, since alpha oscillations differed between hits and misses but not between hits and correct rejections. Namely, it is possible that participants weren't paying attention during those trials which led to a miss response later on. More importantly, this result also converges with previous research on alpha power and performance on various tasks (Doppelmayr et al., 2000, 2005; Klimesch, 1999; Klimesch, Vogt, & Doppelmayr, 2000; Klimesch et al., 2007; Mathewson et al., 2012). In addition, correlations between measures of alpha oscillations and memory-related ERPs during both study and test are also consistent with previous research on alpha power (Klimesch et al., 1993, 1990; Jensen et al., 2002). Furthermore, the regression model suggested that theta duration during hits (both at study and test) and during correct rejections were the main predictors of d'. Criss et al. (2013) conducted a fMRI study examined brain activity between hits and correct rejections during the test phase of an old/new recognition task. They found that more percent signal change in angular gyrus region was correlated with d'. In other words, the bigger the signal change difference in angular gyrus, the bigger the d', the better a participant could discriminate old from new items. Criss et al. (2013) suggested that the activity in angular gyrus could reflect memory strength differentiation. Adopting the same logic here, the cognitive process we captured in the theta old/new contrast (hits–correct rejections) might also reflect match of the probe to memory which can differentiate old and new items.

Prior research has suggested parietal-lobe contributions to memory retrieval are more closely linked to meta-memory processes, such as confidence rating judgements of recollection, than to veridical recognition itself (Ally et al., 2008; Cabeza et al., 2008; Wagner et al., 2005; Woroch & Gonsalves, 2010). Chen et al. (2014) suggested that the Left Parietal Positivity may not reflect recognition success, but rather discriminating the old from new items. Moreover, the theta-oscillation old/new effect contrast did not correlate with the Left

Parietal Positivity. If, indeed, both the theta oscillations and the Left Parietal Positivity reflect some process involved in differentiating memory strength between old and new items, at least, they contribute to the process differently. In addition, it is possible that measures of theta oscillations do reflect recollection processes (correlation with d') in a way that the Left Parietal Positivity does not.

In summary, a pattern emerges from the correlation results whereby alpha oscillations are correlated with memory-related ERPs but not with memory performance, and theta oscillations, on the other hand, are correlated with memory performance but not with memory-related ERPs. Both the alpha and theta oscillations are evidently important for successful encoding and retrieval of memory; our replications of the significant subsequent memory effect and retrieval-success effect, with the BOSC method, confirm that reduced alpha oscillations and increased theta oscillations indicate successful memory. Although the precise functions of these two oscillations in recognition-memory still require further investigation, our results suggest that alpha oscillations might index the participant's attention-level. This could include both visual attention and inward attention that could each facilitate encoding and retrieval in different ways. Those cognitive processes indexed by alpha oscillations are also reflected in the memory-related ERP amplitude; however, the duration and power alpha oscillations do not translate directly to better memory performance, at least as measured with old/new judgements.

Prior research has built a strong case for theta oscillations supporting memory. We have shown that the theta oscillations not only differ between remembered and forgotten words, but also correlate with memory performance across participants. Intriguingly, we find no correlation between theta oscillations and memory-related ERPs, even those thought to reflect the same or similar cognitive processes (the Slow Wave and Late Parietal Positivity). It is plausible that theta oscillations would correlate with other ERP measures that we did not test; it is equally possible that our understanding of these ERP features and theta oscillations requires refinement.

3.4.4 Comparison with conventional measures of power

We focused on a measure derived from the BOSC method in order to be conservative about classifying measured activity as rhythmic. Thus, results obtained with the $P_{episode}$ measure may be more susceptible to Type II than to Type I error. In addition, $P_{episode}$ measures duration of oscillations, given that power exceeds the tuned threshold; thus, any modulation of power within those detected oscillatory episodes is ignored by $P_{episode}$. To check whether our emphasis on this selective oscillation-duration measure may have hidden any pertinent results, we conducted parallel analyses using mean-power as the measure. If amplitude modulations showed any of the effects of interest, we would have found significant effects using mean-power that were not significant with $P_{episode}$ as the measure. We found no such cases. On the other hand, mean-power is not selective for oscillatory activity; if oscillations are present, large in amplitude and/or long-lasting, they will tend to dominate the power measure, but if they are sporadic, mean-power will be weighted more by non-oscillatory signal such as one expects from the colored-noise background spectrum. This may explain why some results were statistically less robust using mean-power than $P_{episode}$. These exceptions were still in the same direction: 1) the correlation between the alpha-band retrieval-success effect and the FN400 (mean power: $r(64) = 0.18,\ p > 0.1$) and 2) the correlation between the theta-band old/new effect and d' (mean power: $r(64) = 0.16,\ p > 0.1$). Thus, using mean-power as an alternative measure produced no results that contradicted the results obtained with $P_{episode}$. Although no conflict between the two measures was found in the current data set, it is still advisable, in future studies, to analyze both, especially to test the possibility that modulations of power within oscillations may track behavioural or cognitive functions even when oscillation-durations do not change. Together, including both $P_{episode}$ and mean-power measures could provide us with more comprehensive picture of oscillation functions.

3.5 Conclusion

We used a large sample size to exploit individual variability by correlating measures of memory-related oscillations, in the alpha and theta bands, with behavioural outcomes and memory-related ERPs. Alpha and theta oscillations appear to play crucial roles in recognition memory; however, they seem to contribute to memory differently. The correlations between alpha oscillations and memory-related ERPs suggested that alpha oscillations help engage participants in effective memory encoding and retrieval. The correlation between theta oscillations at study and d' provided convergent evidence that the theta oscillations helps to support successful encoding of new information in recognition memory. Moreover, theta oscillations at test (with the old/new contrast, but not with the retrieval-success contrast) correlating with memory outcome provided support for differentiation models, suggesting that the prevalence of theta oscillations may reflect differentiation. Furthermore, this effect did not overlap with the function of the Left Parietal Positivity, which may also contribute to differentiation. Theta oscillations might support item memory encoding and retrieval by contributing to relational memory processes; however, the involvement of theta oscillations in relational memory must be different from those indexed by ERP measures.

Chapter 4

Association memory: study and test event-related potentials affect associative recognition memory performance

Abstract

Although association memory is an essential part of memory functioning, the neural mechanisms of association memory remain largely unknown. Here we track how brain activity, measured by event-related potentials (ERPs), at study leads to brain activity at test, in turn influencing memory outcome. Participants studied lists of word pairs, and were tested with associative recognition. That is, they judged if the test probe was the same pairing from the study set ("intact") or was made of words drawn from other studied word pairs ("rearranged"). Taking an individual-differences approach, we asked whether pairs of memory-related ERP features explained common variance across participants, and whether those memory-related ERP features explained individual differences in memory performance. Two early ERP features, the Late Positive Component at study and early retrieval success effect at test correlated with each other. In addition, those features were also correlated with memory performance (d'). The slow wave has been suggested to reflect item-item association encoding; however, this feature did not correlate with associative recognition memory performance, nor with any of the test-phase ERP features. These results suggest that the Late Positive Component at study may influence the early retrieval success effect ERP at test, and they, together, affect behavioural outcomes of the associative recognition memory task.

4.1 Introduction

We form association memories every day, such as the location where I park my car (parkade–car) or the name of a new colleague (John–John's face). Often, we are also faced with associative memory judgments: Did I park my car in the parkade (parkade–car?); Is James the name of my new colleague (James–John's face?). Understanding the cognitive and neural underpinnings of association memory encoding and retrieval has been an important topic in memory research (see Mayes, Montaldi, & Migo, 2007, for a review). Association memory can be examined using different experimental procedures, but associative recognition has been the most widely employed to examine brain activity at both study and test. In this task, participants are presented with a list of to-be-remembered word pairs (i.e., A-B, C-D, E-F ...), then are asked to judge if the probe pairs at test are "intact" (A-B) or "rearranged" from study pairs (A-F). The assumption is that successful distinction of "intact" from "rearranged" probes relies on successful memory of item–item associations, not just memory of the items individually, since all items have been studied during encoding. Moreover, associative recognition only requires a one-key response, which means that brain activity recorded from test phase has less muscle and eye movement.

Prior research, using event-related potentials (ERPs), has identified ERP features related to successful memory encoding and retrieval. At study, brain activity can be separated based on later memory outcomes: subsequently remembered and subsequently forgotten. The voltage difference between the later remembered and later forgotten, known as the subsequent memory effect, may reflect cognitive processes that contribute to successful encoding (see Paller & Wagner, 2002, for a review). Similarly, at test, brain activity can also be separated by memory outcome to reflect the cognitive processes contributing to successful retrieval. The old/new effect identifies brain activity that differentiates correctly identified target items (hits) from correctly identified lure items (correct rejections; Warren, 1980). Much of the ERP research has been done with item-memory procedures, and many have proposed that the study ERP features and test ERP features reflect similar cognitive functions (Fabiani et al., 1986, 1990; Friedman, 1990a, 1990b; Guo et al., 2006; Smith, 1993; Weyerts et al., 1997). Chen et al. (2014) explored the idea of possible relationships between the study and test ERP features, and asked if amplitude difference in one study ERP feature could lead to differences in another test ERP feature, which then explains item recognition memory

(Chapter 2). We found, indeed, there were significant correlations between the study and test ERPs, which suggest functional connections between those ERP features. Moreover, Chen et al. (2014) also considered the retrieval success effect ERP measure during the test phase. The retrieval success effect identifies brain activities differentiate correctly identified target items, remembered (hits) from forgotten target items (misses; Dolcos et al., 2005). Both the old/new effect and retrieval success effect have been used in examining retrieval processes and have similar ERP morphology. However, despite the visual similarities, Chen et al. (2014) found they might reflect different processes. While old/new effect measures the processes involved in the distinguishing targets from lures, retrieval success effect provides additional measures for remembered and forgotten targets. Thus, we used both ERP contrasts to measure retrieval processes at test.

Using the same logic as Chen et al. (2014), the present study employs the associative recognition task to investigate the neural and cognitive processes that may contribute to successful association memory at both study and test. We wondered whether there are functional relationships among the study and test ERP features. More concretely, do the study ERP features reflect some study processes that result in better associative recognition performance, which, in turn, is reflected in other test ERP features? Furthermore, we examined if our current understanding of processes contribute to item-memory-related ERPs extending to association memory, since association memory has been suggested to be dependent on item memory (Murdock, 1974). Although many researchers have argued that processes involved in item and associative information encoding and retrieval differ (Clark, 1992; Clark & Burchett, 1994; Gronlund & Ratcliff, 1989; Hockley, 1992, 1994; Hockley & Cristi, 1996b; Yonelinas, 1997), item information might be the basic building block for associative recognition. For example, Hockley and Cristi (1996a) examined encoding processes involved in both item and associative information. Participants were instructed to study a list of word pairs by either focusing on the item information or focus on the association information. Afterward, participants were given an item-recognition task and an associative-recognition task. They found that the participants who focused on the association information performed better on the associative recognition task compared to those who focused on the item information. More importantly, participants performed equally well on the item recognition task regardless of their encoding emphasis. This suggested that item and associative recognition memory are not entirely independent.

We sought to replicate and to extend the previous work in item-recognition-memory ERPs, explore the neural and cognitive processes of associative recognition by using an individual-differences approach to examine 1) how the study and test ERPs relate to memory-performance and 2) how the study and test ERPs relate to one another across memory phase.

4.1.1 ERPs at study and test

There are two major ERP features at study, the Late Positive Component (400–700 ms after the onset of stimulus) and the Slow Wave (starting around 800 ms). Both features show subsequent memory effects, with later-remembered ERPs are more positive in amplitude than later-forgotten ERPs, particularly at centro-parietal electrodes (Friedman & Johnson Jr., 2000). In item-memory tasks, many studies have functionally differentiated the two features. For example, Fabiani et al. (1990) studied item memory encoding by instructing participants to use different strategies when memorizing a list of words. They found that participants who were instructed to use rote strategies (e.g., repeating the words over and over again) elicited larger Late Positive Components for later-recalled than later-not-recalled items, whereas participants who employed elaborative strategies (e.g., generating sentences using the words in the study list) had no difference in Late Positive Components. Instead, those participants elicited larger Slow Waves between later-recalled and later-not-recalled items. The elaborative strategies employed by Fabiani et al. (1990) instructed participants to form mental images that combine words in the study list, which resembled strategies that are known to support verbal association-memory. Thus, item memory effects may be influenced by associative encoding processes. Therefore, the Slow Wave has been suggested to reflect associative encoding processes that could also support item–item associations. An instructive example of this kind of finding was reported by Kim et al. (2009, 2012), who studied associative memory encoding. They found the subsequent memory effect in both the Late Positive Component and the Slow Wave. More importantly, the effect was more pronounced during the Late Slow Wave time window. In addition, the Slow Wave effect was maximal at frontal electrodes. In short, the frontal Slow Wave was then specifically suggested to reflect encoding of associative information that supports item–item associations (Jäger, Mecklinger, & Kipp, 2006; Kim et al., 2009, 2012; Kounios, Smith, Yang, Bachman, & D‘Esposito, 2002; Weyerts et al., 1997).

During the test phase of recognition tasks, specifically item recognition, two main ERP features, the FN400 and the Left Parietal Positivity, show old/new effects, where voltage of hits ("old") is more positive than correct rejections ("new"). The FN400 appears symmetrically at frontal electrodes and has a negative-going potential peaking around 400 ms after probe onset. The Left Parietal Positivity, appearing in left parietal electrodes, is a positive-going wave that peaks around 500–800 ms after probe onset. The usual inference is that this old–new difference reflects processes that are related to successful recognition judgments. According to dual-process theory, two distinct processes, familiarity and recollection, are involved in recognition memory judgments (see Yonelinas, 2002, for a review). Familiarity-based retrieval is continuous, strength-like information which provides a sense of vaguely knowing the item. On the other hand, recollection-based retrieval contains specific contextual information about the item gathered from the study phase. The two ERP features have been suggested to index two retrieval processes: FN400 for familiarity-based retrieval and the Left Parietal Positivity for recollection-based retrieval (see Rugg & Curran, 2007, for a review). Alternatively, single-process theory suggests that recognition decisions are made based on a single memory strength of the item (Yonelinas, 2002; Criss, 2009). For example, Woroch and Gonsalves (2010) asked participants to judge their confidence level on their old/new response, and found that the amplitude of FN400 varied with levels of confidence. Since the levels of confidence were related to the memory strength of the item, higher confidence means higher memory strength and vice versa. Therefore, Woroch and Gonsalves (2010) suggested that FN400 amplitude reflects the memory strength of an item.

In an associative recognition task, the target probes are "intact" pairs, where both items are studied and presented together as a pair; the lure probes are "rearranged" pairs where both items have been previously studied, but come from different studied pairs. Yonelinas (2002) argued, under the dual-process theory framework, that if familiarity reflects the strength of item-memory, it should only help to discriminate between studied and unstudied items. Given that all items presented in an associative recognition task have previously been studied, item-strength should not help participants discriminate between intact and rearranged probes successfully. Recollection-based retrieval, on the other hand, provides more enriched details about a studied item, such as spatial and temporal context. The associative recognition judgment is more likely to depend on contextual details retrieved in the recollection process, which are more likely be indexed by the Left Parietal Positivity (Rugg & Curran, 2007). Employing the associative recognition procedure, Donaldson and

Rugg (1998) found significant old/new effects at the left parietal and right frontal electrode sites. Donaldson and Rugg (1998) suggested that these two ERP features, the Left Parietal Positivity and right frontal old/new effect, reflect recovery of contextual information via recollection-based retrieval, leading to associative recognition discrimination. Many studies that followed, using a similar procedure, have also reported the right frontal old/new effect, suggesting that this ERP feature reflects retrieval processes that are important for successful associative recognition judgments (Mark & Rugg, 1998; Ranganath & Paller, 1999; Senkfor & van Petten, 1998; Trott et al., 1999; Weyerts et al., 1997).

Taken together, at study, the difference in the Slow Wave may index elaborative processes that facilitate the encoding of associative memory. At test, the difference in the Left Parietal Positivity and the right frontal old/new effect may reflect recollection-based processes that lead to the retrieval of associative information.

4.1.2 Relating study and test ERPs

Despite the complexity of study and test ERPs and their possible cognitive functions related to association memory, one can see parallels emerging between study and test ERPs. Firstly, the Late Positive Component and FN400 have both been linked to non-relational, single-item memory. Secondly, the Slow Wave, the Left Parietal Positivity and the right frontal old/new effect have been linked to deep levels of processing, elaborative encoding strategies, and specifically, item–item associative processes. It is possible that study activity affects test activity, affecting subsequent memory outcomes. In other words, a large Late Positive Component subsequent memory effect at study could result in a large FN400 old/new effect at test, which in turn produces a better memory outcome. Similarly, a large Slow Wave subsequent memory effect at study could result in a large Late Parietal Positivity and right frontal old/new effect at test, which in turn produces a better memory outcome. Our aim, therefore, was to test these hypotheses by correlating study and test ERP features using an individual-differences approach. We measured the magnitude of the subsequent memory effect and old/new effect for each participant using difference waves: hits–misses at study for subsequent memory effect and hits–correct rejections for old/new effect. Memory outcome was measured by d' and response time (RT). We then correlated the measures across participants. If the Late Positive Component and the FN400 reflect similar cognitive processes which track information going in and the same information coming out of memory, then they should explain common variance across participants. Thus, we would predict a positive correlation between the two features. If, for instance, the magnitude in the Late Positive Component is greater for a given participant, the magnitude of the FN400 should be relatively greater for the same participant. Consequently, if an ERP feature at study reflects an encoding process that results in better memory performance, it will be indexed by a (different) ERP feature at test. It is important to clarify that we are not expecting the same ERP features at study and at test, but rather, we are expecting the encoding processes that are reflected in study ERP features result in later memory outcome, which are indexed by other test ERP features.

Design of the current study We used a verbal associative-recognition procedure consistent with prior procedures and obtained both a large number of trials per participant (112 intact probes and an equal number of rearranged pairs as lure probes) and a large sample size (59 included participants). We did not include new items, since the new items could help participants make the associative-recognition judgment based on item-memory alone, or setting different judging criteria for "new", "intact" and "rearranged" (Opitz & Cornell, 2006; Yonelinas, 2002). We included only the studied items at test, and constructed two probe types: intact (identical) and rearranged probes. As before (Chen et al., 2014), we wanted there to be sufficient individual variability in study and test. We therefore did not instruct participants to study in any specific way, with the hope of addressing brain activity that is more closely linked to successful (versus unsuccessful) associative-recognition memory. Moreover, we kept the presentation rate relatively fast (2500 ms per pair). This was to reduce the chance that participants could implement complex, rich encoding strategies which might produce less stimulus-locked memory-related activity measured by ERPs.

4.2 Methods

4.2.1 Participants

Sixty-eight (9 self-reported left-handed, 59 self-reported right-handed; 32 female) undergraduate students enrolled in an introductory psychology course at the University of Alberta, aged 17–26 (mean = 19, SD = 2.03) participated for course credit. Data from nine participants were excluded from analyses: six due to low rates of misses ($< 10\%$), three due to excessive levels of artifacts in the EEG. All participants were required to have English as their first language and had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment in accordance with the University of Alberta's ethical review board.

4.2.2 Materials

The stimuli were nouns drawn from the Toronto Word Pool (Friendly et al., 1982) composed of 4–8 letters. Kucera-Francis frequency was between 1–712 per million. The experiment was created and run using the the Python Experiment-Programming Library (Geller, Schleifer, Sederberg, Jacobs, & Kahana, 2007). Study items and test probes were presented in a white "Courier New" font on a black background. Paired words were presented simultaneously in the centre of the computer screen.

