Associative Recognition: Exploring the Contribution of Recollection and Familiarity.

Jamie George Murray

University of Stirling

Submitted as a requirement for degree of PhD

2014

Declaration

I declare that this thesis was composed by myself and contains no other work, unless explicitly stated otherwise in the text, which has been previously submitted for award of any other degree. I further declare that no part of this thesis has already been submitted, or concurrently being submitted for any such degree, diploma or other qualification at the University of Stirling or any other University of similar institution.

Jamie George Murray

Acknowledgements

I would like to thank Professor David Donaldson for his excellent supervision. His love for science has been a continuous source of inspiration throughout my PhD. I would also like to thank Catriona Bruce, our lab technician, for her expertise in ERP preparation and general technical know-how. I also wish to thank Professor Roger Watt, my secondary supervisor, for his theoretical contributions during the early stages of my thesis. I am also grateful to the University of Stirling Horizon studentship programme which funded this PhD.

I would also like to thank all my friends at the Psychological Imaging Laboratory (PIL), past and present, who have taught me so much over the last six years. A PhD is never undertaken in isolation, and I will always have fond memories of the numerous bowling nights, parties, dinners, drinks and ceilidhs.

I dedicate this thesis to my wife Kimberley and our son Harrison.

Abstract

Episodic memory refers to the storage and retrieval of information about events in our past. According to dual process models, episodic memory is supported by familiarity which refers to the rapid and automatic sense of oldness about a previously encoded stimulus, and recollection which refers to the retrieval of contextual information, such as spatial, temporal or other contextual details that bring a specific item to mind. To be clear, familiarity is traditionally assumed to support recognition of item information, whereas recollection supports the recognition of associative information. Event Related Potential (ERP) studies provide support for dual process models, by demonstrating qualitatively distinct patterns of neural activity associated with familiarity (Mid-Frontal old/new effect) and recollection (Left-Parietal old/new effect). In the current thesis, ERPs were used to address two important questions regarding associative recognition – namely, the function of the neural signal supporting recollection and whether familiarity can contribute to the retrieval of novel associative information.

The first series of experiments was aimed at addressing how recollection operates by employing a recently developed continuous source task designed to directly measure the accuracy of retrieval success. To date, the function of recollection has been fiercely debated, with some arguing that recollection reflects the operation of a continuous retrieval process, whereby test cues always elicit some information from memory. Alternatively, recollection may reflect the operation of a thresholded process that allows for retrieval failure, whereby test cues sometimes elicit no information from memory at all. In the current thesis, the Left Parietal effect was found to be sensitive to the precision of memory responses when recollection succeeded, but was entirely absent when recollection failed. The result clarifies the nature of the neural mechanism underlying successful retrieval whilst also providing novel evidence in support of threshold models of recollection.

The second series of experiments addressed whether familiarity could contribute to the retrieval of novel associative information. Recent associative recognition studies have suggested that unitization (whereby multi-component stimuli are encoded as a single item rather than as a set of associated parts) can improve episodic memory by increasing the availability of familiarity during retrieval. To date, however, ERP studies have failed to provide any evidence of unitization for novel associations, whereas behavioural support for unitization is heavily reliant on model specific measures such as ROC analysis. Over three separate associative recognition studies employing unrelated word pairs, the magnitude of the Mid-Frontal old/new effect was found to be modulated by encoding instructions designed to manipulate the level of unitization. Importantly, the results also suggest that different encoding strategies designed to manipulate the level of unitization may be more successful than others. Finally, the results also revealed that differences in behavioural performance and modulation of the Mid-Frontal old/new effect between unitized and non-unitized instructions is greater for unrelated compared to related word pairs. In essence, the results suggest that unitization is better suited to learning completely novel associations as opposed to word pairs sharing a pre-existing conceptual relationship.

Overall, the data presented in this thesis supports dual process accounts of episodic memory, suggesting that at a neural level of analysis, recollection is both thresholded and variable, whilst also supporting the assumption that familiarity can contribute to successful retrieval of novel associative information. The results have important implications for our current understanding of cognitive decline and the development of behavioural interventions aimed at alleviating associative deficits.

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Chapter 1

General Introduction

The ability to learn, store and retrieve experiences from past events is vital to an organism's survival. Most children, for example, will remember to look both ways before crossing a road or that the teacher said never to run with scissors. Memory, however, is far more than a survival mechanism – it defines who we are by guiding our future actions, shaping our beliefs and allowing us to form close relationships with others. Modern theories of memory have been guided by the computer analogy proposed by early cognitive theorists, in which memory is described by three main stages: encoding (whereby information is first learnt), storage (the organization and maintenance of processed information) and retrieval (the recovery of stored information). The ability to successfully remember therefore requires sufficient encoding of information, which is stored appropriately, and is easily accessible for retrieval. When the processing of any of these stages is disrupted, memory failure is likely to occur. Developing an accurate understanding of how memory operates is an important goal of current scientific research; particularly in light of an ageing population who are vulnerable to memory deficits.