4.2.3 Procedure

The session took place in an electrically shielded, sound-attenuated chamber. In each session, a participant studied and tested on one practice set (excluded from analyses) followed by 28 experimental sets involving 8 pairs each. The study phase instructed participants to study word pairs displayed one pair at a time. Each study set contained 8 pairs, presented one pair at a time. Pairs were presented for 2500 ms with a jittered uniform-random intertrial interval between 500–800 ms. The end-of-list distractor task, included to reduce recency effects that can contribute nuisance variability to the memory measure, consisted of three equations of the form of $A + B + C =$, where A, B, and C were randomly selected digits between two and eight. Each equation remained on the the centre of the screen for 5000 ms. Participants were asked to type the correct answer. In the recognition judgment phase, which immediately followed the distractor task, 8 probes were presented at test, half of which were previously studied pairs ("intact" probes) and half of which were previously studied words rearranged into new pairs ("rearranged" probes). The words from the "intact" probes were never paired with words from the "rearranged" probes. Additionally, the left and right position of each word was kept consistent from study to test. Each probe remained on the screen until the participant made a response by pressing the corresponding key for either "intact" or "rearranged", which appeared in the bottom corners of the screen (with sides conterbalanced across participants. Figure 5.1). For each trial, response time (RT) and accuracy were recorded.

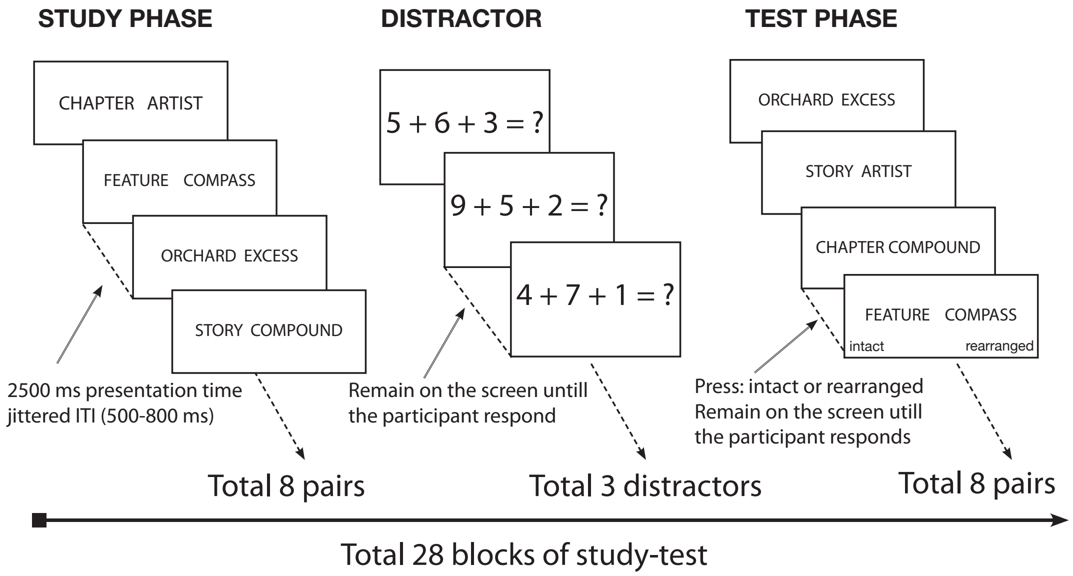


Figure 4.1: The experimental procedure. Each box illustrates the computer screen at a particular stage in the task (text has been enlarged relative to the screen size to improve clarity of the figure). There were 28 blocks of study–test.

4.2.4 Electroencephalography (EEG) Recording and Analyses

EEG was recorded using a high-density 256-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, OR), amplified at a gain of 1000 and sampled at 250 Hz. Impedances were kept below 50 kΩ and EEG was initially referenced to the vertex electrode (Cz). Data was analyzed by custom MATLAB scripts in conjunction with the open-source EEGLAB toolbox (Delorme & Makeig, 2004, `http://sccn.ucsd.edu/eeglab`). The signal was average re-referenced, and digitally bandpass filtered between 0.5–30 Hz. Artifacts were corrected via Independent Component Analysis, implemented in EEGLAB (Jung et al., 2000). The selection of components was based on visual inspection of the spatial topographies, time courses, and power spectral characteristics of all components. The components accounting for stereotyped artifacts including eye blinks, eye movements, and muscle movements were removed from the dataset. Event latencies were corrected with a time lag correction due to a known hardware calibration problem identified by EGI. Based on the participants' responses during the test phase, trials were separated into subsequently remembered associations (subsequent memory effect hits) and subsequently forgotten associations (subsequent memory effect misses). The subsequent memory effect components were analyzed at central and frontal electrodes Fz, F3, F4 and Pz. We analyzed the subsequent memory effect at three different time windows based on previous studies (e.g., Chen et al., 2014; Fabiani et al., 1986; Kim et al., 2009, 2012): 400–700 ms, 700–900 ms and 900–1200 ms latency post–stimulus. We assumed that the earlier time window could capture the difference in the Late Positive Component, while the later time window could capture the Slow Wave. In addition, we also included a later time window of 1500–2000 ms to examine the Late Slow Wave (Kim et al., 2009). The test ERPs, both old/new effect contrast (hits vs. correct rejections) and the retrieval success effect contrast (hits vs. misses) were analyzed in the time window of 400–600 ms post–stimulus for the FN400 at electrode Fz, and 600–800 ms post–stimulus for the Left Parietal Positivity at the parietal electrodes Pz, P3, and P4 and the frontal old/new effect at electrode Fz. The same time windows and electrodes were used for the retrieval-success effect analyses.

Electrodes of interest and time windows were devised based on prior studies, not by looking at the data. However, to avoid confirmation bias, it is important to examine if our ERP correlation results were sensitive to the precise choice of time window, especially given that the time window used in previous research has varied. To assess the robustness of our correlation results to the selection of time windows, we also examined our correlation analyses at all time points in the ERP. These analyses were intended to test for the robustness of the time window selection.

All statistical analyses were carried out using MATLAB and Statistic Toolbox Release 2008b (The MathWorks, Inc., Natick, Massachusetts, United States) and IBM SPSS Statistics for Mac, Version 21.0. (IBM Corp., Armonk, NY) on the mean voltage differences at the corresponding electrodes and time windows.

Condition	[%]	Response time [ms]
hits (intact)	74 (15.2)	1665 (284)
misses (intact)	26 (15.2)	1651 (336)
correct rejections (rearranged)	81.4 (13.5)	1654 (269)
false alarms (rearranged)	18.6 (13.5)	1732 (534)

Table 4.1: Accuracy (percentage) and response time (ms) values, along with their standard deviations across subjects in parentheses.

4.3 Results

Accuracy and response time are summarized in Table 5.1. We compared the response time between correct and incorrect responses for two probe types. A probe type [2] (intact/rearranged) × accuracy [2] (correct/incorrect) repeated measures ANOVA revealed no significant main effect of probe type $F(1.8, 66) = 1.81,\ p > 0.1$, and no significant main effect of accuracy, $F(1.1, 66) = 1.12,\ p > 0.1$. The interaction approached significance ($p = 0.09$). The mean d' value was 1.58 ($SD = 0.78$). Reassuringly, accuracy is not near ceiling or floor, and the standard deviations of both accuracies and response times are large; thus, we expect that there is meaningful variability across participants that could support our planned correlation analyses.

First, we analyzed ERPs at both study and test separately to check whether we could replicate the subsequent memory effects at study, and retrieval success effect and old/new effects at test. Then, we investigated the possible relationship between study and test ERPs. Finally, we tested the behavioural relevance of those ERP features by correlating memory-outcome measures with the ERP features.

4.3.1 Replication of study and test ERPs

Study ERPs

During the study phase, we compared the ERPs for later correctly identified intact pairs (SME hits) with the ERPs for later incorrectly identified intact pairs (SME misses). The subsequent memory effect was analyzed at three frontal electrodes (Fz, F3 and F4) and central-parietal electrode (Pz). We used four time windows to capture the extent of the subsequent memory effect, and the results are summarized in the Table 4.2. The grand average ERPs are shown in Figure 4.2. The subsequent memory effect recorded at electrode

Electrode	400–700 ms	700–900 ms	900–1200 ms	1500–2000 ms
Fz	$-1.8\dagger$	-1.16	-0.21	-1.62
F3	**-2.95***	**-2.12***	-0.4	**-2.91***
F4	-1.47	**-1.98***	-0.27	-0.97
Pz	0.66	-0.22	-0.53	**2.34***

Table 4.2: Paired-sample, two-tailed *t*-tests ($df = 58$) results comparing mean voltage between subsequent hits and subsequent misses during study for four time windows at electrodes of interest. $*$ denotes $p<0.05$, † denotes $p<0.1$.

Pz was similar to that observed in prior item memory experiments (reviewed in Friedman & Trott, 2000). The effect recorded at frontal electrodes showed a negative polarity where subsequent misses were more positive than subsequent hits (Figure 4.2).

The negative polarity subsequent memory effect at frontal electrode sites recorded in our study resembles the Mangels et al. (2001) results. They found an N340 effect (around the same time window as the Late Positive Component) during item-memory encoding. The N340 showed a negative subsequent memory effect over left fronto-temporal electrodes. Mangels et al. (2001) suggested that the N340 was related to encoding of item and its contextual information. It is possible that the negative frontal Late Positive Component subsequent memory effect reflects the processes involved in combining information together, such as item to its context or item to item associations. Notably, Caplan et al. (2009) did not find this N340 effect during encoding of item–item associations. It is possible that the difference in ERP features were due to the experimental paradigm used. Caplan et al. (2009) employed cued recall as the measure for association memory, where Mangels et al. (2001) and the present study employed recognition as the measure for association memory. Different ways of testing association memory might cause participants to use different encoding strategies, which then led to differences in the ERP features.

In addition to the frontal subsequent memory effects, we also found the typical positive subsequent memory effect (Hits > Misses) recorded in many item-memory tasks at parietal electrodes sites; in particular, the Late Slow Wave differentiated remembered from forgotten pairs. This Slow-wave result resembles Kim et al.'s (2009) association-encoding slow wave findings.

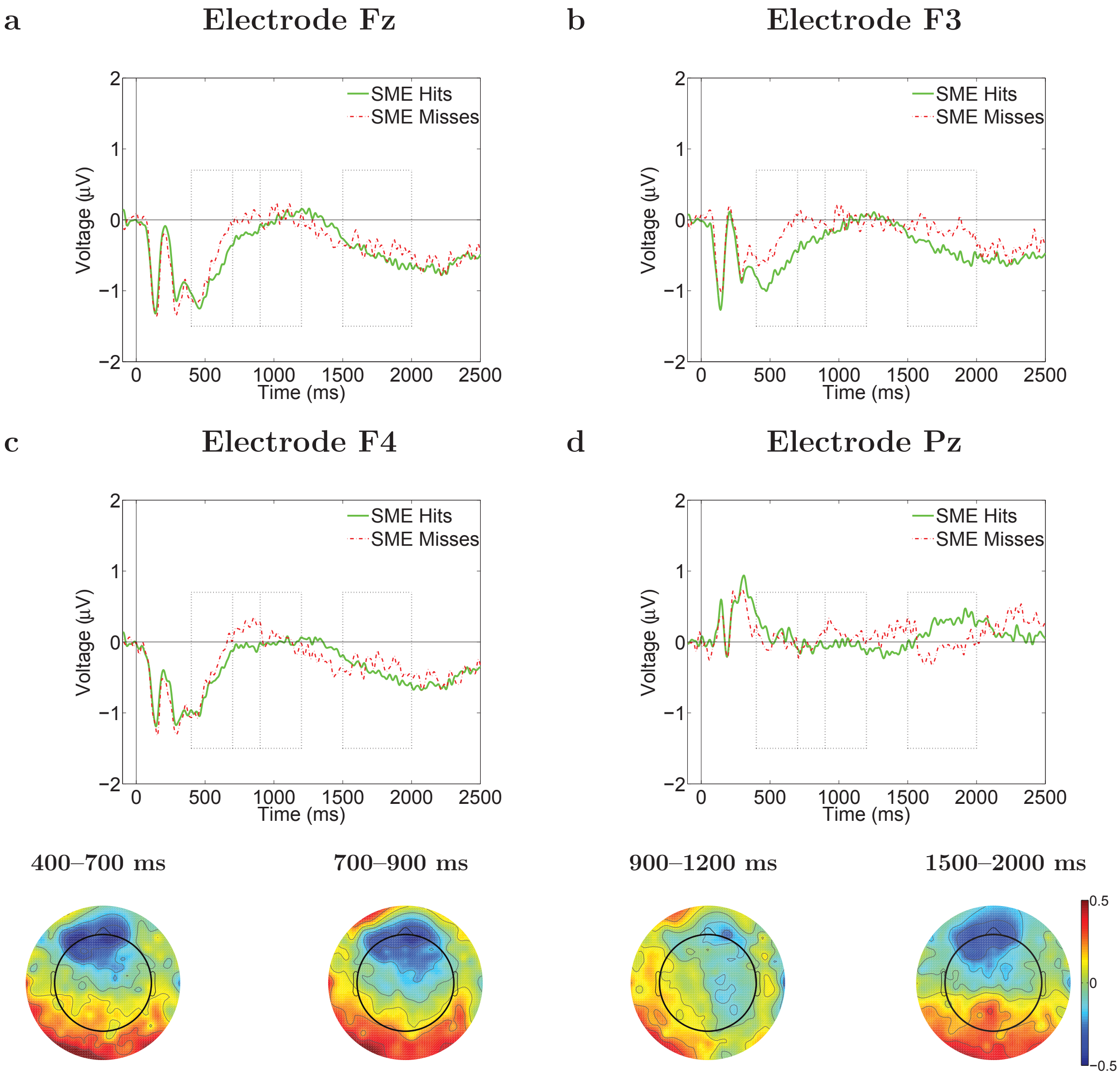


Figure 4.2: Grand-average Subsequent Memory Effect ERPs at Fz, F3, F4 and Pz. Study ERPs for subsequently remembered trials (SME hits, green) are contrasted with subsequently forgotten (SME misses, red) trials. Topographic maps are spline plots, where color reflects mean voltage $[\mu V]$ over the corresponding time window.

4.3.2 Test ERPs

During the test phase, we analyzed ERPs using two approaches: the old/new effect and the retrieval success effect. While the FN400, the Left Parietal Positivity and the right frontal old/new effect are the main ERP features during test, there were many sustained voltage changes in the ERPs. To capture the full effects of the ERPs, we analyzed the test ERPs at parietal electrodes (Pz, P3 and P4) and central frontal electrode (Fz). The old/new effect and the retrieval success effect results are summarized in the Table 4.3, and the grand average ERPs are shown in Figure 4.3.

FN400 There was no significant difference between hits and correct rejections (old/new effect) nor between hits and misses (retrieval success effect) at electrode Fz. This result is in line with Yonelinas's (2002) the idea that familiarity is less involved in the associative recognition judgment and the FN400 was the index of familiarity process (Rugg & Curran, 2007). Alternatively, the amplitude of FN400 has been suggested to reflect the memory-strength of an item (Woroch & Gonsalves, 2010). It is possible that our participants make the associative recognition judgments based on the memory-strength of the items in the probe. However, there was no significant old/new effect nor retrieval success effect in FN400, suggesting item memory strength were similar between trial types and item memory strength did not influence associative recognition judgments in this task. Or, perhaps the assumption that FN400 amplitude difference reflect memory strength does not apply in associative recognition tasks.

Left Parietal Positivity The ERP at electrode P3 showed a hint of the Left Parietal Positivity (Figure 4.3); however, the difference between hits and correct rejections was not significant. There was no significant difference between hits and misses. We expected to find significant Left Parietal Positivity old/new effect, as Yonelinas (2002) suggested associative recognition may rely on recollection-based retrieval which was reflected in the Left Parietal Positivity. It is possible that the Left Parietal Positivity reflect recollection-based retrieval processes in item memory tasks; however, these retrieval processes do not seem to be relevant in our associative recognition task.

Right frontal old/new effect We did not find a right frontal old/new effect where hits were more positive than correct rejections; instead, we found an ERP feature where correct rejections were more positive than hits. This result resembles the ERP effect found in the Bridger and Wilding (2010) study: when participants were asked to retrieve contextual information of the item, the remembered ERP was less positive than the forgotten ERP, suggesting that "negative" old/new effect reflected some active processes that facilitate contextual information retrieval.

In sum, ERPs for hits became more negative than those for correct rejections and misses

Old/new effect (Hits vs. Correct rejections)		
Electrodes	400–600 ms	600–800 ms
Fz	0.03	-0.31
Pz	1.03	1.21
P3	1.12	1.63
P4	0.12	**-1.98***
Retrieval success effect (Hits vs. Misses)		
Electrodes	400–600 ms	600–800 ms
Fz	1.33	0.48
Pz	0.42	0.47
P3	0.04	0.03
P4	**-2.05***	**-1.98***

Table 4.3: Paired-sample, two-tailed *t*-tests ($df = 58$) results comparing mean voltage between hits and misses (retrieval success effect), between hits and correct rejections (old/new effect) during test for three time windows at electrodes of interest. $*$ denotes p¡0.05

from approximately 400 ms post stimulus onset. This effect displays a right parietal negative maximum.

4.3.3 Relationship between ERPs across memory phase

To directly test the relationship between study ERPs and test ERPs, we first measured the voltage difference between subsequent hits and subsequent misses at study (subsequent memory effect) for the Late Positive Component and the Slow Wave, the voltage difference between hits and misses at test (retrieval success effect), and voltage difference between hits and correct rejections at test (old/new effect) for the early and late time window of the interest. We then correlated the subsequent memory effect measures with the old/new effect measures across participants, and reported in Table 4.4. We next correlated the subsequent memory effect measures with the retrieval-success-effect measures across participants, as reported in Table 4.5.

There was no significant correlations between the study ERPs (the Late Positive Component and the Slow Waves) and the old/new effect test ERPs. In addition, there was a significant positive correlation between the Late Positive Component at electrode F3 and early retrieval success effect at electrode P4. In addition, the correlations between the Late Positive Component and late retrieval success effect; and between the Late Positive Component and early old/new effect showed a positive trend effect.

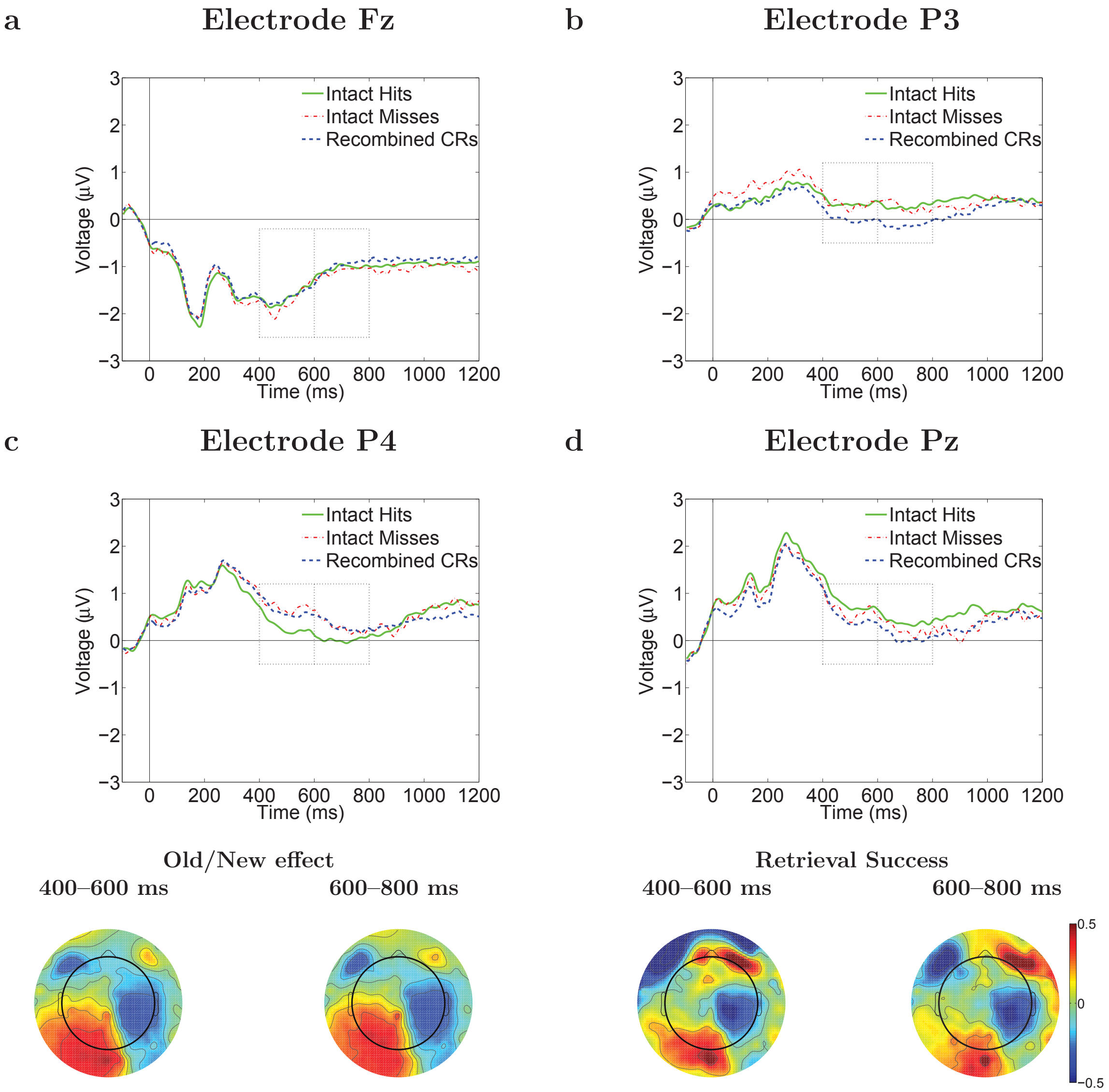


Figure 4.3: Grand-average of test ERPs at Fz, P3, P4 and Pz. Study ERPs for hits (green), misses (red) and correct rejections (blue). Topographic maps are spline plots for the old/new effect and retrieval success effect, where color reflects mean voltage $[\mu V]$ over the corresponding time window.

The across-phase correlation revealed that the Late Positive Component was correlated early retrieval success effect and also late retrieval success effect (trend effect). Since the two retrieval success effect were dependent ($r(58) = 0.87, p < 0.05$), a partial correlation analysis was conducted to explain the relationship cross-phase. Partial correlation, controlling for the late retrieval success effect, indicated a positive correlation between the Late Positive Component and the early retrieval success effect ($r(58) = 0.32, p < 0.05$); in contrast, partial

Subsequent memory effect

		F3 400–700 ms	700–900 ms	1500–2000 ms	Pz 1500–2000 ms
ONE	P4				
	400–600 ms	0.25†	0.17	0.10	-0.03
	600–800 ms	0.18	0.13	0.02	-0.01

Table 4.4: Pearson correlation (df = 58) between study ERPs (subsequent memory effect) and test ERPs (old/new effect, ONE) across participants. $*$ denotes p<0.05. † denotes p<0.1

Subsequent memory effect

		F3 400–700 ms	700–900 ms	1500–2000 ms	Pz 1500–2000 ms
RSE	P4				
	400–600 ms	**0.37***	0.21	0.10	0.07
	600–800 ms	[0.25†]	0.12	-0.02	0.16

Table 4.5: Pearson correlation (df = 58) between study ERPs (subsequent memory effect) and test ERPs (retrieval-success effect) across participants. $*$ denotes p<0.05. † denotes p<0.1. [] indicates that this trend effect become nonsignificant after the partial correlation analysis

correlation, controlling for the early retrieval success effect, found no significant correlation between the the Late Positive Component and late retrieval success effect ($r(58) = -0.15, p > 0.1$). This suggests that the positive correlation between the Late Positive Component and the late retrieval success effect was mediated by the early retrieval success effect. It is also important to note that the topographic distributions between the early and late ERP effects were very similar. The late effect might be the same as the early effect, which was sustained for another 200 ms. Thus, the only relationship identified by the across-subject correlation analyses was the Late Positive Component at electrode F3 and early retrieval success effect at electrode P4.

4.3.4 Behavioral relevance of the ERPs

In order to understand the relationship between memory-related ERPs and their behavioural relevance both at study and test, we examined if those memory related ERP measures could explain variance in memory performance across participants. We chose electrodes that had shown a significant subsequent memory effect at study (electrode F3 and Pz), and significant old/new effect and retrieval success effect (electrode P4) to correlate with the memory behavior measures (d’ and response time). There was a significant negative correlation between the Late Positive Component at study and d’ (Table 4.6), suggesting that if one person had a big difference between hits – misses (more negative), this person would also perform well in this associative recognition task. At test, there were significant negative correlations between both measures of old/new effect and d’. In addition, there were significant negative correlations between both measures of retrieval success effect and d’ (Table 4.7). There were no significant correlations between study or test ERPs with response time of hits.

	F3 400–700 ms	700–900 ms	1500–2000 ms	Pz 1500–2000 ms
d’	**-0.32***	-0.16	-0.24	-0.09
RT	0.010	0.07	0.06	-0.11

Table 4.6: Pearson correlation (df = 58) between study ERPs (subsequent memory effect) at electrode F3 and Pz and behavior measures (d’ and response time, RT) $*$ denotes p<0.05.

	Old/New effect (test)		Retrieval success effect (test)	
	P4 400–600 ms	600–800 ms	P4 400–600 ms	600–800 ms
d’	**-0.26***	**-0.29***	**-0.30***	**-0.26***
RT	-0.08	-0.10	-0.08	-0.12

Table 4.7: Pearson correlation (df = 58) between test ERPs (both Old/New Effect and Retrieval Success Effect) and behavior measures (d’ and response time, RT). $*$ denotes p<0.05.

4.4 Robustness to the selection of time windows

One of the big challenges in ERP research is the selection of time windows of analysis. Because the time window used in previous research has varied, maybe our results were sensitive to the precise choice of a time window. To assess the robustness of the correlation results (uncorrected for multiple comparisons) to the choice of the time window of analysis, we plotted the full, timepoint-by-timepoint correlation value in Figure 4.4. There were patches of significance outside the windows of interest, the general impression one gets from these figures is that the pattern of results we obtained was relatively robust to the selection of time windows. This applies both to the old/new effect analysis (a) and the retrieval-success effect analysis (d). In future studies, we could conduct an exploratory analysis and inspect further other significant correlations on these figures.

4.5 Discussion

Using an individual-difference approach, we evaluated if memory-related ERP features reflect common or distinct processes by correlating memory-related ERPs at study to those at test. Moreover, we asked if those ERP features could explain individual variance in memory performance. We found that the Late Positive Component at study covaried with the early retrieval success effect significantly. Furthermore, the Late Positive Component was the main predictor of memory success (d'). This approach refines our current understanding of existing memory-related ERPs in a verbal associative recognition tasks. Moreover, the study-test relationship refines our current thinking on the processes involved in associative information encoding and retrieval, as we will discuss below.

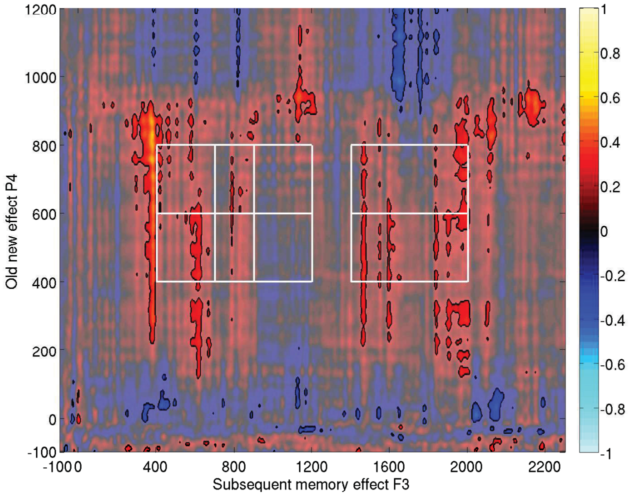
4.5.1 Study ERPs

Subsequent memory effect ERP features were thought to reflect successful-encoding processes at the subject level (Paller & Wagner, 2002). Two main ERP features observed in the present study showed significant subsequent memory effects: the Late Positive Component and late Slow Wave. These features presented a *negative*-polarity subsequent memory effect at the frontal region, and a positive polarity subsequent memory effect at the parietal region. The negative frontal Late Positive Component was correlated with d', but not with response time of hits across participants. In addition, the parietal Late Positive Component and the late Slow Wave were not correlated with memory behaviour (d' and response time).

While the subsequent memory effect recorded at electrode Pz was similar to results from prior item-memory experiments (Friedman & Johnson Jr., 2000; Paller & Wagner, 2002), the frontal subsequent memory effect showed a negative polarity effect wherein later-forgotten trials were more positive than the later-remembered trials. Prior research has found similar negative subsequent memory effects. For example, Otten and Rugg (2001) examined the study-ERPs in an incidental item recognition memory task. During the study phase of the experiment, participants were instructed to judge the words in two ways: 1) if a word was

Correlation across participants at different memory stages and electrodes

a Subsequent memory effect (P3) & old/new effect (P4)



b Subsequent memory effect (Pz) & retrieval success effect (P3)

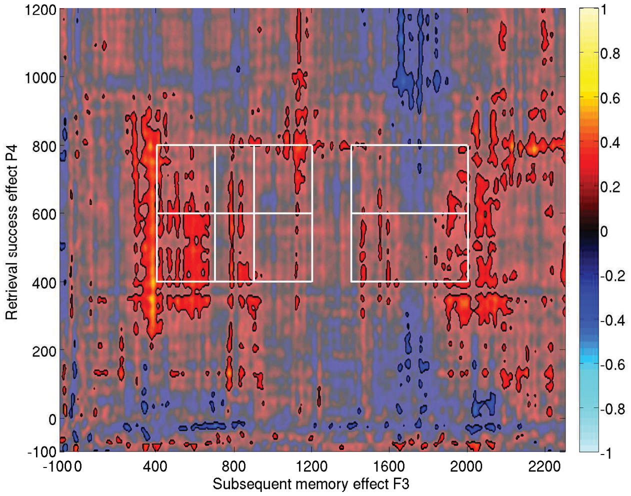


Figure 4.4: Correlation between study and test ERPs across all participants, for all combinations of study and test times. The horizontal axis represents the time course at electrode F3 during study (subsequent memory effect). The vertical axis represents the time course at electrode P4 during test (old/new effect or retrieval-success effect), with the 100 ms prestimulus baseline, 2500 ms post-stimulus time for study ERP and 1200 ms post-stimulus time for test ERP. The subsequent memory effect (encoding hits–misses) is correlated with the old/new effect (hits–correct rejections; a), or retrieval-success effect (hits–misses; b) at every pair of time samples. The semi-transparent white screen masks out any non–significant points ($p > 0.05$, pointwise). The boxes on the figure indicate the time windows selected for the main correlation analyses. "*" denotes significance ($p < 0.05$) when the corresponding time windows were averaged across.

animate (animacy task), 2) if the first and last letters of a word were in alphabetical order (alphabetic task). The study-ERPs showed significant subsequent memory effects differentiating later remembered items from later forgotten items; however, the direction of the subsequent memory effect differed. The animacy task showed the typical subsequent memory effect (remembered > forgotten), and the alphabetic task condition showed a negative subsequent memory effect (forgotten > remembered) in both the Late Positive Component and the Slow Wave time window. Otten and Rugg (2001) argued that the difference in polarity of the subsequent memory effect did not mean that the engagement of cognitive function is weaker, but rather, reflected differences in the encoding process that were task-specific. Our current task differs in many ways from the Otten and Rugg (2001) study. First, although both studies examined the study ERP using the subsequent memory effect, our participants were presented with word pairs, whereas their participants were presented with single items. Second, our participants were explicitly told to study and remember the word pairs (intentional encoding), whereas their participants were given a surprise memory task (incidental encoding). Lastly, the topographic distributions of the subsequent memory effect also differ between two studies. It is likely that we were measuring a different source of activity that led to the negative polarity of the subsequent memory effect.

On the other hand, Bridger and Wilding (2010) offered an alternative explanation for the negative subsequent memory effect that could explain the effects in our study. They asked participants to study a list of words, presented one at a time on either the left or right side of the screen, and later made both old/new and location judgments. In the location task, participants judged if the probe item was presented on the left or right side of the screen (source memory task). Using two time-windows to analyze the subsequent memory effect, Bridger and Wilding (2010) found a negative subsequent memory effect at both the 300–500 ms (Late Positive Component) and the 800–1300 ms (Slow Wave) time window when comparing location judgment accuracy (forgotten locations were more positive than remembered locations). In addition, Bridger and Wilding (2010) also found a positive subsequent memory effect at both the Late Positive Component and the Slow Wave time window when comparing recognition memory accuracy (remembered items were more positive than the forgotten items). They suggested that the negative subsequent memory effect reflected processes important for later recollection-based retrieval. The location source memory task can be viewed as an association task, where items were associated with their locations on the screen. The results of Bridger and Wilding (2010) could also be re-interpreted as suggesting that the negative subsequent memory effect indexes association-related encoding processes. Our result converges with this idea, as the negative Late Positive Component was negatively correlated with d' across participants. This means that if someone had a strong negative effect at the Late Positive Component, this person would also perform well in the associative recognition task. This result is in line with the arguments made by Caplan et al. (2009) that the Late Positive Component could also reflect successful encoding of associative information.

The later study ERP feature, Slow Wave, has been reported at different electrode sites. Based on topographic patterns alone, it would seem that there are multiple Slow Waves relevant to memory encoding. The Slow Wave recorded from the frontal region has long been suspected to reflect associative-related encoding processes. Fabiani et al. (1990) asked participants to use elaborative strategies to study items, and found a frontal Slow Wave onset associated with successful recall around 500 ms. Although it was an item-oriented task, the study strategy employed tapped into relational processing as participants were asked to connect or organize the words by making sentences, or forming images or pictures. Furthermore, Kim et al. (2009, 2012), who also reported frontal Slow Wave in an word–word association task, suggested that the frontal Slow Wave reflects processes involved in learning relational and associative information.

We observed two Slow Waves in our study based on the topographic distribution: a positive Slow-Wave subsequent memory effect at electrode Pz, and a negative Slow-Wave subsequent memory effect at frontal electrodes. When we examined the relationship between memory performance (d') and the size difference in Slow Waves at electrode F3 and Fz, we did not find significant correlations between d' and Slow Waves across participants at either electrode. In other words, the Slow Wave within-subjects effect of a given participant did not explain the participant's memory performance on this associative recognition task.

In sum, the negative subsequent memory effect recorded from the frontal electrodes may reflect unique encoding processes that are crucial for successful associative recognition. Furthermore, the frontal Slow Wave, which has been suggested to reflect associative memory encoding related processes, showed within-subject effects, but those effects did not explain individual differences in memory performance.

4.5.2 Test ERPs

At test, we examined two ERP features, the FN400 at electrode Fz and the Left Parietal Positivity at electrode P3, using the old/new effect approach (hits versus correct rejections) and the retrieval success effect (hits versus misses). We did not find significant old/new effects, nor retrieval success effects during the time window of FN400. The null result in the FN400 is in line with the dual-process theory of recognition: the FN400 reflects familiarity-based retrieval that does not contribute to successful associative recognition (Yonelinas, 2002). Alternatively, FN400 has been suggested to reflect the memory-strength of an item (Woroch & Gonsalves, 2010). It is possible that our participants make associative recognition judgments based on the memory-strength of the items in the probe. Therefore, we could expect to see a significant difference between hits and misses, as items in hit trials could have higher strength than items in the miss trials. Similarly, we could also expect to see a significant difference between hits and correct rejections as items in hit trials could have higher strength than items in the correct rejection trials. However, there was no significant old/new effect nor retrieval success effect in FN400, suggesting item memory strength was similar between trial types and item memory strength did not influence performance.

Yonelinas (2002) summarized prior research and suggested that the associative recognition judgments were largely dependent on the recollection-based retrieval, which was indexed by the Left Parietal Positivity (Rugg & Curran, 2007). The assumption is that in a given pair, A–B, item A could provide a context for item B, and vice versa. Given that all items were from the study set, knowledge of the items in the probes were not enough to successfully discriminate intact from rearranged probes. Recollection would be able to differentiate intact from rearranged probes since it enabled the retrieval of contextual information (the other item of the pair). Therefore, it would be reasonable to expect a significant old/new effect and retrieval-success effect in the Left Parietal Positivity. However, our results showed no significant effect. It is possible that the Left Parietal Positivity may not, in fact, be sensitive to recollection-based processes. For example, Curran (2000) asked whether the Left Parietal Positivity reflected recollection-based retrieval. The participants were instructed to discriminate studied targets from very similar lures (i.e., "chair" versus "chairs"). The Left Parietal Positivity did not differ between targets and similar lures. Thus, Curran (2000) argued that the Left Parietal Positivity may not index the form of recollection-based retrieval that could help discriminate targets from similar lures. Therefore, the null effect in the Left Parietal Positivity could suggest that either the discrimination between the probe types do not involve recollection as predicted by dual-process theory, or the Left Parietal Positivity does not reflect recollection involved in associative recognition judgments.

Although many have argued that recollection-based retrieval contributes to successful associative recognition judgments, others have suggested that familiarity-based retrieval could also support associative recognition when a pair is processed as a single item, so-called "unitization" (see Murray & Kensinger, 2013, for a review). Diana et al. (2011) found, when participants were instructed to form one single representation of two items in a pair, they showed a strong old/new effect at FN400, suggesting familiarity-based retrieval. We did not find significant effects in our FN400 measures. It is likely that our participants did not use unitization encoding strategies for learning the word pairs.

Apart from the FN400 and the Left Parietal Positivity, the frontal old/new effect (Hits > Correct rejections) recorded by others in the associative recognition paradigm (Donaldson & Rugg, 1998; Senkfor & van Petten, 1998; Trott et al., 1999) was also not observed in the present study. Instead, we found a negative old/new effect, where the voltages of correct rejection ERPs were more positive than those of the hit ERPs. From the topographic distribution of amplitude difference between ERPs of old and new responses, the negative old/new effect seems to concentrate on the right hemisphere. Similar old/new effects have been found in many source memory retrieval tasks. Source memory studies, as described in the Introduction, can be viewed as encoding and retrieving associations between the item and its location. For example, Cycowicz, Friedman, and Snodgrass (2001) asked participants to study a set of pictures outlined in either red or green, and later had them judge if a picture was from the study set (item recognition) and if the outline colour of the pictures was accurate (source memory). In this case, the source memory task is testing the association between the picture and its outline colours. They examined source memory retrieval by contrasting the ERPs from correct source retrieval, incorrect source retrieval, and new items. Correct-source-retrieval ERPs had the most negative voltage, while the new–item ERPs had the least negative voltage. It is also worth noting that they did not find the Left Parietal Positivity in their study. Cycowicz et al. (2001) argued that the retrieval of source memory (associative information) might not be facilitated by recollection-based retrieval, as indexed by the Left Parietal Positivity, but rather, by unique processes related to source-memory retrieval. Our task was not a source-memory task, but may be similar in that it involves associative information processing. It is possible that we were measuring similar neural or cognitive processes that were tapped by Cycowicz et al. (2001). Furthermore, Donaldson and Rugg (1999) examined the ERP correlates of association memory retrieval comparing associative recognition and cued recall. Interestingly, they found a negative old/new effect in the cued recall procedure and a positive old/new effect in the associative recognition condition. Our ERP results highly resembled the cued recall ERPs in the Donaldson and Rugg (1999) study. It is possible our participants used recall-like retrieval to make associative recognition judgments through recall-to-reject or recall-to-accept processes which we will discuss next.

Some experimental psychologists have theorized that the associative recognition decision is based on a recall-like process, either the "recall-to-reject" process (Clark, 1992; Clark & Burchett, 1994; Clark & Gronlund, 1996; Gronlund & Ratcliff, 1989; Hintzman & Curran, 1994; Rotello & Heit, 1999, 2000) or the "recall-to-accept" process (Rotello & Heit, 1999). The assumption is that after studying a list of pairs (i.e., A-B, C-D, E-F, ...), when participants are given pair *A-D* to judge, the participant would use A as the cue to probe for its counterpart (B). After recalling B, the participant would see if it matched with the other item presented (D). If the two items matched, the participant would respond "intact" (recall-to-accept) or if the two items mismatched, the participant would respond "rearranged" (recall-to-reject). In other words, the associative recognition judgment is achieved via cued recall.