Memory is also not a unitary system, but comprises many functionally distinct systems and sub-systems, each with their own particular processes. The current thesis is concerned with episodic memory – i.e., the ability to retrieve events from one's past. Episodic memory is vital to our ability to function in society allowing us to remember where we left the house keys in the kitchen, or to recollect whether gran pointed to the sherry rather than vodka when ordering her drink. Episodic memory defines our sense of self, allowing us to remember our likes and dislikes and to recognize close and distant relationships. When our ability to form new episodic memories deteriorates, every-day functioning becomes increasingly challenging and in those very rare cases where episodic memory fails completely, we become trapped in time; unable to form explicit, declarative memories from the events in our lives.

The current chapter will provide a brief overview of memory, and recognition in particular in order to set the thesis in context. First, the theories and evidence in support of multiple memory systems are discussed, beginning with the broad division between short-term and long-term memory, before focusing on episodic memory. Second, a brief review of the different theories of episodic retrieval is presented before describing the methods used to investigate recognition. Finally, this chapter will discuss evidence from behavioral, neuropsychological and neuroimaging domains in support of dual process theory, which predicts the existence of two functionally independent and neuroanatomically dissociable retrieval process that support episodic memory.

1.1. The organization of memory

1.1.1. What are memory systems?

The current thesis will be set within the multiple memory systems approach[1], originally proposed by Tulving and Schacter (1990, 1994). By this perspective, dissociations

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[1] By contrast, the processing approach defines memory in terms of distinct processes that are engaged by specific tasks. Originally, the memory systems approach and processing approach were considered to be alternative perspectives. More recently, however, the two perspectives are considered compatible with one another (Roediger, Buckner, & McDermott, 1999; Schacter, 1992; Schacter, 1990).

between direct (test instructions that make reference to a previous study episode) and indirect (no reference at test to a prior study episode) tests of memory occur because they are supported by functionally independent underlying memory systems. Schacter and Tulving (1994) originally proposed that a memory system should be defined by what it is not (Schacter & Tulving, 1990). Firstly, a memory system is not a memory process: whereby a process is defined as a specific operation carried out to support memory performance – i.e., encoding, retrieval and rehearsal. Secondly, a memory system is not a task. A recognition task, for example, does not imply a recognition memory system that is distinct from other memory systems. Many different memory processes and systems will likely interact to support successful retrieval from memory, and therefore memory tasks will not reflect a pure measure of any particular memory process or system (Jacoby, 1991). Lastly, according to Schacter and Tulving (1990), implicit and explicit memory does not constitute distinct systems but rather the expression of memory with awareness (explicit) or without awareness (implicit) of the original study episode.

Later, Schacter and Tulving (1994) set out a number of criteria to help distinguish between different memory systems. The first criterion is ‘class inclusion’, which states that each memory system must be able to perform a variety of tasks within a certain category or class, irrespective of the specific details of the task. The second criterion is ‘properties and relations’, which states that a memory system must be described in terms of its relation to other systems and properties. Such properties include the rules that govern the memory systems operation, the type of information that is processed and the underlying neural substrates that support the system. Third, the criterion of 'convergent dissociations', refers to the requirement to demonstrate dissociations between memory systems using a variety of different tasks, stimuli and populations. Only when these multiple dissociations converge to support the same conclusion can a memory system be distinguished from other systems.

1.1.2. Memory structure

Memory is often described as a hierarchy of memory systems that are divided into further sub-systems with distinct processes (Squire, 1992; see Figure 1.1). Although dividing memory into separate independent systems may prove to be a gross oversimplification, it does allow memory to be defined, measured and tested. Perhaps the oldest and most widely accepted division of memory is between Short Term Memory (STM) and Long Term Memory (LTM) – as described by multi-store models (e.g., Atkinson & Shiffrin, 1968). STM refers to the temporary storage (up to a few seconds except when rehearsed) of recently encoded information which is limited in capacity (often cited as 7 ± 2 distinct elements: see Miller, 1956). By contrast, information in LTM can be stored for long periods of time. The existence of a double dissociation between STM and LTM memory has been taken as evidence that the two systems are separate[2]. For example, brain damaged patients have been found to exhibit preserved LTM memory but impaired STM (Warrington & Shallice, 1969), and in other cases the reverse pattern has been observed with preserved STM but impaired LTM (Wickelgren, 1968).

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[2] A double dissociation refers to instances whereby a particular task will have an effect on system A but not B, whereas an alternative task will have an effect on system B but not A. If each system is assumed to be supported by distinct neural substrates, and that each task engages a single cognitive process, then the presence of a double dissociation can be taken as evidence for separable systems (Schacter & Tulving, 1994).