Since our negative old/new effect ERPs resemble those of cued recall ERPs— not recalled probes had more positive ERP amplitude than the recalled probes (Donaldson & Rugg, 1999), we suspect that our participants employed these recall-like strategies to discriminate the probes. In addition, memory performance (d') was significantly correlated with the old/new effect ERP contrast and the retrieval success effect ERP contrast across participants. In other words, if one participant had large negative ERP contrast (for both old/new effect and retrieval success), this participant would perform well in this associative recognition task. It is difficult to determine whether our participants used recall-to-reject or recall-to-accept, or may be both; however, the recall-like process, indexed by negative old/new effect, influenced memory performance.

4.5.3 Connecting study and test ERPs

One of the main goals of the present study was to extend our current understanding of the cognitive processes tapped by memory-related study and test ERPs. The across-phase correlations can provide insight into this. The Late Positive Component at study was significantly correlated with the early retrieval success effect at test. This means that if one participant had a big negative subsequent memory effect at the Late Positive Component, the same person would also have a big negative early retrieval success effect at test. Interestingly, both ERP features in the present study bear a high resemblance to the ERP features that are thought to reflect cognitive processes related to successful encoding and retrieval of source memory. Our results suggest that word–word associations can be achieved using the same processes involved in item-context associations.

Furthermore, results found in the present study are very similar to the ERP correlation results in Chapter 3 (Chen et al., 2014). In Chapter 3, we found that the Late Positive Component at study and FN400 at test were correlated with d'. Similarly, we also found the Late Positive Component and early retrieval success effect (albeit in negative polarity) were also correlated with d'. Given the close coupling of item and association memory, it is possible that processes that contribute to successful item memory encoding and retrieval could also contribute to association memory. Therefore, the Late Positive Component at study and the early retrieval success effect at test might index item memory related processes that then led to successful association memory.

4.6 Conclusion

Many complex processes could be involved in successful associative memory functioning. We found a negative subsequent memory effect at study and negative old/new and retrieval-success effects at test, indexing successful encoding and retrieval within subjects. In addition, the Late Positive Component at study appears to play an important role both in associative recognition within-subjects and in explaining memory performance between-subjects. Furthermore, the Late Positive Component at study was correlated with the early retrieval success effect at test, suggesting that they might be linked to source-memory-like processing. Lastly, the null effect result of the Late Parietal Positivity added more evidence that challenged its role in memory success. In short, the differences measured in Late Positive

Component at study leads to difference measures in the early retrieval-success effect at test, which in turns leads to better performance on the associative recognition task. This pattern of results echoed the findings in the item-recognition memory task, suggesting a possible common neural mechanism for verbal recognition memory in general.

Chapter 5

Rhythmic activity and individual variability in associative recognition memory

Abstract

Theta ($4 - 8\ Hz$) and alpha ($\sim 10\ Hz$) oscillations have been suggested to play important roles in memory functioning. In particular, more theta oscillations and less alpha oscillations are associated with effective encoding (subsequent memory effect) at study and successful retrieval (retrieval success effect) at test. Here, we seek to understand the functions of those oscillations in a verbal associative recognition memory task. Taking an individual-difference approach, we test two main hypotheses. First, we asked whether those within-subjects memory effects, namely, subsequent memory effect and retrieval success effect in theta and alpha oscillations explain individual difference in memory performance. Theta oscillations at study and at test correlated with memory performance (d') across participants, supporting the prediction; however, no support was found for alpha oscillations. Second, we tested whether the memory-related theta and alpha oscillation measures reflect the same cognitive processes that are reflected in the memory-related event-related potential (ERP) features, specifically the features have been implicated to reflect processes involved in successful associative recognition memory. Alpha oscillations correlated with some of the ERP features, where theta oscillations did not correlate with any memory-related ERP measures. Our findings are consistent with item-recognition oscillation results, where theta oscillations correlated with memory performance and alpha oscillations correlated with memory-related ERPs. The two oscillations might be a part of a neural network that is essential to memory regardless of the verbal memory tasks.

5.1 Introduction

Learning new associations between items involves complex cognitive processes. Neural oscillations recorded from the human scalp have been linked to some of those processes. Theta ($4-8\ Hz$) and alpha ($\sim 10\ Hz$) oscillations in particular are thought to play important roles in various aspects of association memory, where more theta activity and less alpha activity is indicative of successful memory encoding and retrieval (Doppelmayr et al., 1998, 2000, 2005; Klimesch, 1996, 1999; Klimesch et al., 2005, 1990, 1993, 1994; Jensen et al., 2002). Association memory can be tested using many procedures, for example associative recognition and cued recall (Kahana, 2012). In an associative recognition procedure, participants are instructed to study lists of word pairs (i.e., A-B, C-D, E-F...), and are then asked to judge a new list of probes composed with identical "intact" pairs (A-B) or "rearranged" pairs made up of studied words from different pairs (A-F). The use of an associative recognition task provides an opportunity to examine brain activity recorded from both the study and the test phase. Compared to cued recall, where after studying lists of word pairs, participants are given a probe (cue) and asked to recall the other item of the pair (i.e., A - ?) via type or vocal responses, associative recognition only requires a one-key response. This means that brain activity recorded from test phase has less muscle and eye movement.

EEG oscillations recorded at study can be analysed using the subsequent memory paradigm, where activity is separated into later-remembered and later-forgotten trials using the memory outcome from the test phase. This contrast enables the researchers to isolate brain activity related to successful encoding (Paller & Wagner, 2002). Similarly, during the test phase, brain activity can be separated into remembered and forgotten trials, just like the subsequent memory effect, but at test. The retrieval success effect could reflect processes that contribute to successful retrieval (Dolcos et al., 2005).

Murdock (1974) has made the distinction between memory for items and memory for associations, and suggested that association memory is highly dependent on item memory. For example, Hockley and Cristi (1996a) studied item and associative information by given participants a list of word pairs to study. Half of the participants were instructed to focus on the items, where the other half were instructed to focus on the associations between items. Then participants were tested using item recognition for item memories and associative recognition for association memories. They found that the association-focused group performed better on the associative recognition task, and performed equally well on the item recognition task compared to the item-focused group. This result suggested that association memory and item memory were somewhat dependent. Although the processes involved in remembering item and associative information might differ (Clark, 1992; Clark & Burchett, 1994; Gronlund & Ratcliff, 1989; Hockley, 1992, 1994; Hockley & Cristi, 1996b; Yonelinas, 1997), it is possible that the processes involved in successful item memory encoding and retrieval might also support the successful encoding and retrieval of association memory. Chen and Caplan (2017) studied the functions of theta and alpha oscillations in an item-recognition task by correlating those oscillatory measures with memory performance and memory-related event-related potentials (ERPs) across participants (Chapter 3). We found that theta and alpha oscillations contribute to memory function differently. While theta oscillations explained individual differences in memory performance, alpha oscillations were correlated with memory-related ERPs across participants. We suggested that theta oscillations might be supporting successful item memory in an associative manner. For example, participants might remember the item in relation to other items that came before or after it, or remember the item in terms of its list context. Thur, using the same logic and approach, the aim of the present study is 1) to determine the functional significance of the theta and alpha oscillations in memory for associations and 2) to examine whether the measures of theta and alpha oscillations match findings from event-related potentials (ERPs) about the cognitive processes involved.

5.1.1 Functions of theta and alpha oscillations and association memory

Theta oscillations have long been thought to play important roles in successful encoding and retrieval (see Jensen et al., 2007; Kahana et al., 2001; Klimesch, 1997, 1999; Klimesch et al., 2010, for reviews). In item memory tasks, more theta activity reflects successful memory in encoding. Klimesch (1999) reviewed oscillation studies that used the subsequent memory effect procedure, and found an increased level of theta activity for later-remembered trials than for later-forgotten trials. Similarly, Doppelmayr et al. (1998) examined theta activity between good and bad performers during the test phase of an item recognition task. They found that not only remembered trials had more theta activity than the forgotten trials, but also the difference in theta activity between remembered and forgotten trials (retrieval success effect) was bigger in good performers than bad performers. Doppelmayr et al. (1998) suspected that the theta activity retrieval-success effect recorded from the scalp might be related to hippocampal theta activity, within bigger hippocampo-cortical feedback loops. This theta-oscillation engaged loop could be important for association memory. Since Sirota et al. (2008) proposed that the theta oscillations modulate the communication between the hippocampus and neocortex, and Ranganath (2010) reviewed a body of research and suggested that hippocampus and medial temporal lobe were responsible for the binding relational information, it is possible that the theta oscillations recorded from the scalp were a reflection of that brain network activity, which could support association memory. In line with this idea, Summerfield and Mangels (2005) asked participants to remember a list of word–colour associations, and then tested their memory for words and the associated colours. They found that increased theta activity during study was associated with better subsequent memory, and thus suggested that theta oscillations help to bind an item (word) to its context (colour) during encoding. Therefore, theta oscillations might facilitate association memory encoding and retrieval. Furthermore, Caplan and Glaholt (2007) measured theta oscillations during the study phase of a relational memory task (learning word-pairs and word-triples). They found that there were more theta oscillations present for more accurate and faster participants. These results further the notion that theta oscillations are critical in learning item–item associations.

During the test phase of an associative recognition procedure, participants are instructed to make “intact” and “rearranged” judgments. Various theoretical frameworks have been proposed to explain how participants make associative recognition judgments. The dual-process theory extended the item-recognition framework to associative recognition judgments. In this view, there are two separate processes involved in recognition judgments, familiarity and recollection. Familiarity is thought to be a relatively simple strength signal, whereas recollection is supposed to reflect additional, detailed contextual retrieval (Yonelinas, 2002). Since “intact” and “rearranged” probes in the associative recognition task are all assembled from studied items, but paired differently in the “rearranged” pairs, Yonelinas (2002) argued that associative recognition judgment relies on recollection-based retrieval which includes specific contextual details that familiarity-based retrieval would not be able to provide. In other words, one word of a pair is the “context” for the other word. Nyhus and Curran (2010) reviewed many item-memory oscillation studies, and found that more theta activity was associated with recollection-based responses. If associative recognition judgments indeed rely on recollection-based retrieval, theta oscillations could potentially facilitate the process.

In short, theta oscillations might be essential for learning item–item associations and making correct recollection-based judgments, which then support associative recognition memory.

Alpha oscillations, on the other hand, have been thought to have many functions in various tasks. For example, alpha oscillations showed activity difference in attentional demands (see Klimesch et al., 1999, for a review), verbal stimulus type (abstract versus concrete words Schack et al., 2003), and mental visual imagery of the words (Bartsch et al., 2015). More importantly, alpha oscillations have also been implicated in memory functions (see Klimesch, 1996; Klimesch, Doppelmayr, & Hanslmayr, 2006; Klimesch et al., 2010, for reviews). Moreover, there are some lines of evidence that alpha oscillations are also important for learning item–item associations. For example, Molle, Marshall, Fehm, and Born (2002) instructed participants to study pairs of words or pairs of faces. After studying the word–word pairs, the association was tested using cued recall (given one word as probe, recall the other word of the pair); or after studying the face–face pairs, the association was tested using matching (given the probe face, find the target face from 18 given alternatives). A block would be considered as a "good performance" block if more than 4 out of 9 pairs of words were recalled, or more than 1 out 3 pairs of faces were matched, otherwise, it would be a "poor performance" block. They found that alpha activity was reduced during the "good performance" blocks compared to the "poor performance" blocks. The results of this study suggested that less alpha activity (alpha desynchronization) is beneficial in learning associative information. Similar alpha effects have been found for item memory as well (see Klimesch, 1997; Klimesch et al., 2007, for reviews). In addition, Klimesch, Doppelmayr, and Pachinger (1997) studied the functions of alpha oscillations in a paired-associate learning task. Participants were split into "good" and "bad" memory performers based on their accuracy, and the amount of alpha activity was decreased more for the "good" performers than for the "bad" performers. The results from these studies provided some evidence that decreased alpha activity might not only index attention, but also reflect memory processes involved in an associative memory task. In addition, Klimesch (1997) reviewed several studies of alpha oscillations and memory performance (both item and association memory), and determined that at both the study and test phase of memory experiments, less alpha activity was associated with better memory performance. Klimesch (1997) concluded that apart from indexing attentional processes, less alpha activity might also reflect processes that were crucial for successful memory encoding and retrieval.

The studies summarized above have demonstrated that theta and alpha oscillations differ between remembered and not remembered trials (i.e., subsequent memory effect at study and retrieval success effect at test). The within-subjects differences in brain activity could reflect processes involved in memory functioning. If the processes indexed by theta and alpha oscillations were the underpinning neural mechanism for memory functioning, we would expect to see those differences explaining the individual variability. The results from Doppelmayr et al. (1998); Klimesch, Doppelmayr, and Pachinger (1997); Molle et al. (2002) suggested that alpha and theta oscillations could distinguish good and bad memory performers. Thus, it is possible that these within-subjects effects measured by oscillations vary as a function of memory performance in a continuous manner, which might explain individual differences. For example, Caplan and Glaholt (2007) have demonstrated that theta oscillations at study phase of a relational task covaried positively with accuracy, but negatively with response time. In this present study, we seek to replicate the within-subjects memory effects of theta and alpha oscillations in an associative recognition task and to extend the behavioural relevance of those two oscillations. If an oscillation measure could explain individual differences in memory performance, it would strengthen the argument for their behavioural relevance; if not, that would weaken the argument, and suggest that alpha and theta oscillations might reflect processes that were not directly related to association memory. Since there was more theta activity, and less alpha activity, in the good memory performers than the bad memory performers, we expect to see a positive correlation between measures of theta oscillations and memory performance (d'), and a negative correlation between measures of alpha oscillations and memory performance.

5.1.2 Possible cognitive roles of theta and alpha oscillations examined using event-related potentials

Prior studies that used the ERP technique have identified a few ERP features that are thought to reflect encoding and retrieval of association memory. For example, Kim et al. (2009, 2012) examined the ERP features from the study phase of a paired-associate learning task and found that the subsequent memory effect was most pronounced around 800–1200 ms after the onset of stimulus (Slow Wave) recorded from the frontal electrode sites. They suggested that the Slow Wave might reflect processes involved in item–item associations. Other studies that used associative tasks also found similar Slow Wave effects (Jäger et al., 2006; Kounios et al., 2002; Weyerts et al., 1997). At test, there are two main ERP features, the FN400 and the Left Parietal Positivity, that have been associated with item-recognition memory. Instead of using the retrieval success effect contrast, many used old/new effect, contrasting remembered studied items (hits) and correctly rejected new items (correct rejections). The rationale behind the old/new effect contrast is that if one can successfully identify old items from the new, one must have memories for the old items. Both contrasts have been used in ERP studies, and the ERP morphology has looked very visually similar. However, Chen et al. (2014) and Chapter 4 have demonstrated that despite the morphological similarity, those two contrasts might index different processes. We examined both retrieval success and old/new effects in the present study. Under the dual-process theory framework, the FN400 was thought to reflect familiarity-based retrieval, where the Left Parietal Positivity was thought to reflect recollection-based retrieval (see Rugg & Curran, 2007, for a review). Since the dual-process theory suggested that associative recognition judgments rely on recollection-based retrieval, the Left Parietal Positivity has been the target ERP feature in associative recognition tasks. For example, using the associative recognition procedure, Donaldson and Rugg (1998) found strong old/new effect at the left parietal electrodes, and thus suggested that the Left Parietal Positivity reflected retrieval of contextual information via recollection. Other studies that used similar associative recognition procedures also found similar test ERPs effects (Mark & Rugg, 1998; Ranganath & Paller, 1999; Senkfor & van Petten, 1998; Trott et al., 1999; Brewer et al., 1998).

In Chapter 4, we conducted a verbal associative recognition memory ERP study examining the connection between study and test ERP features. We found significant subsequent memory effects at study, and it was in reverse polarity from some of those reported ERP studies. We did not find a significant old/new effect, nor retrieval success effect in the FN400 or the Left Parietal Positivity. Instead, the ERP effects we observed bear a high resemblance to the ERP findings in source memory tasks. Source memory was developed to objectively test the recollection-based retrieval under the dual-process theory framework. In many cases, participants were asked about their own judgment (i.e., remember/know responses, response confidence rating), and the responses were highly subjective. In source memory tasks, participants were asked about the contextual details of the item, for example, the colour of the font or the location of the stimulus. If participants were able to successfully retrieve those contextual details (source), then it was assumed that recollection-based retrieval was engaged. In Chapter 4, we suggested that source memory tasks are comparable to paired associative learning task, in which an item is associated with its context.

In oscillation studies of item recognition-memory, it has been proposed that theta activity is involved specifically in the recollection process (e.g., Guderian & Düzel, 2005; Guderian et al., 2009; Gruber et al., 2008; Osipova et al., 2006). If, indeed, the associative recognition judgment relies on recollection-based retrieval alone, and theta oscillations reflect recollection, we should expect to see a strong correlation between the ERP measures of recollection and oscillation measures of recollection where the same cognitive process is contributing to both.

Design of the current study We used a verbal associative-recognition procedure that was consistent with prior procedures and obtained both a large number of trials per participant (112 intact probes and an equal number of rearranged pairs as lure probes) and a large sample size (58 participants). We did not include new items, since the new items could allow participants to make associative-recognition judgments based on item-memory alone, and participants may have two criteria for the probes (intact versus rearranged versus new) which further complicates the task (Kahana, 2012; Osipova et al., 2006; Yonelinas, 2002). We included only the studied items at test, and constructed two probe types: intact (identical) and rearranged pairs.

5.2 Methods

5.2.1 Participants

The study includes the same data as reported in Chapter 4. Sixty-eight (9 self-reported left-handed [1], 59 self-reported right-handed; 32 female) undergraduate students enrolled in an introductory psychology course at the University of Alberta, aged 17–26 (mean = 19, SD = 2.03) participated for partial course credit. Data from nine participants were excluded

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[1] When we excluded these 9 participants from the analyses, the pattern of results was not affected

from analyses: six due to low rates of misses ($< 10\%$), four due to excessive amounts of artifacts in the EEG, for a total of 58 participants included. All participants were required to have English as their first language and had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment in accordance with the University of Alberta's ethical review board.

5.2.2 Materials

The stimuli were nouns drawn from the Toronto Word Pool (Friendly et al., 1982) composed of 4–8 letters. Kucera-Francis frequency was between 1–712 per million. The experiment was created and run using the the Python Experiment-Programming Library (Geller et al., 2007). Study items and test probes were presented in a white "Courier New" font on a black background. Paired words were presented simultaneously in the centre of the computer screen.

5.2.3 Procedure

The methods are the same as in Chapter 4, the session took place in an electrically shielded, sound-attenuated chamber. In each session, a participant studied and tested on one practice set (excluded from analyses) followed by 28 experimental sets involving 8 pairs each. The study phase instructed participants to study word pairs displayed one pair at a time. Each study set comprised 8 pairs, 16 words. Pairs were presented for 2500 ms with jittered uniform-random intertrial interval between 500–800 ms. The end-of-list distractor task, included to reduce recency effects that can contribute nuisance variability to the memory measure, consisted of three equations of the form of $A + B + C =$, where A, B, and C were randomly selected digits between two and eight. Each equation remained on the the centre of the screen for 5000 ms. The participant was asked to type the correct answer. In the recognition judgment phase, which immediately followed the distractor task, 8 probes were presented at test, half of which were previously studied pairs ("intact" probes) and half of which were previously studied words rearranged into new pairs ("rearranged" probes). Additionally, the left and right position of each word was kept consistent from study to test. Each probe remained on the screen until the participant made a response by pressing the corresponding key for either "intact" or "rearranged", which appeared in the bottom corners of the screen (with sides conterbalanced across participants. Figure 5.1). For each trial, response time (RT) and accuracy were recorded.

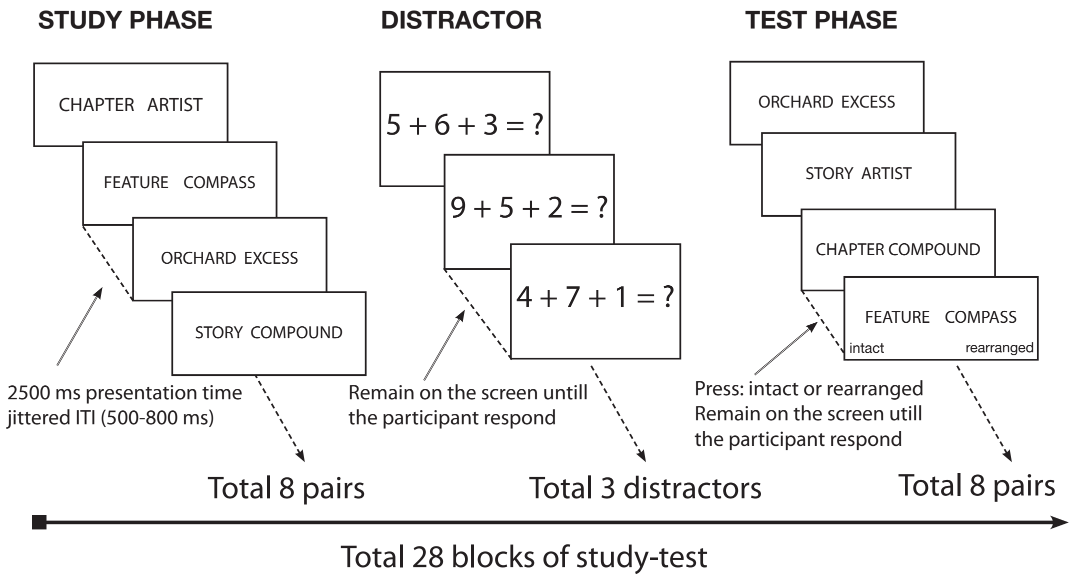

Figure 5.1: The experimental procedure. Each box illustrates the computer screen at a particular stage in the task (text has been enlarged relative to the screen size to improve clarity of the figure). There were 28 blocks of study–test.

5.2.4 Electroencephalography (EEG) Recording and Analyses

EEG was recorded using a high-density 256-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, OR), amplified at a gain of 1000 and sampled at 250 Hz. Impedance were kept below 50 kΩ and EEG was initially referenced to the vertex electrode (Cz). Data were analyzed by custom MATLAB scripts in conjunction with the open-source EEGLAB toolbox (Delorme & Makeig, 2004, `http://sccn.ucsd.edu/eeglab`). Artifacts were corrected via Independent Component Analysis, implemented in EEGLAB (Jung et al., 2000). The selection of components was based on visual inspection of the spatial topographies, time courses, and power spectral characteristics of all components. The components accounting for stereotyped artifacts including eye blinks, eye movements, and muscle movements were removed from the data. Independent Component Analysis were done separately for ERP and oscillation analyses due to the difference in filter bandwidth ($0.5 - 30\ Hz$ for ERPs and $0.1 - 50\ Hz$ for oscillations), see details below. Event latencies were corrected with a time lag correction due to a known hardware calibration problem identified by EGI.

ERP analysis

ERPs were analyzed as in Chapter 4. Signal was average re-referenced, and digitally bandpass filtered between 0.5–30 Hz. ERP trials were time-locked to the onset of pairs and referenced to a 100 ms pre-stimulus baseline. Electrodes and time windows were selected based on previous measurements of our ERP features of interests. For the study activity, the subsequent memory effect components were analyzed at electrode Fz and Pz in the time window of 400–700 ms latency post–stimulus for the Late Positive Component, 700–900 ms for the Slow Wave, and 1500–2000 ms for the Late Slow Wave. For the test activity, the retrieval success effect was analyzed by comparing hit with miss trials and the old/new effect was analyzed by comparing hit with correct-rejection trials. Both ERP effects were analyzed in two time windows, an early time window 400–600 ms and a late time window 600–800 ms at electrode Fz and P4. The selections of electrodes and time windows were the same as Chapter 4.

5.2.5 Oscillation analysis

EEG signal was average re-referenced, and digitally bandpass filtered between 0.1–50 Hz before it was subject to oscillation analysis. To ensure our results related to rhythmic activity, rather than non-rhythmic (non-repeating) activity that happens to have measurable power at our frequencies of interest, oscillations were detected using the wavelet-based oscillation detection method, BOSC (Better OSCillation detection; for further details, see Caplan et al., 2001; Whitten et al., 2011). In applying this method, signals were only classified as rhythmic if they exceeded power threshold for a given frequency for a minimum length of time (duration threshold). The power threshold was set to the 95^{th} percentile of the probability distribution of power values at a given frequency. The duration threshold was set at each frequency to three cycles. This method is thus more selective for rhythmic (repeating) activity than other methods (Caplan et al., 2001; Whitten et al., 2011). The proportion of time BOSC detected oscillations occurring each frequency, f, is denoted $P_{episode}(f)$. Frequency band of interests were defined as theta, 4.00 Hz, 4.78 Hz, 5.66 Hz and 6.72 Hz; and alpha, 8.00 Hz, 9.51 Hz and 11.31 Hz. Frequencies within a band were collapsed by averaging the proportion of oscillations present within that particular bandwidth. Analysis was confined to the frontal and parietal electrodes (i.e., electrode Fz and Pz). All trials were time-locked to the onset of the study stimulus, and $P_{episode}$ of all frequency for each trial was calculated using the time window of 1–1200 ms latency post-stimulus (which captures the same time duration as the ERP measures). Because the defining frequencies for a rhythm band vary from study to study, this makes it important to examine each sampled frequency individually. To check the robustness of our frequency bands, we also examined our correlation analyses at all frequencies sampled over the full 1–45 Hz range.

All statistical analyses were carried out using MATLAB and Statistics Toolbox Release 2008b (The MathWorks, Inc., Natick, Massachusetts, United States) and IBM SPSS Statistics for Mac, Version 21.0. (IBM Corp., Armonk, NY).

5.3 Results

Accuracy and response time are summarized in Table 5.1. The mean d' value was 1.58 (SD = 0.78). Accuracy was not near ceiling or floor, the large standard deviations of d', accuracy and response time suggest a meaningful variability across participants. The variability could support our planned correlation analyses.

Condition	[%]	Response time [ms]
hits (intact)	74 (14)	1486 (206)
misses (intact)	26 (14)	1855 (436)
correct rejections (rearranged)	81.4 (15)	1682 (286)
false alarms (rearranged)	18.6 (11.4)	1971 (494)

Table 5.1: Accuracy (percentage) and response time (ms) values, along with their standard deviations across subjects in parentheses.

First, we analyzed oscillations at both study and test separately to check whether we could replicate the subsequent memory effects at study, and retrieval success effect and old/new effects at test. Then, we tested the behavioural relevance of alpha and theta oscillations by correlating memory-outcome measures with the oscillation measures. Finally, we investigated the possible relationship between memory-related ERPs with the oscillation measures.

Study

Electrodes	α	θ
Fz	1.17	**2.23***
Pz	**-2.73***	-1.34

Test

Retrieval success effect			old/new effect	
Electrodes	α	θ	α	θ
Fz	1.86	**5.64***	-1.00	**5.07***
Pz	**-2.21***	-1.21	-1.19	-0.35

Table 5.2: t-values from paired-samples, two-tailed t-tests ($df = 58$) comparing mean $P_{episode}$ between subsequent hits and subsequent misses during study, between hits and misses (retrieval success effect), and between hits and correct rejections (old/new effect) during test for alpha and theta oscillations at electrodes of interests. $*$ denotes $p < 0.05$.

5.3.1 Replication of subsequent-memory, retrieval-success and old/new effects

The subsequent memory effect was analyzed at electrode Fz for theta oscillations and Pz for alpha oscillations (Figure 5.2 a,b). We conducted paired-samples, two-tailed t tests comparing the duration of oscillatory activity ($P_{episode}$) between subsequent hits and subsequent misses. Subsequent hits had theta oscillations at electrode Fz more of the time than subsequent misses, and subsequent hits had alpha oscillations at electrode Pz less of the time than subsequent misses in the alpha band (Table 5.2).

A similar pattern was found at test when we conducted a retrieval-success effect analysis, comparing theta and alpha activity for the hits to misses (Figure 5.2 c,d). Paired-samples, two-tailed t tests comparing mean $P_{episode}$ values confirmed the retrieval-success effect in both the theta (at Fz) and alpha (at Pz) bands (Table 5.2). In addition, parallel to the retrieval-success effect at test, we conducted an old/new effect analysis, comparing theta and alpha activity for the hits (old) to correct rejections (new, Figure 5.2 e,f). The paired-samples, two-tailed t-test, comparing mean $P_{episode}$ between hits and correct rejections during test, was significant for the theta band at electrode Fz (Table 5.2), replicating prior results (Klimesch, 1999; Klimesch, Doppelmayr, Stadler, et al., 2001). There was no significant difference between hits and correct rejections in the alpha band at electrode Pz. Moreover, in an item-memory recognition task, Chen and Caplan (2017) did not find significant old/new effect in the alpha band. Similar alpha results have been reported in other recognition memory studies as well (see Klimesch, Doppelmayr, Schwaiger, Winkler, & Gryber, 2000, for a review). Decreased alpha oscillations might reflect engagement of attentional processes which led to correct responses for both intact and rearranged probes.

5.3.2 Relationship between oscillations and individual variability in memory-outcome

We next examined if the within-subjects memory effects explain individual difference in memory. If oscillation measures could be shown to explain variance in memory performance across participants, that would corroborate the within-subjects results, and strengthen the role of theta and alpha oscillations in this associative recognition task. We first correlated the theta and alpha oscillation subsequent memory effects with the behavioural measures (d' and mean response time for hits) across participants, and likewise for the retrieval-success effects and old/new effect (Table 5.3). We found significant positive correlations between 1) d' and theta subsequent memory effect, 2) d' and theta retrieval success effect, and lastly 3) d' and theta old/new effect across participants. This means that with more presence of theta oscillation at both study and test, the participants would perform better on this associative recognition task. On the other hand, we found no significant correlations between d' and any alpha oscillation measure. Furthermore, we found no significant correlation between any alpha and theta oscillation measures and response time. Although both alpha and theta oscillations showed significant within-subjects memory effects, only the within-subjects measures of theta oscillations related to individual differences in memory performance (d'). Moreover, there is no significant correlation between alpha oscillations measures and theta oscillation measures at study (subsequent memory effect, $r(57) = 0.13, p > 0.1$) and at test (retrieval success effect, $r(57) = 0.09, p > 0.1$). This suggests that the two oscillations were independent, may be reflecting distinct cognitive and neural processes.

Again, to assess the robustness of these results, we conducted a broadband version of this analysis and plotted correlation values (not corrected for multiple comparisons) as functions of all frequencies at electrodes Fz and Pz (Figure 5.3). In general, the broadband analyses confirmed the results of the band-averaged analyses. It is worth noting that although there was no significant correlation between response time and theta-band oscillation measures, oscillations measured at 4.00 Hz, 4.78 Hz and 5.66 Hz at electrode Fz correlated nega-

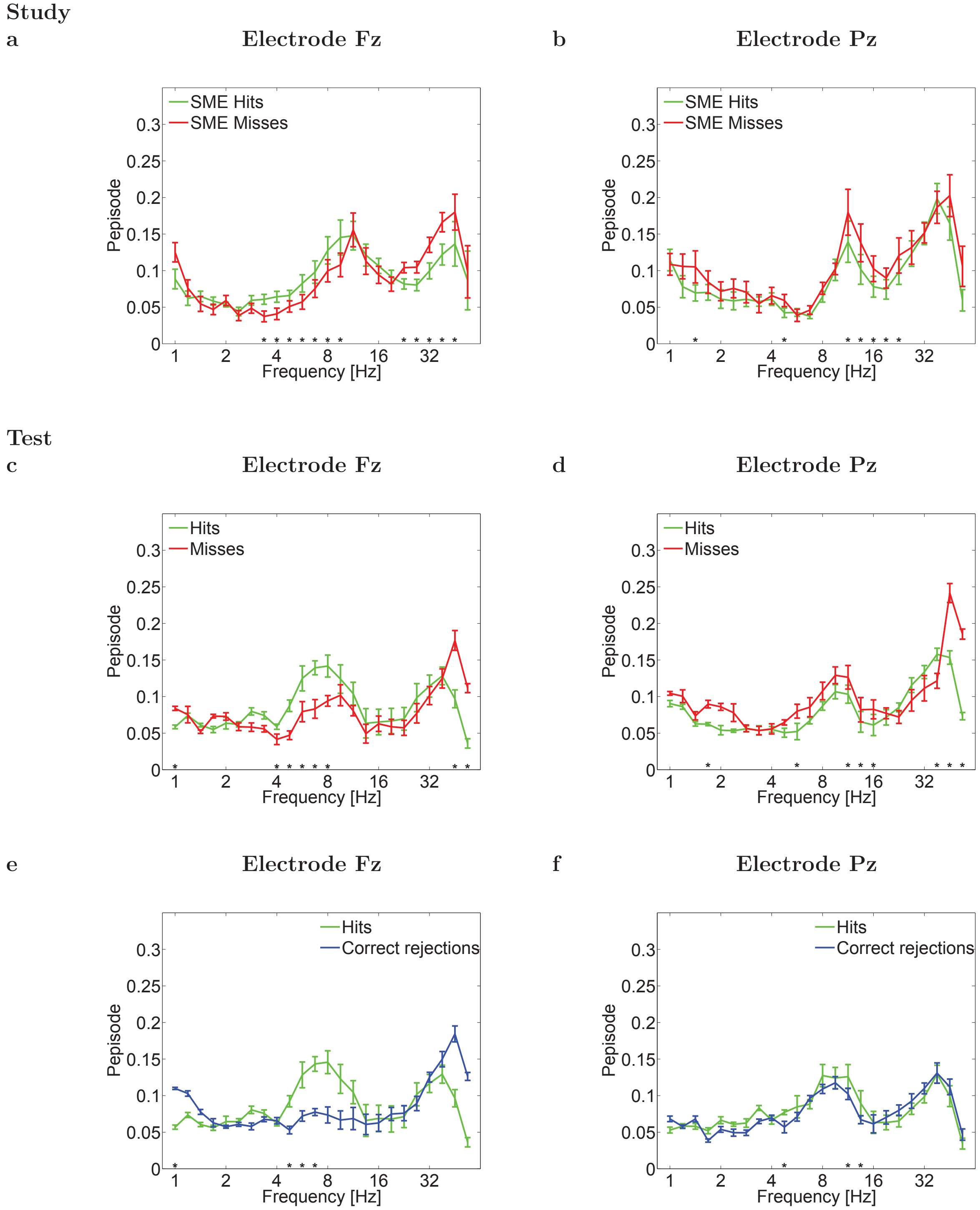

Figure 5.2: Average proportion of oscillatory activity ($P_{episode}$) is plotted as functions of frequency between hits (green) and misses (red) during study and test, and between hits (green) and correct rejections (blue) at test. Error bars represent 95% confidence intervals * denotes significant ($p < 0.05$) differences.

	Study Subsequent memory effect	
	α	θ
d’	-0.10 (-0.34, 0.16)	**0.35*** (0.03, 0.51)
RT	-0.06 (-0.31, 0.19)	0.14 (-0.29, 0.21)
electrode F3		
Late Positive Component	0.13 (-0.13, 0.37)	-0.04 (-0.28, 0.22)
Slow Wave-Early	0.15 (-0.11, 0.39)	0.02 (-0.23, 0.27)
Slow Wave-Late	0.12 (-0.14, 0.36)	-0.02 (-0.27, 0.24)
electrode Pz		
Slow Wave-Late	**0.27*** (0.04, 0.36)	-0.02 (-0.27, 0.24)

	Test Retrieval success effect		Old/new effect
	α	θ	θ
d’	-0.001 (-0.26, 0.25)	**0.34*** (-0.05, 0.48)	**0.25*** (-0.01, 0.46)
RT	0.11 (-0.15, 0.35)	-0.24† (-0.46, 0.01)	-0.18 (-0.41, 0.08)
Retrieval-success effect			
400–600 ms	[0.23† (-0.04, 0.45)]	0.14 (-0.11, 0.38)	–
600–800 ms	**0.27*** (-0.01, 0.47)	0.12 (-0.03, 0.32)	–
Old/new effect			
400–600 ms	–	–	0.09 (-0.16, 0.34)
600–800 ms	–	–	0.17 (-0.08, 0.41)

Table 5.3: Pearson correlation ($df = 57$) between 1) mean $P_{episode}$ alpha (recorded at Pz) and theta (recorded at Fz) oscillations with behavioral measures (d’ and response time, RT); 2) study mean $P_{episode}$ alpha and theta oscillations with study ERPs (the Subsequent Memory Effect); 3) retrieval mean $P_{episode}$ alpha and theta oscillations with retrieval ERPs (retrieval success effect); 4) retrieval mean $P_{episode}$ alpha and theta oscillations with retrieval ERPs (old/new effect). Reported along with 95% confidence interval, $*$ denotes $p < 0.05$; $\dagger$ denotes $p < 0.1$. [] indicates that this significant correlation become non-significant after the partial-correlation analysis (see text).

tively with response time, approaching significance (uncorrected for multiple comparisons, Figure 5.3,d). It is possible that some of those effects were washed out by averaging.

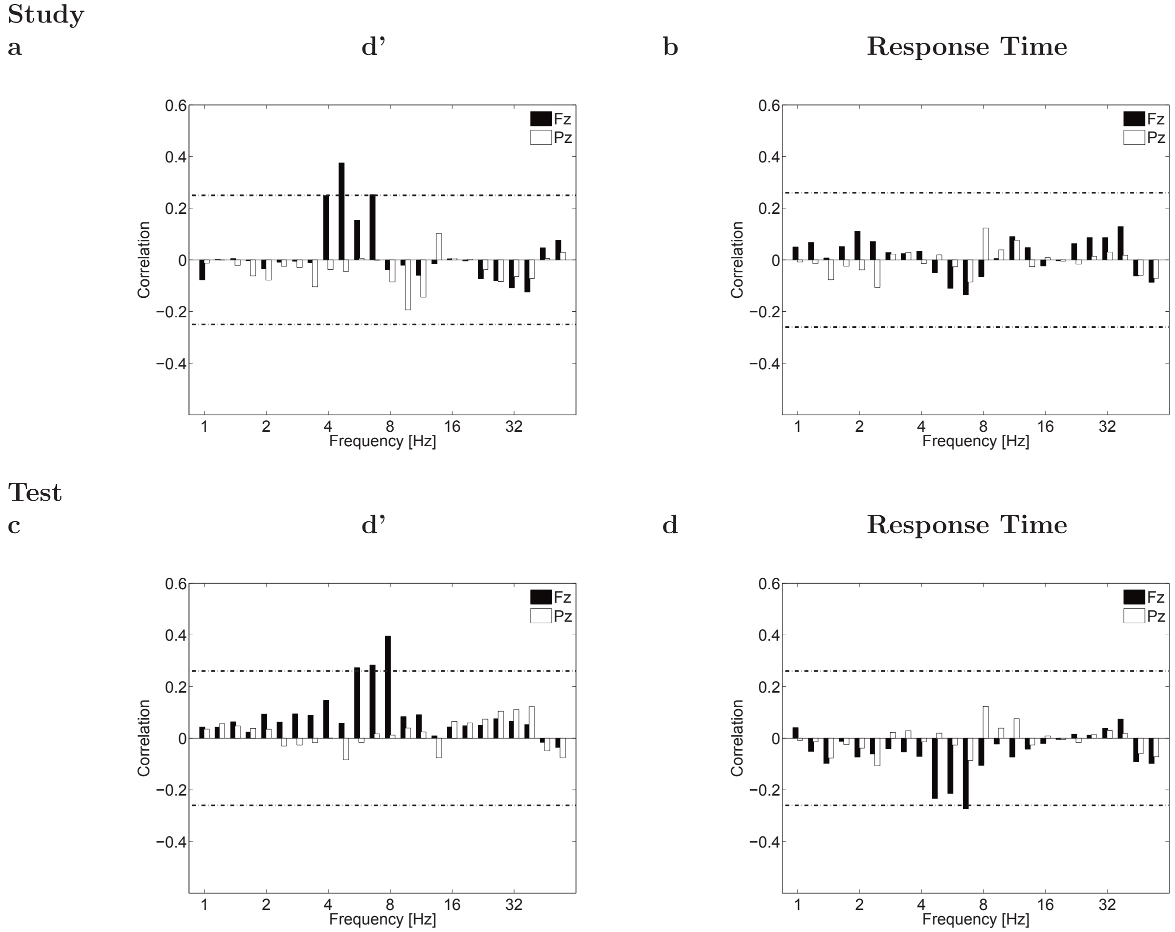

Figure 5.3: Pearson correlation ($df = 57$) plotted for all $P_{episode}$ frequencies at study (a,b) and test (c,d) correlating with d' (a,c) and response time (b,d). Oscillations were recorded at electrode Fz and Pz. The dashed lines denote the significance thresholds ($p < 0.05$, two-tailed).