While multi-model theories of memory provide a detailed description of STM, their description of LTM is often oversimplified. Research into LTM, for instance, has found that it can be further divided between declarative and non-declarative systems (see Figure 1.1). The declarative system refers to memory that is accessible to consciousness (i.e., explicit memory), such as personal information and world knowledge. By contrast, the non-declarative system operates below the level of consciousness (e.g., implicit memory), and reflects memory for motor and cognitive skills (i.e., procedural knowledge), perceptual priming, and simple behaviors that derive from conditioning or habituation. The engagement of the non-declarative system is often revealed when previous experience facilitates behavior on a task that is not dependent on intentional retrieval of prior experience.

The declarative and non-declarative systems are typically assessed with explicit and implicit memory tasks respectively. Explicit memory tasks are often intentional (i.e., participants know that they will take part in a memory test) and direct (test instructions that make reference to a previous study episode). One example of an explicit memory task is recognition memory, whereby participants are given a list of items to study and are later required to discriminate between previously studied items from newly presented items. By contrast, implicit tasks are often incidental (i.e., participants do not know they are taking part in a memory test) and indirect (i.e., there is no reference at test to a prior study episode). Word stem completion, for example, is an implicit memory test whereby participants who have previously studied a list of words are later given incomplete word fragments to complete. At test there is no mention of the previous list of words and there is often a significant delay between study and test phases. Non-declarative memory is demonstrated when participants complete word fragments that are identical to the items that have been previously studied. Word fragmentation tasks provide a measure of repetition priming – i.e., when prior exposure to a stimulus facilitates processing of current information, even when the original study episode cannot be explicitly recognized (Tulving, Shacter & Stark, 1982).

Several dissociations have been found that support the division of declarative and non-declarative systems. In healthy populations, dissociations between performance on direct and indirect tests provides some evidence that declarative and non-declarative memory systems are separate. Increased retention intervals, for instance, affect performance on direct, but not indirect tests. For example, Tulving, Shacter and Stark (1982) demonstrated that recognition performance was affected by a 7 day delay, whereas no observable difference was found on word stem completion performance over the same period. In addition, both retroactive and proactive interference impair performance on direct cued recall tasks, but have no effect on indirect word stem completion tasks (Graf & Schacter, 1987). Studies of amnesic patients also provide further evidence in support of the dissociation between declarative and non-declarative systems with some patients demonstrating preserved performance on indirect tasks such as word stem completion but impaired performance on recognition and recall tests (Warrington & Weiskrantz, 1968; Corkin, 1968).[3]

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[3] It should be noted that the presence of a single dissociation does not provide evidence for a separate memory system (Shacter & Tulving, 1991). However, researchers have been confident in distinguishing between declarative and non-declarative systems because of the converging functional dissociations demonstrated across a variety of materials, populations and tasks.

Declarative memory can further be divided into semantic and episodic memory systems. Episodic memory refers to specific experiences and events that are linked to a particular spatial and temporal context, whereas semantic memory refers to general knowledge about the world. To give an example, attempting to remember the capital of Germany would be supported by semantic memory, whilst remembering when you first had bratwurst would involve episodic memory. Both memory systems are considered declarative because retrieval is explicit and participants are aware of the information that is accessed. From a neuroanatomical level of analysis, episodic and semantic memory systems are believed to be supported by distinct brain regions. For example, a meta review of Positron Emission Tomography (PET) and functional Magnetic Resonance Imaging (fMRI) data revealed that, overall, semantic memory is associated with activity in the left pre-frontal and temporal regions, whereas episodic memory is related to activity in the prefrontal, medial temporal and posterior midline regions (Cabeza & Nyberg, 2000).

Further dissociations between semantic and episodic memory have also been found with amnesic patients. A double dissociation, for instance, is reported in two separate case studies of patients K.C. (Tulving, 1991) and L.P. (De Renzie et al., 1987). Patient K.C. suffered damage to the hippocampus and surrounding medial temporal structures (Rosenbaum et al., 2005), resulting in a loss of episodic memory but preserved semantic memory. More precisely, K.C. retained knowledge for facts, such as where kitchen utensils were stored, but could not remember events from his past. By contrast, patient L.P. who suffered an attack of encephalitis could not recognize familiar faces or recall the identity of famous individuals, but her episodic memory for events in her life was preserved demonstrating preserved episodic but impaired semantic memory. Collectively, the presence of the double dissociation and the evidence from neuroimaging studies converge to support the separation of semantic and episodic memory systems.

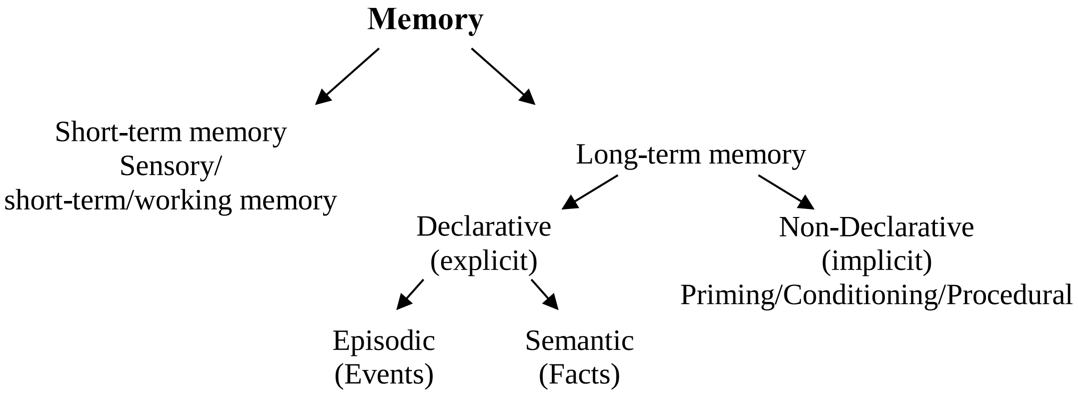

Figure 1.1: Schematic illustration of memory systems. Adapted from Squire (1992).

The questions addressed in the current thesis are primarily concerned with the operation of episodic memory, and more specifically how episodic memories are retrieved. That is not to say, however, that the experimental tasks described in the data chapters will provide a process pure measure of episodic memory. As with the majority of other studies of episodic memory, the potential ‘leaking in’ of non-declarative systems is expected, and is considered in Chapter 9. Regardless, as the retrieval of episodic memories is the main topic of this thesis, the rest of the chapter will focus in more detail on this specific memory system.

1.2. Episodic retrieval

As previously highlighted in the discussion above, episodic memory retrieval is typically investigated using a study-test paradigm. The study-test paradigm can either be a test of recall or recognition. Recall tests require participants to learn a list of items and attempt to remember at test as many items as possible (i.e., free recall) or are required to learn associations between pairs of items and must recall the partner of items presented at test (i.e., cued recall). Recognition tests, by contrast, require participants to learn lists of items and at test are required to make judgments about whether test items are ‘old’ (i.e., previously presented at study) or are ‘new’ (i.e., not presented at study). Whilst recognition has received considerably more attention within the episodic memory literature than recall, there is still considerable debate surrounding the retrieval processes involved in successful recognition. To date, different competing views have been put forward that attempt to explain recognition memory – generally classified as the single and dual process theories. Below these different accounts of recognition memory are reviewed, beginning with single process theory.

1.2.1. Single process theory

Despite the name, single process theory is a term for a number of memory models[4] which propose that recognition is supported by a single strength-based retrieval process. Single process theories are inherently attractive because they provide a parsimonious account of memory retrieval. In short, single process theories assume that stronger memories provide more information and thus better recognition than weaker memories. In their simplest form, all single process models are variations of Signal Detection Theory (SDT: see Green and Swets, 1966). The standard SDT model involves two

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[4] Including, but not limited to, TODAM (Murdock, 1997); MINERVA 2 (Hintzman, 1988) and SAM (Gillund & Shiffrin, 1984).

equal-variance Gaussian distributions (illustrated in Figure 1.2) and a decision criterion. When applied to recognition tests, SDT assumes that studied items have greater memory strength than unstudied items, although variability in memory strength for studied and unstudied items is traditionally assumed to be equal. When the memory strength of a test item exceeds the decision criterion an ‘old’ judgment is made; otherwise the item is declared as ‘new.’

In some instances unstudied items will carry a greater memory strength signal than studied items, and conversely studied items will have less memory strength than some unstudied items (see Figure 1.2). As a result, there are four possible recognition judgments. To be clear, a correct ‘old’ response to a studied item is classified as a Hit, whereas the same response to an unstudied item is a mistake and is called a False Alarm. Comparatively, a correct ‘new’ response to an unstudied item is called a Correct Rejection, whereas the same response to a studied item is a mistake and is called a Miss. Importantly; these four potential responses are not all independent. For example, the proportion of Hits and Misses will add up to 1 (because participants can respond ‘old’ and ‘new’ when the signal is present). Similarly, when the signal is absent, the proportion of Correct Rejections and False Alarms will also add to 1. In short, all the information about performance will be reflected by the proportion of Hits and False Alarms.