Follow-up analysis of theta oscillations and memory outcome

Theta oscillation measures were found to covary with d' during test for both the old/new effect and retrieval-success effect contrasts. We moved beyond the difference measures and explore future the contribution of theta oscillations during different types of trials at both study and test. A multiple regression was run with d' as the measure and $P_{episode}$(theta) during study for later-hits, during study for later-misses, during hits at test, during misses at test and during correct rejections at test as the five predictors (Table 5.4). We did not include false alarms during test due to low trial counts. The significant predictors were theta-oscillation during study for later-hits, and during hits at test. Thus, only theta oscillations associated with successful memory for the intact pairs (hits at both study and test) were the main predictors of d'. This suggests that the presence of theta oscillations helps to encode a pair initially, and the presence of theta oscillations is also required during correct judgment of intact pairs (hits) but not rearranged pairs (correct rejections). It is possible that presence of theta oscillations provided brain states that were uniquely important for remembered information.

predictors	beta	t
θ Hits (study)	0.55	2.01*
θ Misses (study)	-0.07	-0.24
θ Hits (test)	0.61	2.61*
θ Misses (test)	-0.36	-1.14
θ Correct Rejection (test)	-0.37	-0.88

Table 5.4: Regression model for theta activity predicting d'. The theta activity measure is the proportion of oscillations ($P_{episode}$) for hits and misses during study, and hits, misses and correct rejections during test, recorded at electrode Fz. $*$ denotes $p < 0.05$.

5.3.3 Relationship between oscillations and memory-related ERPs

We aimed to extend our understanding of the possible functions of the alpha and theta oscillations to associative recognition-memory by seeking possible relationships between well-studied memory-related ERPs and oscillation measures. Using the same dataset, in Chapter 4, we isolated a few target ERP features for this analysis. At study, we measured significant subsequent memory effect at the Late Positive Component and the Slow Wave at frontal electrode F3, and the Slow Wave at centro-parietal electrode Pz. At test, we measured significant retrieval success effect (hits$-$misses) and significant old/new effect (hits$-$correct rejections) at electrode P4 for two time windows, 400–600 ms (early) and 600–800 ms (late). Then, we correlated theta and alpha oscillation measures with mean-voltage measures of ERPs implicated in associative recognition (Table 5.3). Theta oscillations at study and test were not correlated with any ERP measures, but alpha oscillations at study were significantly correlated with the Slow Wave-Late at electrode Pz and the alpha oscillations at test were significantly correlated with ERP measures from both time windows of the retrieval success

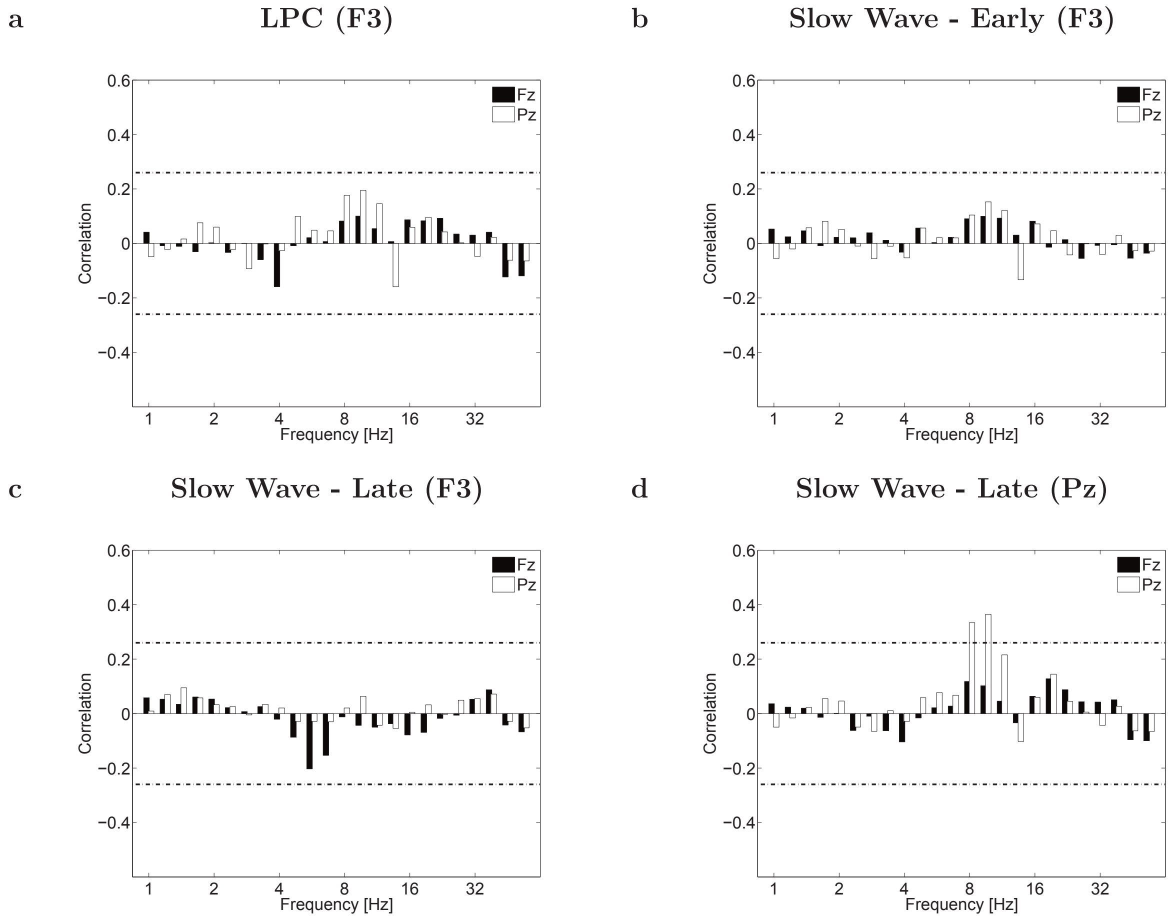

Figure 5.4: Pearson correlation ($df = 57$) plotted for all $P_{episode}$ frequencies at study correlating with subsequent memory effect ERPs (a, LPC at electrode F3, b, Slow Wave Early at electrode F3, c, Slow Wave Late at electrode F3, d, Slow Wave Late at electrode Pz). Oscillations were recorded at electrode Fz and Pz. The dashed lines denote the significance thresholds ($p < 0.05$, two-tailed).

effect.

It is important to note that in Chapter 4, we found that the retrieval success effect ERPs in these two time windows correlated with one another. To further understand the relationship between alpha oscillations and these ERPs, we carried out partial correlations. While controlling for the early retrieval success effect, the alpha oscillation measure and the late retrieval success effect remained significantly correlated ($r(57) = 0.25, p < 0.05$). However, when controlling for the late retrieval success effect, the correlation between alpha oscillation measure and the early retrieval success effect were no longer significant. This correlation pattern suggests that the shared variance between the alpha oscillations measure

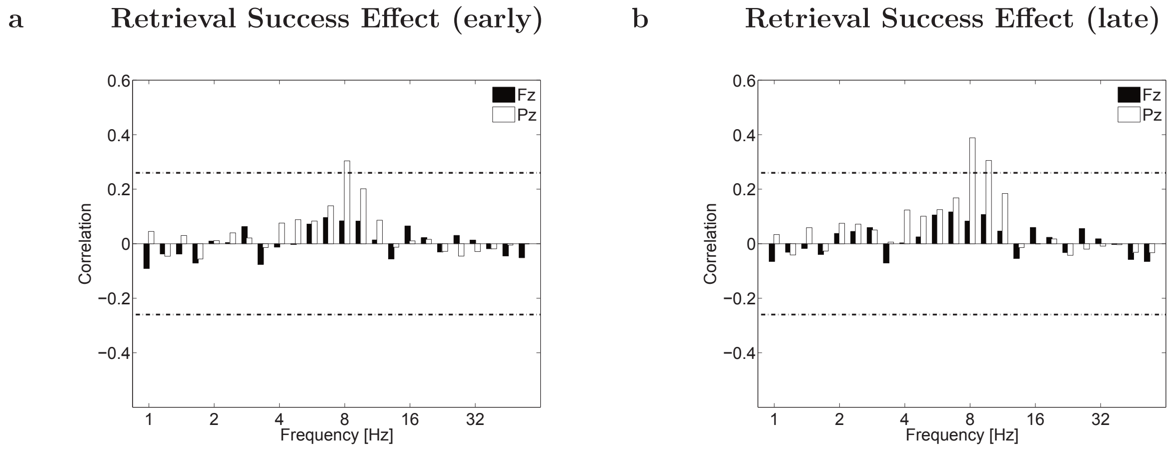

Figure 5.5: Pearson correlation ($df = 57$) plotted for all $P_{episode}$ frequencies at test correlating with retrieval success ERPs (a, retrieval success effect at early time window (400–600 ms) at electrode P4, b, retrieval success effect at late time window (600–800 ms) at electrode P4. Oscillations were recorded at electrode Fz and Pz. The dashed lines denote the significance thresholds ($p < 0.05$, two-tailed).

and the early retrieval success effect was mediated by the late retrieval success effect. It seems backwards that later retrieval success effect activity is mediating the early retrieval success effect. Since those two retrieval success effect ERP features were correlated, they might be reflecting similar processes, cognitive or neural. It is possible the signal reflecting those processes started in early retrieval success effect time window and ramped up in the later retrieval success effect time window. Therefore, we are seeing the late retrieval success effect mediating the early effect.

5.4 Discussion

Using an individual difference approach, we correlated measures of alpha and theta oscillations with behavioural memory outcomes and memory-related ERPs in an associative recognition task. Our findings suggested new possible functions of alpha and theta oscillations, and extended our understanding of cognitive processes involved in associative recognition.

5.4.1 Relevance of alpha and theta oscillations to memory outcome

Our first goal was to test the behavioural relevance of the theta and alpha oscillations in a verbal associative recognition task. Chen and Caplan (2017) found that theta oscillations during test were positively correlated with memory performance (d') across participants in an item recognition task. This correlation was only significant when using the difference measure of hits and correct rejections (old/new effect). In the present study, using an associative recognition task, we found that alpha oscillations showed a significant within-subjects memory effect (subsequent memory effect and retrieval success effect); however, those within-subjects effects did not correlate with any behavioural measures (d' and response time) across participants. Theta oscillations also showed significant within subject effects (subsequent memory effect, retrieval success effect and old/new effect). All of these within subject effects were correlated with d', but not with response time. This result is in line with the idea that theta oscillations facilitate relational and association information encoding and retrieval (Caplan & Glaholt, 2007; Nyhus & Curran, 2010; Summerfield & Mangels, 2005). To further examine the functions of theta oscillations in this associative recognition task, we conducted regression analyses to specify how theta oscillation during hits and misses at study and hits, misses and correct rejections at test contribute to memory performance d'. We found that only theta oscillations during hits at both study and test contributed significantly to d'. It seems that theta oscillations provided a "state" where participants can encode and retrieve successfully, where presence of theta oscillations enable the cognitive processes for associative recognition (Düzel, Penny, & Burgess, 2010). Following this idea, it is possible that the presence of theta oscillations could contribute to the false recognition of rearranged probes. However, we have limited trial counts for false alarms, thus, we could not include it as a predictor of d' in the regression analyses. In future studies, we could consider adding false alarm as a predictor for d' to explore the possibility that "theta-state" leads to false recognition. If the theta oscillations during false alarm trials were a significant contributor to d', we could suggest that the presence of theta oscillations gives participants a sense of "remembering" during test, which could lead to "intact" judgments.

Furthermore, Caplan and Glaholt (2007) examined theta oscillations during study where participants learning word-pairs and word-triples. They found the theta oscillations positively correlated with accuracy, but negatively correlated with response time. In the present study, we found a positive correlation between theta oscillations (subsequent memory effect) and memory performance (d'), but no significant correlation was found with response time. It is impossible that the choice of experimental paradigm changed the correlation patterns. Caplan and Glaholt (2007) used cued recall to measure memory performance, whereas we used associative recognition to measure memory performance. Moreover, participants in Caplan and Glaholt's (2007) study were instructed to learn both word-pairs and word-triples, whereas we only instructed participants to learn word-pairs. The differences between paradigms might contribute to the different correlation results seen in two studies.

Alpha oscillations are associated with visual attention, where decreased alpha activity is related to visual attention, and increased alpha activity indicates visual inattention (Klimesch et al., 1999). The level of alpha activity has been linked to memory performance on paired associate tasks as well (Klimesch, 1997). The results from these studies provided some evidence that decreased alpha activity might not only index attention, but also indicate a relationship to associative memory performance. We found no significant correlation between alpha oscillation measures and memory outcomes. Our results added more evidence that alpha might be reflecting visual attention. This was demonstrated by alpha activity differing between hits and misses within subjects, but did not explain individual differences in memory performance. It is possible that participants were not paying attention during some of the trials at study which led to a miss response later on, and level of alpha activity was indicative of attention allocation, thus leading to the within subject effects in alpha oscillations.

In sum, similar to the item recognition memory study (Chapter 3, Chen & Caplan, 2017), theta oscillations facilitate successful encoding and retrieval of associative information, where although alpha oscillations showed within subject memory effects, those effects did not explain individual memory difference.

5.4.2 Memory-related oscillations and memory-related ERPs

ERPs have been used to investigate recognition memory more extensively in relation to oscillations. During a recognition test, Yonelinas (2002) suggested that under the framework of dual-process theory, recollection-based retrieval enabled the retrieval of an item and its contextual details. In the case of associative recognition, for a pair A–B, item B can be served as the context of item A and vice versa. It is possible that recollection-based retrieval was used during the associative recognition judgment; however, we did not find significant FN400 or Left Parietal Positivity effects in Chapter 4. This suggested that either our participants did not use recollection-based retrieval for their associative judgments, or the ERP measures that were initially thought to index recollection did not capture the process. On the other hand, theta oscillations have also been suggested to index recollection. As we suggested in the Chen and Caplan (2017) study, if indeed the Left Parietal Positivity and theta oscillations were both indexing recollection, they might have been indexing different types of recollection processes. In line with this interpretation, we did not see a significant correlation between the theta oscillation measures and the test ERP measures. Therefore, we may be capturing different types of retrieval processes which could explain individual differences in memory performance.

Many have argued that associative recognition relies more on recollection-based retrieval (Hockley & Consoli, 1999; Rotello & Heit, 2000; Yonelinas, 2002; Yonelinas & Jacoby, 1994; Yonelinas et al., 1998). However, other researchers have found that familiarity-based retrieval could also support associative recognition judgments when a pair is processed as a single item— "unitization" (see Murray & Kensinger, 2013, for a review). Unitization is when the two items of the pair form a single representation for encoding (Graf & Schacter, 1989; Wollen et al., 1972). Diana et al. (2011) have found that using unitization encoding manipulation, high-unitization pairs showed a strong old/new effect at frontal-central ERP features suggesting familiarity-based retrieval. We did not find support for familiarity-based retrieval using ERP measures, as there were no significant FN400 effects (Chapter 4). Nyhus and Curran (2010) presented evidence that theta oscillations are implicated in recollection-based retrieval, with some studies finding that theta oscillations are also involved in familiarity-based retrieval in item memory. It is possible that theta oscillations also reflect familiarity-based retrieval that was enabled by the unitization of the items. However, the retrieval processes involved would evidently be different from those reflected in the ERP features.

It is difficult to determine which types of retrieval processes are involved in the present study (could be familiarity-based retrieval or recollection-based retrieval or possibly both). The results suggested that theta oscillations reflect processes that are not only able to differentiate remembered and not remembered pairs within a subject, but also able to explain individual differences in memory performance. Those processes do not share any variance with any ERP features that we measured in the present study. Maybe theta oscillations do not reflect familiarity or recollection-based retrieval, but rather other processes that are essential for associative recognition. However, it is equally possible that theta oscillations index other types of familiarity or recollection-based retrieval that was not measured by the ERP features.

Alpha oscillations, on the other hand, showed a very different result pattern than the theta oscillations. The alpha oscillation subsequent memory effect at study was correlated with Late Slow Wave at electrode Pz, and alpha oscillation retrieval success effect at test was correlated with late retrieval-success effect (after partial correlation). The Slow Wave has been thought to index elaborative memorization strategies (Fabiani et al., 1990), which could include "deep" levels of processing as well as relational or imagery-based strategies (Caplan et al., 2009; Kim et al., 2009). It is reasonable to assume that the Slow Wave might also reflect processes involved in item–item association memory. In Chapter 4, we found significant subsequent memory effects in Slow Waves at electrodes F3 and Pz, but none of these Slow Waves correlated with memory performance (d') across participants. Here, when we correlated alpha oscillations with the Slow Waves, we found that the Slow Wave recorded from electrode Pz, but not from electrode P3, was significantly correlated with alpha oscillations. This suggested that there might be multiple sources that contribute to Slow Waves, and Slow Waves recorded from different electrodes might reflect different cognitive processes. It is possible that alpha oscillations and Slow Wave Late might be reflecting inward attention as suggested by Chen and Caplan (2017), where if one participant had big differences in alpha activity during study (subsequent memory effect), the same participants would also have a bigger amplitude difference in the Late Slow Wave. Regardless of what the processes the Slow Wave and alpha oscillations might index, they do not affect individual differences in memory performance directly.

In Chapter 4, we did not find the Late Positivity Component that was associated with recollection-based retrieval. Instead, we found two ERP features showed significant retrieval success effect at test. Both the early and late features were correlated with d', suggesting that the amplitude measures observed in these features might reflect successful retrieval of associative information. In the present study, we found that alpha oscillations (retrieval success effect) were correlated with the Late retrieval success effect ERP features, was not correlated with d'. This suggested that alpha oscillations might play a role in memory retrieval, but again not directly related to memory performance.

There is a clear pattern that emerges from the correlation results, where theta oscillations are correlated with memory performance but not with memory-related ERPs, and alpha oscillations are correlated with memory-related ERPs, but not with memory performance. We had similar results in Chapter 3 (Chen & Caplan, 2017) using an item-recognition task. There are two possible takeaways from this pattern of results. First, both alpha and theta oscillations are important for memory functioning. It is possible they are a part of neural underpinning that is essential to memory, regardless of the task. Klimesch, Doppelmayr, et al. (2000) has suggested that theta and alpha oscillations might be two modes of a dynamic network that facilitates memory encoding and retrieval. Although we did not find the "trade-off" relationship in our item-recognition task (Chapter 3), nor in the present associative-recognition task, it is possible that those two oscillations are modes of a dynamic network, without the "trade-off" relationship. Second, the ERP amplitude difference might be a direct result of alpha oscillation phase reset. Many researchers have suggested that the phase resetting of oscillations is the neural mechanism of ERP (see Sauseng et al., 2007, for a review). The logic is that the ongoing oscillations reset their phase in response to a stimulus, the synchronized phases across frequencies would lead to an additive effect in the EEG signal and generate an ERP. It is possible that ERP features we recorded in the present study were the result of phase reset of alpha oscillations more so than theta oscillations. Therefore, a significant correlation between alpha oscillations and ERPs might be purely based on the additive nature of those two signals rather than some other deeper cognitive process connections.