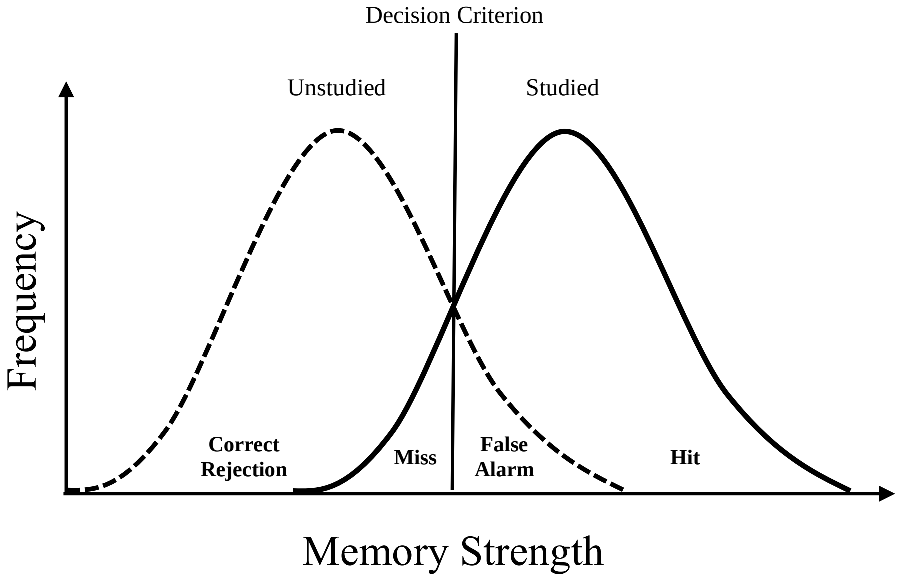

Figure 1.2: Illustration of the Signal Detection model. The memory strengths of studied and unstudied items follow a normal distribution. Plotted on the x axis is the continuous memory strength variable and the y axis plots the frequency of test items. The decision criterion is placed by the participant on the strength axis. When the memory strength of items is above this criterion items are judged ‘old’ and when the strength falls below the criterion items are judged ‘new.’ A correct judgment to studied items is classified as Hits and correct judgments to unstudied items being classified as Correct Rejections. The overlap between the two distributions reflects incorrect responses, with studied items receiving a ‘new’ judgment being classified as a Miss, whilst unstudied items being judged ‘old’ being classified as False Alarms.

Whilst SAT accurately accounts for all the response operations, the interpretation of performance based on the proportion of Hits and False Alarms is difficult because both values depend crucially upon two different measures of memory performance. The first is known as discriminability and reflects the separation between signal and noise (i.e., the difficulty of the task). High discrimination refers to when there is a large distance between studied and unstudied items, resulting in a higher proportion of Hits and smaller proportion of False Alarms (see Figure 1.3: right side). When there is less distance and greater overlap in the memory strength of studied and unstudied items, there will be a smaller proportion of Hits and greater proportion of False Alarms (see Figure 1.3: left side), indicating poorer discrimination.

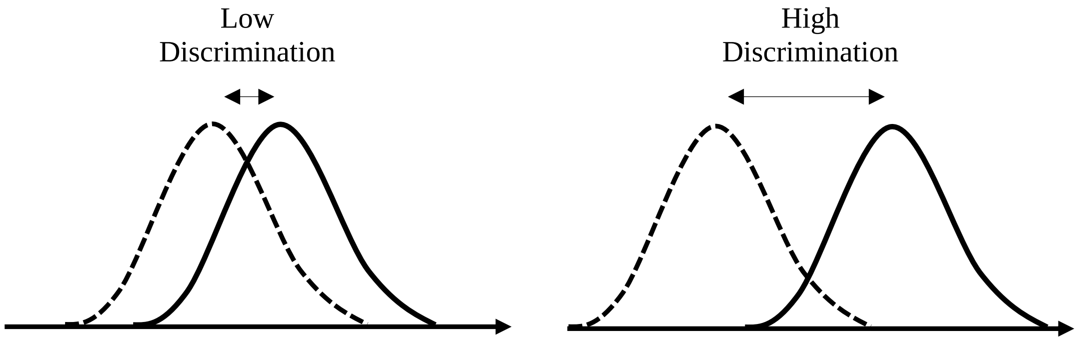

Figure 1.3: Memory strength distribution of studied (black line) and unstudied (dashed line) items for low (left) and high (right) discrimination. Memory strength is located on the x axis and frequency on the y axis.

The second measure is known as response bias, which reflects the placement of the decision criterion. To be clear, the criterion can be freely varied by the participant, and its position determines the bias of responses. A low criterion means that the participant will tend to respond ‘old’ on a greater proportion of trials (i.e., a liberal response bias: see Figure 1.4 left side) resulting in a greater number of False Alarms. By contrast, when the criterion is high, participants will tend to respond ‘new’ on a greater number of trials (i.e., a conservative bias: see Figure 1.4 right side) resulting in more Missed responses.

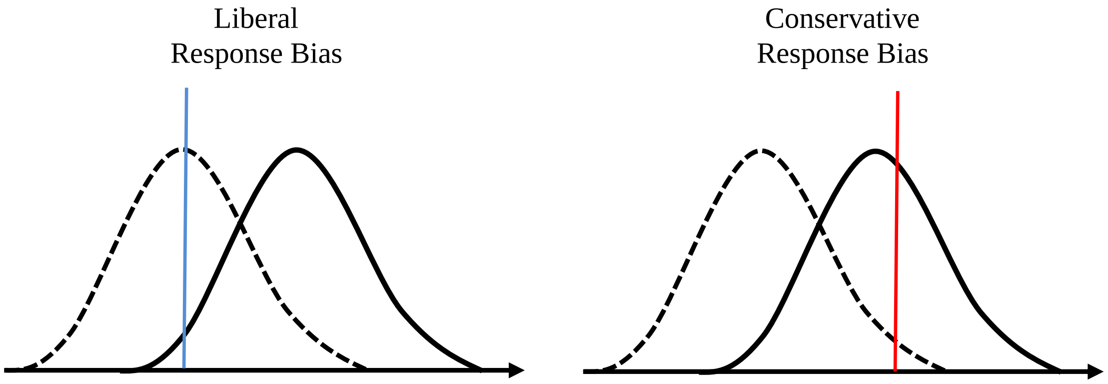

Figure 1.4: Equal strength distributions with liberal (blue) and conservative (red) response bias.

Modelling episodic retrieval on a single strength-based process, however, is difficult to reconcile with studies finding a dissociation in performance between recall and recognition tasks. If retrieval is supported by a single process, for example, then the same experimental manipulation will result in the same effect regardless of the task that is employed. Studies looking at the mirror effect, however, have found that performance on recall and recognition differs under the same experimental conditions. To be clear, the mirror effect refers to the common finding that low frequency words generally elicit a higher hit rate and smaller false alarm rate compared to high frequency words. When word frequency is tested with recall, however, high frequency words are remembered more often than low frequency words, whereas in recognition tests low frequency words are recognized with greater accuracy than high frequency words (Gregg, 1976; Kinsbourne and George, 1974; Glanzer and Adams, 1985, 1990). In short, the mirror effect is relatively difficult to reconcile with a single strength based process which has lead researchers to propose an alternative account of episodic retrieval.

1.2.2. Dual process theory

A number of different dual process models have been proposed, all of which assume recognition judgments are supported by two independent retrieval processes. Familiarity, for example, reflects a rapid signal of memory strength providing a quantitative measure of the likelihood that an item has been previously studied, and is often accompanied by a phenomenological experience of encountering a stimulus before. By contrast, recollection supports the qualitative retrieval of associative information, such as contextual or spatial information associated with an item. Recollection is often accompanied by the phenomenological experience of remembering specific details about a prior event. The distinction between familiarity and recollection is best illustrated by Mandler (1980), who describes an instance whereby you find someone familiar, but are unable to recollect who they are, or where you know them from.

From the classic Mandler example it is clear that recollection and familiarity give rise to separate phenomenological experiences of remembering. This does not mean, however, that recollection and familiarity need to necessarily be defined as isolated processes. Instead, recollection and familiarity are likely to arise from the interaction of several different cognitive processes including attention, orientation, perception, search processes and post-retrieval monitoring (among many others that remain unidentified). The implications of this distinction are important. Taken at a neural level of analysis, for instance, it may be practical for research purposes to identify a brain region that supports recollection, but it is misleading to identify that brain region as reflecting the recollection process. For the purposes of this thesis, recollection and familiarity are not defined as unitary processes, but instead are viewed as reflecting different retrieval processes that incorporate other cognitive mechanisms. The aim of the remainder of this section will briefly discuss three alternative models (a more extensive review is provided by Yonelinas, 2002) to illustrate where there is both consensus and disagreement among dual process theorists, before reviewing the different methods that are used to investigate familiarity and recollection.

According to the conditional search model proposed by Atkinson and Juola (1973, 1974), familiarity is characterized as a fast acting process, engaged during recognition and supporting the retrieval of perceptual information. Recollection, by contrast, is a slow acting process that is only engaged when familiarity fails, and supports the retrieval of semantic information. To be clear, familiarity is argued to reflect the activation of nodes within a lexical network in which each individual node represents a different word or object. According to this account, the familiarity process is characterized by signal detection (see Section 1.2.1), however, unlike early SDT models, participants set an additional lower criterion. When item recognition is ambiguous (i.e., the familiarity strength of an item falls between the upper and lower criteria), an additional recollection process is engaged that searches semantic memory. One significant feature of the conditional search model is that it explicitly proposes that learning of novel information is supported purely by recollection because familiarity reflects the activation of existing lexical nodes.

An alternative perceptual fluency heuristic model was initially proposed by Jacoby and Dallas (1981). Similar to the Atkinson and Juola model, familiarity is believed to operate faster than recollection, although both processes are viewed as operating independently and can therefore occur in parallel. According to this account, familiarity reflects the assessment of processing fluency, whereas recollection reflects the retrieval of contextual information about an item. Emphasis is placed on recollection being a controlled and effortful process, whereas familiarity reflects a relatively automatic process. Unlike the previous Atkinson and Juola model, however, familiarity is not considered as an inherent property of an event, but instead arises due the ease of processing of an item (i.e., fluency), either due to prior exposure to that item or because of saliency of the perceptual features of an item. By this account, familiarity and priming (either conceptual or perceptual) are related (Jacoby & Kelly, 1984).