5.5 Conclusion

We exploited individual variability in an associative recognition task by correlating measures of memory-related oscillation effects in alpha and theta bands with behavioural outcomes (d' and response time) and with memory-related ERPs. Both theta and alpha oscillations showed within-subjects memory effects, the subsequent memory effect at study and retrieval success effect and old/new effect (theta oscillations only) at test, suggesting that they facilitate the processes involved in associative recognition. However, theta and alpha oscillations contribute to memory functioning differently. The theta oscillation within subject memory effect explained individual differences in memory outcomes, but did not correlate with any memory-related ERPs. On the other hand, the alpha oscillation within subject memory effects did not explain any individual differences in memory outcomes, but correlated with memory-related ERPs. The theta oscillations may be setting a state to enable successful encoding and retrieval which directly influences the outcomes of the recognition task. The alpha oscillations may index attention, or other cognitive processes that could affect memory outcome, but it is done so through via the correlation with memory-related ERPs. In sum, we might be seeing a functional double dissociation of theta and alpha oscillations, where theta oscillations drive behavioural outcomes and alpha oscillations affects ERP features.

Chapter 6

General Discussion and Conclusion

The purpose of the preceding experiments was to investigate the neural mechanisms underlying human recognition memory. To understand how brain activity at study and at test might affect the individual difference in memory outcome, I used ERPs and oscillations as my measures of brain activity in item-recognition and associative-recognition tasks. In this final chapter, after summarizing the principal findings for each experimental chapter, there will be a broad discussion of some basic experimental findings in the context of existing theories and research regarding memory-related brain activity measures and recognition memory. This discussion will then focus on the significance of the research findings with respect to within-subject and between-subject memory measures, as well as connections between item and association memory. Finally, some objectives for future research will be identified.

6.1 Summary of principal findings

6.1.1 Chapters 2 and 4: the relationships between study and test ERPs and their effects on recognition memory performance

Chapter 2 examined the relationships among study and test ERPs and how these memory-related ERPs influence item recognition memory. The Late Positive Component and the Slow Wave are two classic ERP features at study that have been thought to index successful memory encoding (Friedman & Johnson Jr., 2000; Paller & Wagner, 2002; Wagner et al., 1999). Both features are found around the centro-parietal region (electrode Pz). The Late Positive Component is thought to reflect shallow encoding processes such as repetition, whereas the Slow Wave is thought to reflect deep encoding processes such as imagery and relational-information. Similarly, the FN400 and the Left Parietal Positivity are two other

ERP features at test that have been thought to index two different retrieval processes that contribute to successful item recognition judgments, namely, familiarity and recollection, as suggested by dual-process theory of recognition (Rugg & Curran, 2007; Rugg & Yonelinas, 2003). These proposed cognitive correlates of memory-related ERP features at study resemble other proposed cognitive correlates of ERP features at test. Specifically, the parallel between the Late Positive Component and the FN400, and the parallel between the Slow Wave and the Left Parietal Positivity. Information encoded using shallow strategies may be retrieved using familiarity-based (shallow) retrieval, and deeply encoded information may be retrieved using recollection-based (deep) retrieval. Put simply, information processing might follow a shallow-in, shallow-out and deep-in, deep-out model.

I measured memory-related ERPs, the Late Positive Component and the Slow Wave at study, and the FN400 and the Left Parietal Positivity at test, replicating the subsequent-memory effect, old/new effect and retrieval-success effect. I found that the study ERPs were indeed related to test ERPs, as I predicted. Across participants, the Late Positive Component was positively correlated with the FN400, and the Slow Wave was positively correlated with the Left Parietal Positivity. More importantly, the Late Positive Component and the FN400 pair was positively correlated with memory outcomes (d' and response time), but the Slow Wave and the Left Parietal Positivity pair was not. A graphic representation of the results is depicted in Figure 6.1, with the red circle denoting study brain activity, blue circle denoting test brain activity, and yellow circle denoting behavioural measures. The Venn diagrams represent the relationships among different measures.

In summary, I found that the item-memory-related study ERPs mapped onto the test ERPs. However, only the early ERP features, the Late Positive Component at study (subsequent memory effect) and FN400 at test (retrieval success effect) explained individual differences in memory performance. Moreover, not predicted by the hypothesis, the processes indexed by the later ERP features, the Slow Wave and the Left Parietal Positivity, may not be helpful in aiding participants making successful recognition judgments.

Extending the same logic and technique in item-recognition-memory ERPs to association-memory ERPs, Chapter 4 examined the relationships among study and test ERPs and how these memory-related ERPs influence associative recognition memory. Using an associative recognition procedure, participants studied lists of word pairs, and then judged a list of test probes that were either the same pairing from the study set (“intact”) or composed of

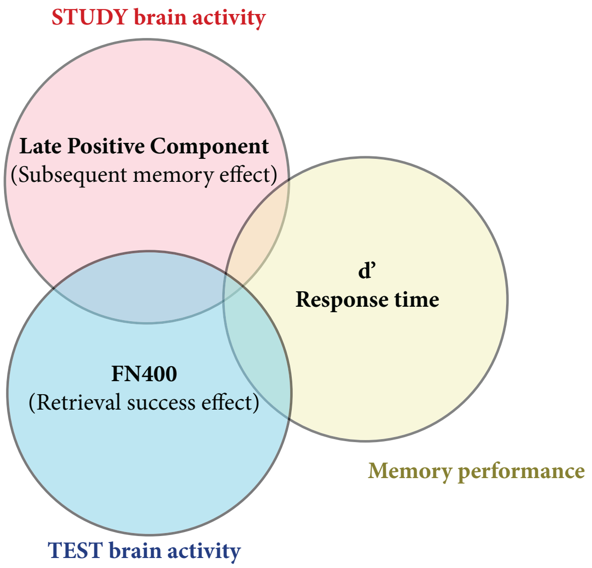

Figure 6.1: The relationships between brain activity measured by ERPs and item recognition memory performance

words drawn from other studied word pairs ("rearranged"). Since items in both probe types are from the studied list, item memory alone cannot be helpful in distinguishing "intact" from "rearranged" probes. Extending the dual-process theory of item recognition, Yonelinas (2002) argued that associative judgments are largely based on recollection-based retrieval, since recollection provides other contextual details that familiarity could not provide. Thus, the two test ERP features that are thought to reflect recollection-based retrieval, the Late Parietal Positivity and the frontal old/new effect, are deemed to also reflect successful associative recognition. However, item memory may be essential for item–item association memory (Murdock, 1974); therefore, I also examined the Late Positive Component and the Slow Wave, item-memory ERP features during study. The processes indexed by Slow Waves, specifically the frontal Slow Wave, has been suggested to resemble item–item association strategies (i.e., make connections between items in the list). Thus, the Frontal Slow Wave is suggested to reflect processes contributing to encoding item–item associations (Kim et al., 2009, 2012). Again, similar cognitive correlates were proposed for association-memory-related ERPs. Specifically, the parallel between the Late Positive Component at study and the FN400 at test, as well as the parallel between the frontal Slow Wave at study and both the Left Parietal Positivity and frontal old/new effect at test.

I measured memory-related ERPs at study, the Late Positive Component and the Slow Waves, and replicated the subsequent memory effect (albeit negative polarity at frontal sites). However, I did not find significant old/new effects or retrieval success effects in the FN400, the Left Parietal Positivity and frontal old/new ERP feature. Instead, I found ERP features that have been suggested to reflect processes involved in retrieval of item–context associations (source memory retrieval), such as the early- and late-retrieval success effect, as well as the early- and late-old/new effect. It is possible similar processes were required for both item–item associations and item–context associations. I correlated the subsequent memory effect ERP measures with the early- and late-retrieval success effect and old/new effect ERP measures. I found the study ERPs were related to test ERPs, similar to the results found in the item recognition study (Chapter 2). Across participants, the Late Positive Component was correlated with the early ERP feature (retrieval success effect). Moreover, these features correlated with memory performance (d'), but not with response time. The frontal Slow Wave that is thought to reflect processes contributing to item–item association did not correlate with memory performance. In addition, the Slow Waves did not correlate with any test ERP features. The pattern of results are summarized in Figure 6.2. These results suggest that the Late Positive Component at study may influence the early ERP features (retrieval success effect) at test, and they were critical for associative recognition memory. More importantly, The frontal Slow Wave, which has long been suggested to facilitate association memory, did not explain individual differences in memory performance. These results echoed the findings in Chapter 2, where earlier ERP features at study and test explain memory outcomes across participants, suggesting a possible common underpinning mechanism for both types of recognition, which will be further discussed in the latter sections.

6.1.2 Chapters 3 and 5: theta and alpha oscillations explain individual variability in recognition memory

In general, more theta activity ($4-8\ Hz$) and less alpha activity ($\sim 10\ Hz$) are thought to benefit memory function (Doppelmayr et al., 1998, 2000, 2005; Klimesch, 1996, 1999; Klimesch et al., 2005, 1990, 1993, 1994; Jensen et al., 2002). Although many functions have attributed to the theta and alpha oscillations in terms of memory, how those oscillations affect recognition memory remain largely unclear.

Chapter 3 examined the possible cognitive roles of theta and alpha oscillations and how

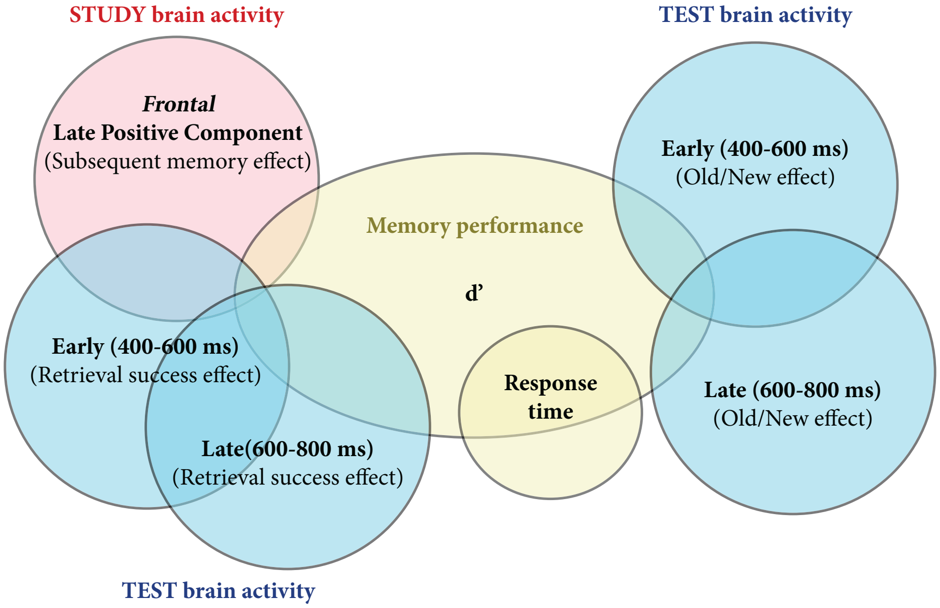

Figure 6.2: The relationships between brain activity measured by ERPs and associative recognition memory performance

these oscillations affect individual memory performance in an item recognition memory task. Therefore, I tested whether the theta and alpha oscillations 1) influence memory performance; 2) reflect the same cognitive processes that contribute to the amplitude differences in the item recognition memory ERPs. The replications of the significant subsequent memory effect and retrieval-success effect confirmed that reduced alpha oscillations and increased theta oscillations indicate successful memory. In addition, I found that only theta oscillations were correlated with memory performance across participants, meaning that more theta oscillations during study and test indicate better memory performance. Moreover, only alpha oscillations were correlated with memory-related ERPs, in particular, the Slow Wave at study and the FN400 at test (Figure 6.3).

Although the precise functions of these two oscillations in recognition-memory still require further investigation, our results suggest that alpha oscillations might index the participants' attention-level. This could include both visual attention and inward attention that could each facilitate encoding and retrieval in different ways. Although the measures of alpha oscillations were correlated with the memory-related ERP amplitude, they do not directly translate to better memory performance, at least when measured with old/new judgments. Furthermore, theta oscillations might index a different kind of recollection-based retrieval. Since both the Left Parietal Positivity and the theta oscillation were thought to index recollection-based retrieval, it is reasonable to expect that these two measures would correlate. However, the non-significant correlation suggests that either recollection was not involved in the task or, if indeed both measures index recollection, they might be indexing different types of recollection-based retrieval.

In summary, both the alpha and theta oscillations are evidently important for successful encoding and retrieval of memory, but they might contribute to item recognition memory performance differently.

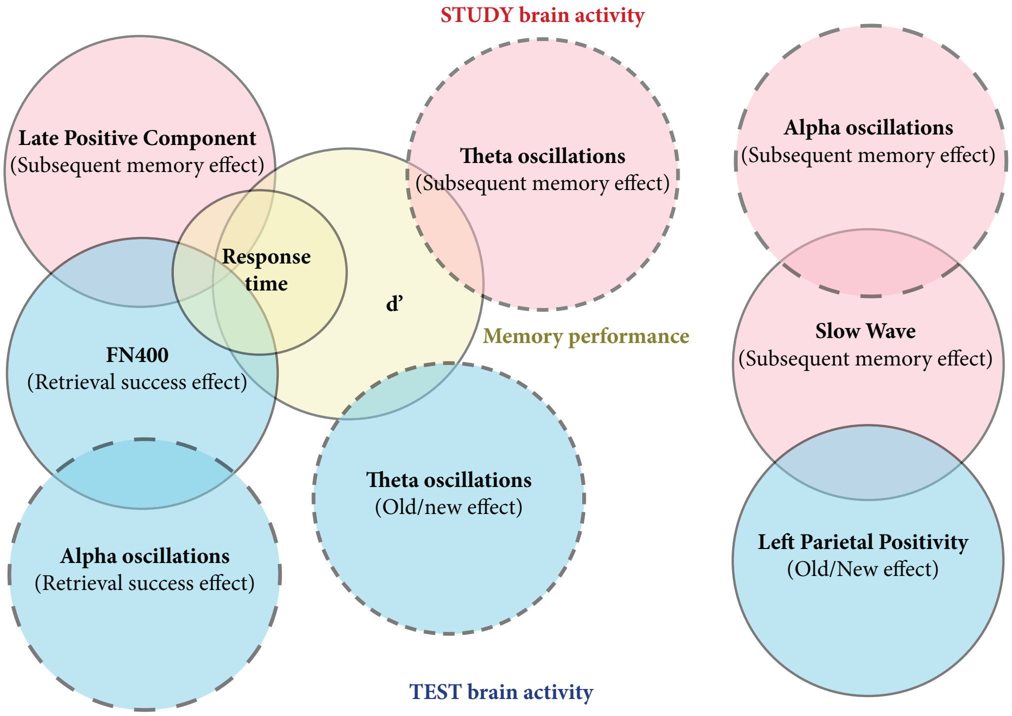

Figure 6.3: The relationships between brain activities measures, both ERPs and oscillations, and item recognition memory performance. This digram builds on the ERP result from Chapter 2 as depicted in Figure 6.1

Extending the same logic and techniques to association memory, Chapter 5 examined the possible roles of theta and alpha oscillations in associative recognition and how these oscillations affect individual memory performance in an associative recognition memory task. Again, I tested whether the theta and alpha osscilations 1) explain individual differences in memory performance; 2) reflect the same cognitive processes that contribute to the difference in the associative recognition memory ERPs. As seen in Chapter 3, I replicated the significant subsequent memory effect and retrieval success effect in both alpha and theta oscillations, where less alpha oscillations and more theta oscillations at study and at test indicate successful memory. When examining the correlation between oscillations and ERP measures, Chapter 5 built upon the ERP results from Chapter 4. While many researchers suggested that recollection-based retrieval contributes to associative recognition judgments (Hockley & Consoli, 1999; Rotello & Heit, 2000; Yonelinas, 2002; Yonelinas & Jacoby, 1994; Yonelinas et al., 1998), I did not find significant memory effect in ERP features that were indicative of recollection-based retrieval. Instead, I found that other ERP features, early and late retrieval success effects, resemble ERP findings in studies requiring item–context associations (source memory). Using these ERP features, only alpha oscillations were found to be correlated with memory-related ERPs, specifically, the Slow Wave at study and a late ERP (retrieval success effect) at test. Moreover, theta oscillations correlated with memory performance (d'), but not with ERP features (Figure 6.4). Thus, the pattern of results parallels that of Chapter 3: theta oscillations—memory performance, and alpha oscillations—memory-related ERPs. Furthermore, these results echo those found with the item-recognition task (Chapter 3), where theta and alpha oscillations, although important for successful memory encoding and retrieval, contribute to memory function differently. I will discuss this further in the latter sections.

6.2 General implications for memory-related brain activity measures and recognition memory

6.2.1 The Late Positive Component and the Slow Wave

Two subsequent memory effect features known as the Late Positive Component and the Slow Wave, have mainly been distinguished by their different latencies (see Friedman & Johnson Jr., 2000; Paller & Wagner, 2002; Wagner et al., 1999, for reviews). Researchers have suggested two different functions these two features might be tapping into (Paller et al., 1987, 1988; Paller & Kutas, 1992; Paller, Kutas, & McIsaac, 1995; Smith, 1993; van Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991; van Petten & Senkfor, 1996). However, when one inspects the study ERPs, it is often not clear where the Late Positive Component ends

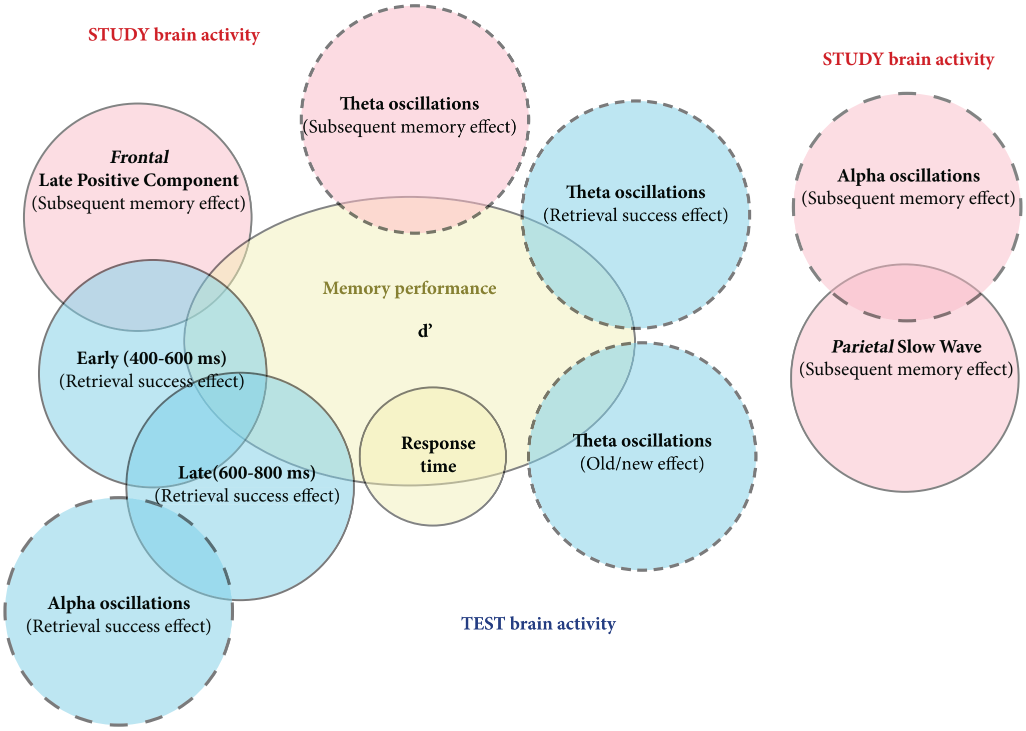

Figure 6.4: The relationships between brain activity measures, both ERPs and oscillations, and associative recognition memory performance. This digram builds on the ERP result from Chapter 4 as depicted in Figure 6.2

and the Slow Wave begins. Therefore, these two ERP features have often been discussed as though it were one single deflection, starting at around the onset of the Late Positive Component and lasting to the end of the Slow Wave (Donaldson & Rugg, 1998; Guo et al., 2004; Marzi & Viggiano, 2010). For example, Guo et al. (2004) examined a sustained subsequent memory effect with a 200–800 ms time window between two different encoding strategies (shallow and deep) and found deeply encoded items elicited a larger subsequent memory effect than the shallow encoded items. Even if the Late Positive Component and the Slow Wave are distinct features, they may still still respond to common cognitive processes.