Finally, the Dual Process Signal Detection (DPSD) model proposed by Yonelinas, (1994) has arguably had the most influence on subsequent studies of episodic memory. The DPSD model is essentially a mixture of signal detection theory and high threshold theory (i.e., only items that exceed a memory threshold are endorsed as being remembered). Familiarity, according to this model, is a continuous process and is characterized by signal detection (described in more detail above), reflecting the assessment of memory strength associated with an item. The original DPSD model also proposed that recollection, by contrast, was probabilistic and characterized as a threshold reflecting the assessment of qualitative information in an ‘all-or-none’ fashion (Yonelinas, 1998). To be clear, participants can recollect the association between different components of an event, but in some instances will fail to retrieve any information from memory. As with the Jacoby and Dallas model (1991), recollection and familiarity are believed to be independent but operate in parallel, with familiarity operating more quickly than recollection.

From the brief review of the dual process models described above it has hopefully become clear that there is a certain level of consensus and disagreement surrounding familiarity and recollection. Most dual process models are in general agreement that familiarity is a quick and automatic process, whereas recollection is slower and more effortful. All three models described also characterize familiarity as a continuous index of memory strength, whereas recollection is involved in the retrieval of specific information about a prior study episode (Yonelinas, 2002). There is disagreement, however, on whether familiarity and recollection operate in a serial fashion (Atkinson & Juola, 1973, 1974), or in parallel (Jacoby and Dallas, 1981; Yonelinas, 1994). Another important source of contention revolves around the possibility that familiarity can support the learning of novel information, with Atkinson and Juola (1974) firmly ruling out the possibility, whereas Yonelinas' (1994) DPSD model suggests that familiarity contributes to associative retrieval under limited circumstances (a topic that concerns the second of the two primary aims of the current thesis and will be discussed in more detail in Chapters 2 and 4). As the current thesis is interpreted within the dual process frame work, it is worth reviewing how the contributions of recollection and familiarity have been measured, before discussing the evidence supporting a functional and neuroanatomical dissociation between the processes.

1.3. Measures of recollection and familiarity

A standard old/new recognition task of item memory (i.e., encoding and retrieval of a single stimulus) is useless for measuring the contributions of recollection and familiarity, because both processes will contribute to a successful recognition decision. To tease apart the contributions of recollection and familiarity researchers have relied on paradigms that either attempt to use tasks that isolate a particular process (i.e., task dissociation procedures), or to derive estimates of the contribution of each process (i.e., process estimation procedures). Both these methods will be described in more detail, beginning with task dissociation procedures.

1.3.1. Task dissociation methods

The speeded response method is one particular type of task dissociation, based on the assumption that familiarity operates more quickly than recollection. With the speeded response method, the amount of time a participant has to respond to a stimulus is manipulated. In theory, speeded responses should rely primarily on familiarity whereas slower responses should comprise of a mixture of both recollection and familiarity. One particular response speed manipulation that has received considerable attention is the response-deadline procedure. For this procedure, participants are forced to make a speeded response judgment within a particular time period (i.e., within 800ms) and performance is compared to non-speeded judgments. The results from response-deadline studies should be interpreted with caution because different test instructions are applied to the different response deadlines, introducing a potential confound that may influence retrieval processes (Yonelinas, 2002). This limitation can be mitigated by employing other response speed manipulations that do not rely on alternative instructions such as the Speed-Accuracy Trade Off (SAT) paradigm (Wicklegren, 1977), or response time methods.

Another example of task dissociation is the comparison of item and associative tasks. Here, item recognition is believed to be supported by the contribution of both familiarity and recollection but associative retrieval is much more dependent on recollection (Yonelinas, 1997; Donaldson & Rugg, 1998; Hockly & Consoli, 1999). To be clear, a typical associative recognition task will require participants to learn pairs of items (i.e., A-B/C-D/E-F), and at test discriminate between previously studied intact pairs (i.e., A-B) and recombined pairs (i.e., C-F/ D-E). As every item at test was presented at study they will all be familiar, forcing participants to recollect the association between items to make a successful judgment.

A slightly more advanced version of the standard item and associative recognition task is to directly compare item and source retrieval performance. In a standard source recognition task for example, participants will be presented with items that can either be located on the left or right side of the screen, spoken in a male or female voice, or presented in different colors. At test, the participant will be given a standard ‘old/new’ recognition task, but for items identified as ‘old’ will be required to recollect the position of the word, whether it was spoken in a male or female voice, or what color it was presented in. The source recognition paradigm allows for the comparison of retrieval of the item without the source (i.e., item retrieval) and retrieval of the item with the source (i.e., source retrieval). In theory, the test is able to isolate recollection because participants must be able to accurately recollect the source to make a successful judgment, whereas item judgments can be made based on familiarity (see Chapter 4 for a more detailed review of source recognition and ERPs that are relevant to the current thesis).