Both Chapters 2 and 4 correlated the Late Positive Component and the Slow Wave across participants, and found that those two ERPs were highly correlated. It seems that those two ERP features might reflect common processes. However, the two features are also showing independence. For example, the Late Positive Component was correlated to memory performance, d', but the Slow Wave was not. Furthermore, the Late Positive Component correlated with the FN400, but not with the Left Parietal Positivity; whereas the Slow Wave correlated with the Left Parietal Positivity, but not with the FN400. The data suggests that while they may overlap, the Late Positive Component is functionally different from the Slow Wave. There are at least two possible explanations for the high correlation between the two features. First, the choice of the time window might not be precise. As explained above, sometimes it is not clear when the Late Positive Component ends and the Slow Wave begins. The ERP time window selections are largely based on previous studies which may not reflect the true separation between two features in my studies. Thus, the high correlation between the two features might be because one feature is correlating with itself, which is miscategorized by the time window selection. Second, multiple processes might contribute to the two features, and they may share some of these processes. An ERP feature might reflect different processes, so it is possible that the different correlation patterns between the Late Positive Component and the Slow Wave were due to the unshared variance between the two features. This means that the variance shared between the Late Positive Component and FN400 was not shared with the Slow Wave; in other words, the common variance between the Late Positive Component and the Slow Wave was not shared with FN400 nor the Late Positive Component. Therefore, the Late Positive Component and the Slow Wave may respond to some common processes which are not shared with other ERP features. In summary, the Late Positive Component and the Slow Wave may reflect some common processes, but their functions are largely distinct.

6.2.2 The role of the Left Parietal Positivity in memory retrieval

The Left Parietal Positivity has been thought to index recollection-based retrieval under the dual-process theory of recognition framework (Rugg & Curran, 2007). However, many studies have challenged its role in successful memory retrieval. For example, Curran (2000) instructed participants to discriminate targets from similar lures (i.e., “chair” versus “chairs”). They hypothesized that recollection-based retrieval could provide information for participants to accurately reject similar lures. However, the Left Parietal Positivity, which was thought to index recollection-based retrieval, did not show significant amplitude differences between targets and similar lures. Curran (2000) suggested that the Left Parietal Positivity may not index recollection, challenging its role in contributing to successful memory. Adding more evidence to the same argument, the results in the experimental chapters suggest that the Left Parietal Positivity does not reflect recognition success as a consequence of encoding processes. In the item-memory-recognition task (Chapter 2), the Left Parietal Positivity, although significant for both the old/new effect and retrieval success effect, did not correlate with memory performance (d') across participants. Furthermore, in the associative-recognition task (Chapter 4), the Left Parietal Positivity did not show a significant old/new effect or retrieval success effect at all. Numerous sources of evidence state that parietal-lobe contributions to memory retrieval are more closely linked to metamemory processes, such as judgments of recollection, rather than veridical recognition itself (Ally et al., 2008; Cabeza et al., 2008; Wagner et al., 2005; Woroch & Gonsalves, 2010). This explains the pattern of results in Chapter 2 and 4 where there was significant old/new effect in item recognition but not in associative recognition. In item recognition, the test probes consisted of old (studied) items and new (unstudied) items, whereas in associative recognition, the test probes consisted of only studied items, changing the pairing of the items ("rearranged"). Since the Left Parietal Positivity was only involved in old/new discrimination, it would not benefit the "intact" and "rearranged" discrimination. It is possible that the Left Parietal Positivity does not reflect the type of recollection involved in associative recognition judgments. Thus, the role of the Left Parietal Positivity may be less critical in memory retrieval than what prior research has suggested.

6.2.3 The theta–alpha-oscillation neural network for memory functioning

More theta oscillation activity and less alpha oscillation activity have been suggested to reflect successful encoding and retrieval (Doppelmayr et al., 1998, 2000, 2005; Klimesch, 1996, 1999; Klimesch et al., 2005, 1990, 1993, 1994; Jensen et al., 2002). Klimesch (1999) suggested that theta and alpha might be two dynamic modes of a single network that supports memory function, where the theta mode facilitates encoding of new information and the alpha mode facilitates retrieval of memory. Furthermore, Klimesch et al. (2010) extended the theta-alpha network idea, and suggested that alpha and theta oscillations each reflect numerous, but different, cognitive processes relevant to memory. More importantly, theta and alpha oscillations displayed a "trade-off" relationship where alpha oscillations tend to decrease when theta oscillations increase, and vice-versa. This relationship between theta and alpha oscillations across participants was explored in Chapter 3 and 5, but the correlation results indicated that there was no significant negative correlation between theta and alpha oscillations in both item and associative recognition memory tasks. Thus, a trade-off relationship between alpha and theta activity did not appear to be present in both tasks. However, results from Chapter 3 and 5, despite of different memory tasks, showed striking similarities. Theta oscillations correlated with memory performance (d') and alpha oscillations correlated with memory-related ERP features. It is possible that both theta and alpha oscillations are involved in a common neural network for memory, regardless of memory task, while also being functionally independent. Theta oscillations might set a "state" for the participants where the presence of theta oscillations enables successful encoding and retrieval. Alpha oscillations, on the other hand, apart from indexing attentional processes, also shared closer connections with memory-related ERP features. Thus, these two oscillations may represent a common network that facilitates successful memory functioning.

6.2.4 Old/new effect versus retrieval success effect

Brain activity at test is measured by both the old/new effect and the retrieval success effect. van Petten and Senkfor (1996) reported one of the few ERP studies that examined test activity using the retrieval-success effect, and obtained similar findings to those reported using the old/new effect. Presumably, given the similar morphology of the ERP features, this distinction between the two effects has not been seen as important in many situations. However, the data presented here suggests that differences in these two effects are cognitively relevant. For example, in Chapter 2, the FN400 correlated with the Late Positive Component only when the retrieval success effect was used. Similarly, the Left Parietal Positivity correlated with the Slow Wave only when the old/new effect was used. Additionally, in Chapter 4, only the early retrieval success effect was correlated with the Late Positive Component. While the possible interpretations of these correlation differences were discussed in depth in each chapter, these two retrieval effects are clearly sensitive to different measures. The old/new effect measures memory through discrimination of old from new, with the assumption that if one remembers the studied material (old), one should be able to correctly identify the targets from the lures. Thus, the old/new effect compares only the correct responses: hits and correct rejections. The retrieval success effect, on the other hand, measures memory through the accuracy of the response to only the targets. The assumption is the same as the subsequent memory effect at study; if one remembers the studies material, one should be able to correctly identify the target, and the forgotten targets will be missed. Thus, the retrieval success effect compares only the target probes based on accuracy: hits and misses. While both measures tap into retrieval processes, there are some subtle yet important differences. Finnigan et al. (2002) argued that the processes involved in old/new judgments are very different from those involved in successful retrieval of targets.

Together, these two effects may provide a comprehensive view of processes involved in successful recognition. Furthermore, the regression analyses results demonstrated that sometimes, a clearer and more complete picture can be seen by breaking down brain-activity into different trial types, hits, correct rejections, misses, and false alarms when possible.

6.2.5 Implications for recognition memory

While the studies summarized above cannot resolve the ongoing debate about whether recognition judgments are based on a single continuous source of information or two distinct sources (single-process theory and dual-process theory), the results could offer some valuable insights into theories and models of recognitions memory.

Test ERP features have been claimed to support both theories. In the old/new effect, the FN400 and the Left Parietal Positivity have been thought to index familiarity and recollection based retrievals, as proposed by the dual-process theory (see Rugg & Curran, 2007, for a review). Similarly, the amplitude of the FN400 and the Left Parietal Positivity have been shown to vary according to memory-strength, as suggested by the single-process theory (Finnigan et al., 2002; Woroch & Gonsalves, 2010). Furthermore, theta oscillations have been implicated in both familiarity and recollection-based retrieval (see Nyhus & Curran, 2010, for a review).

I replicated these two retrieval ERP features and theta oscillations in a verbal item memory task (Chapter 2 and 3). The dual-process theory would argue that the Left Parietal Positivity and theta oscillations reflect recollection, which drives the old/new recognition judgments. However, the Left Parietal Positivity did not correlate with theta oscillations. If both the ERP feature and the theta oscillations index recollection, this result suggests that they may be involved in different types of recollection-based retrieval. It is also possible that one or even both of these measures do not reflect recollection. In addition, the Slow Wave at study correlated with the Left Parietal Positivity (old/new effect), suggesting that the discrimination of old and new items can be influenced by encoding processes. A class of strength based models assume that the memory strength of new items could be affected by the encoding processes of the old items. Specifically, Retrieval Effectively from Memory (REM; Shiffrin & Steyvers, 1997) predicts that the more old items are studied, the more new items will be mismatched from the study list (strength-based mirror effect). For example, Criss (2006) found that when the hit rate for targets increased for high memory-strength items compared to low memory-strength items, the correct rejection rate for lures also increased. The Left Parietal Positivity may reflect retrieval processes that are sensitive to a reduced memory match for lures. Furthermore, when theta oscillations were used as predictors for memory performance (d') in a regression, the theta oscillations during both hits and correct rejections were the significant predictors. More importantly, the β value in the regression model was positive for hits and was negative for correct rejections. This result suggests that theta oscillations at test may index memory strength of probe items and display the strength-based mirror effect. Compared to correct rejections, hits might be evoking more theta oscillations, leading to a better match of the memory for the studied list.

In a verbal associative recognition memory task (Chapter 4), I did not find a significant old/new effect or retrieval success effect in both the FN400 and the Left Parietal Positivity. The dual-process theory argued that recollection-based retrieval could provide information for successful associative recognition that familiarity-based retrieval could not provide. The null effect in the FN400 was consistent with the theory. However, the null effect in the Left Parietal Positivity suggested that either the feature did not reflect the type of recollection involved in associative recognition or the feature did not have any cognitive relevance to memory functioning (see Section 6.2.2 *Role of the Left Parietal Positivity in memory retrieval*).

Alternatively, familiarity-based retrieval could contribute to successful associative recognition judgments when two items of a pair form a single representation for memory ("unitization"). For example, Diana et al. (2011) found that the FN400 amplitude differed significantly between pairs learned with or without the use of the unitization strategies, suggesting familiarity-based retrieval. However, the null effect in the FN400 did not support that idea either. In addition, the theta oscillations displayed both significant old/new effect and retrieval success effect in the associative recognition task (Chapter 5). It is difficult to determine whether theta oscillations reflect recollection-based retrieval not indexed by the Left Parietal Positivity or memory strength, as both could contribute to successful associative recognition judgments.

In summary, I found support for both single-process theory and dual-process theory. It is possible that some of the participants used the memory strength information, where others used familiarity/recollection-based retrieval, to make their recognition judgments.

6.3 Significance of the research

The works in this dissertation focused on how memory-related brain activity may explain individual differences in memory performance using an individual-difference approach. This approach provides a new way of exploring the cognitive significance of memory-related brain activity where one can ask whether these measures reflect common or distinct processes. This approach is not to replace the conventional within-subjects approach, but rather provides a complementary method that sharpens our understanding of these brain activity measures.

6.3.1 Within-subjects measures and individual differences

Memory-related measures are often analyzed at the subject level, comparing different trial types for one participant. For example, the subsequent memory effect compares later-remembered and later-forgotten at study, the old/new effect compares hits and correct rejections at test, and the retrieval success effect compares hits and misses at test. These within-subjects measures have provided ways to tap into the neural underpinning of successful memory encoding and retrieval. One might think that between-subjects effects should simply echo within-subjects effects. Assuming that there are some basic processes that govern memory functioning, if these processes are reflected in the within-subject brain activity measures, then the observed amplitude differences in ERP features and activity-level differences in oscillations might be able to explain individual differences in memory performance. However, this is not always the case. Some within-subjects measures may not be sensitive to the between-subjects measures and explain variances in a continuous manner. Thus, there are three possible scenarios between within-subject and between-subject measures, 1) the processes contribute to memory functioning are measured by both the within-subject effects and the between-subject effects; 2) the processes contribute to memory functioning are measured by only the within-subject effects but not by the between-subject effects; 3) the processes not directly linked to memory functioning are measured by the within-subject effect, but not by the between-subject effects. By examining both the within-subjects effects and individual differences, we can understand more about memory-related brain activity.

Within-subjects effects also explain between-subject effects Using the across-participants correlation, we can explore the within-subjects memory effects of oscillations on memory performance. For example, alpha and theta oscillations showed a significant subsequent memory effect at the subject level, where decreased alpha oscillations and increased theta oscillations were observed during subsequently remembered trials. However, when we correlated the subsequent memory effect difference of theta and alpha oscillations with memory performance, only theta oscillations significantly correlated with memory performance (d', Chapter 3 and 5). The positive correlation between theta oscillations and memory performance is in line with Doppelmayr et al.'s (1998) result when they separated the participants into good and bad memory performers based on their recognition memory outcome, and then examined theta activity during test between the performer groups. They found significant retrieval success effect where more theta activity during remembered trials compared to the forgotten trials. More importantly, the difference in theta activity (within-subjects effect) was greater in the good than the bad performer group. However, the median-split method used in Doppelmayr et al.'s (1998) study might be splitting participants into those who were engaged (good performers) and those were disengaged (bad performers). Speaking directly to the Doppelmayr et al.'s (1998) results, the significant correlations found between theta oscillations and memory performance in Chapters 3 and 5 suggest that magnitude of within-subject effects explain individual differences in memory performance in a continuous manner.

Within-subjects effects do not explain between-subject effects The frontal Slow Wave has been suggested to reflect successful item–item association encoding (Kim et al., 2009, 2012; Mangels et al., 2001; Wagner et al., 1999; Weyerts et al., 1997); however, despite showing the significant subsequent memory effect, the difference in frontal Slow Wave (within-subjects effect) did not correlate with d' in the associative recognition task (Chapter 4). The size of the Slow Wave differences has been assumed to reflect a number of encoding processes engaged. For example, Kim et al. (2009) asked participants to learn verbal associates by presenting word 1 and word 2 of a study pair one at a time, separated by a short delay. They found significant the subsequent memory effect in the Slow Wave during both word 1 and word 2. More importantly, the effect was more pronounced during word 2. Kim et al. (2009) reasoned that associations cannot be fully formed until after the presentation of the word 2, and the Slow Wave present after the onset of the second word indexed encoding processes that were crucial for association memory. However, there was no support found in Chapter 4, the frontal Slow Wave did not correlate with memory performance. It is possible that the frontal Slow Wave is sensitive to other memory-related processes, not measured by d' and response time. Perhaps ERP features from different memory tasks or measures may be able to explain individual differences. Moreover, it is equally important to consider that the within-subjects measures are only predictive at the subject level, but not predictive of individual differences. For example, if the Slow Wave reflects cognitive processes, where an increase in its amplitude is beneficial to successful encoding, the amplitude differences between later-hits and later-misses does not carry any functional meaning across participants.

Sometimes, the within-subjects memory effects might result from other processes which are not directly related to memory performance. For example, decreased alpha oscillations have been suggested to reflect visual attention. If participants closed their eyes during half of the study trials, they would not be able to learn those items presented when they had their eyes closed. Thus, items presented during eyes-open trials (less alpha activity) would be remembered and items presented during eyes-closed trials (more alpha activity) would be forgotten. The difference in alpha oscillation activity would then coincide with subsequent memory performance. Unless *all* participants closed their eyes during half of the study trials, this difference in activity will not likely correlate across participants. More often, even if a participant were fully engaged, paying close attention to the task, not all of the studied material would be later retrieved. This means that attention is just one factor for determining memory performance. Attention, indexed by alpha oscillations, is necessary to any cognitive functioning. However, it does not directly drive memory performance, thus, the within-subjects effects would not explain between-subjects effects.

6.3.2 The relationship between item- and associative-recognition memory

Item–item association memory is dependent on item memory. Hockley and Cristi (1996a) examined the relationship between encoding item information and association information. They had participants study a list of word pairs while focusing on either the item information or the association information. Afterward, participants were given either an item-recognition task or an associative recognition task. Hockley and Cristi (1996a) found that when participants were tested using associative recognition, participants who were asked to focus on the association information had better accuracy than the participants who were asked to focus on the item information. However, when participants were tested using item recognition, they performed equally, regardless of their encoding emphasis. These results suggested that item information could be essential to association memory. Although the processes involved in item and associative information encoding and retrieval might differ (Clark, 1992; Clark & Burchett, 1994; Gronlund & Ratcliff, 1989; Hockley, 1992, 1994; Hockley & Cristi, 1996b; Yonelinas, 1997), the neural mechanisms underlying the item recognition memory might also contribute to associative memory. For example, the Late Positive Component (subsequent memory effect) at study correlated with memory performance in both item and associative recognition memory tasks. In addition, the theta oscillations at study and test were correlated with memory performance in both item and associative recognition memory tasks as well. It is possible that successful associative recognition memory judgments rely on the same common neural mechanisms as item recognition memory; thus, the same set of correlations were found for both tasks. Or it is also possible that successful associative recognition is mediated by the item recognition neural mechanisms; thus, successful associative recognition is dependent on successful learning of item memories.

6.4 Limitations and future directions

In this dissertation, I focused on one type of memory procedures, recognition memory, and a small subset of memory-related EEG measures. While the results from the experimental chapters could offer valuable insights, they also present limitations and challenges for future experiments to address.

First of all, the choice of memory paradigm may influence the brain activity measures.

For example, Donaldson and Rugg (1999) examined association memory using both cued recall (a pair A-B, given A as probe, recall B) and associative recognition. They evaluated test ERP features for both conditions and found different morphology and topographic distributions for each. They suggested that the differences observed were largely due to different cognitive processes engaged in the retrieval process. The cross-participants correlations I employed were contingent on the within-subjects memory measures. Thus, slight changes to the experimental paradigm might affect the morphology of the ERP and eventually lead to different patterns of correlation results. To address this, future studies could consider choosing robust ERP features that yield similar effects across many memory paradigms. Alternatively, future studies can apply this individual difference approach to many different memory paradigms to learn the precise function of memory-related measures.

Second, we could not pinpoint the cognitive processes that underlie these memory-related processes. Although many significant correlations have been found to exist among the memory-related brain activity measures (i.e., the Late Positive Component and FN400, alpha oscillations and the Slow Wave, etc.), the common neural and cognitive processes that contribute to these functional connections were largely unknown. The previous sections and chapters presented specific ideas as interpretations of those relationships, future research is still needed for exploring the functional significance of those measures. At the very least, the cognitive functions suggested for one measure could extend to other measures that are significantly correlated.

Finally, our understanding of recognition memory is limited to the choice of brain-activity measures. For example, alpha and theta oscillations were the main oscillations of interest. It is possible that many encoding and retrieval processes are not reflected in these two oscillation bands that I examined. Gamma oscillations ($> 30\ Hz$), for example, have been implicated in successful association memory by binding relevant information together (Nyhus & Curran, 2010). Future studies could include other oscillations, such as gamma oscillations, as the target measures when testing the within-subjects and between-subjects memory effects.

To summarize, the works in this dissertation established an alternative approach to exploring the functions of brain activity in memory tasks. The results extended our knowledge of classical memory-related ERP and oscillation measures. The neural mechanisms underlying recognition memory are complex; however, the relationships between study and test ERP features in conjunction with alpha and theta oscillations might point to a unified neural mechanism for both item and associative recognition memory.

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