The use of task dissociation procedures such as source retrieval has been prevalent within the recognition literature to separate the contributions of recollection and familiarity, particularly in combination with neuroimaging methods. Arguably, however, the estimates of familiarity and recollection derived from task dissociation procedures can be imprecise (Yonelinas, 2002). Estimates of familiarity based on source incorrect trials, for instance, may be contaminated by the contribution of recollection for episodic details that do not support the discrimination required by the task. To be clear, during an examination a student may recollect the exact page in a book that contained the answer to a test question, but nonetheless fails to remember the exact answer. This type of recollection is known as ‘noncriterial recollection’ (Yonelinas & Jacoby, 1996; Parks, 2007) and has been demonstrated to bias estimates of familiarity during studies of source memory (see Parks, 2007; Wais et al., 2010).

The problem of noncriterial recollection can be mitigated to some extent by carefully designing source tasks that make it more likely that participants rely on criterial information about a particular item. In addition, the assumption that correct source retrieval is dependent only on recollection is questionable when considering that under some circumstances, familiarity may contribute to successful associative retrieval. Although associative recognition is believed to be heavily dependent on recollection, the DPSD model proposes that, under certain circumstances, familiarity can support the retrieval of novel associations. Source experiments, for example, have demonstrated that when items and their source are encoded as a single representation, familiarity can contribute to successful retrieval (Diana et al., 2008, 2010). The argument that familiarity can contribute to successful associative retrieval is a theoretically important claim and will be explored in more detail in Chapter 2.

1.3.2. Process-Estimation methods

A modified version of the item/source recognition task is the process dissociation task (developed by Jacoby, 1991). Here, participants take part in two similar recognition tasks that differ slightly in terms of task instruction (i.e., inclusion and exclusion instructions). To give an example, items encoded at study will be presented in different colors (e.g., red or green). During a recognition test, participants are either required to respond ‘old’ to all items that were previously studied (e.g., the inclusion task), or required to respond ‘old’ when items are presented in one of the two colors (e.g., the exclusion task). The process-estimation procedure predicts, based on dual process theory, that the exclusion task is heavily reliant on recollection because participants must retrieve associative details to make a successful judgment. The inclusion task, by contrast, requires retrieval of item information and a successful judgment will therefore reflect contribution of both recollection and familiarity. Parameter estimates of recollection and familiarity are derived from a pair of equations that calculate the probability of successful recollection (see Jacoby, 1991 for more details of these equations). Interpretation of results from process estimation procedures should, however, be made with caution. As with the source paradigm discussed earlier, the process dissociation procedure is also prone to the contribution of noncriterial recollection, which can elevate the estimate of familiarity and underestimate recollection (for a more detailed discussion see Parks, 2007). Proponents of the process dissociation procedure, however, argue that the contribution of noncriterial recollection occurs so infrequently as to not pose a serious problem (Yonelinas & Jacoby, 1996; Yonelinas, 2001).

An alternative process estimation procedure is the Remember/Know paradigm developed by Tulving (1985). The Remember/Know procedure requires participants to introspect about the subjective ‘feeling’ associated with a memory judgment, and to report whether they recognize previously studied information based on Remembering (i.e., recollecting details of a prior episode) or Knowing (i.e., being familiar with a stimulus in the absence of recollection). The Remember/Know procedure has the benefit of not relying on specific types of information to estimate recollection and familiarity, affording researchers some flexibility in the experimental paradigms that can be employed.

Consistent with previously discussed methods, however, the results from the Remember/Know procedure should be interpreted with caution. For instance, whilst the procedure provides a reliable assessment of recollection derived from the proportion of 'Remember' responses, the estimates of familiarity are more ambiguous. In theory, remember responses should reflect recollection and know responses should reflect familiarity. Due to the forced nature of the design, however, the estimates of familiarity can be ambiguous. There are two major problems for the standard Remember/Know method that are specifically caused by the forced choice design. First, because participants are required to either make a Remember response if they recollect and Know response if they do not (i.e., familiar but not recollected), the Remember/Know procedure will overestimate recollection and underestimate the contribution of familiarity. To be clear, Remember responses will comprise of both recollection and familiarity, but Know responses will only be based only on familiarity in the absence of recollection. To compensate for this underestimation, Yonelinas and Jacoby (1995) proposed the Independence Remember/Know (IRK) method, which corrects the estimate of familiarity by rescaling the data (i.e., by dividing the proportion of Know responses by the opportunity to make a Know response). Secondly, the forced choice design of the Remember/Know procedure results in a proportion of responses that include guessing. This is particularly problematic for Know responses, as familiarity and guessing are more likely to reflect decisions made with uncertainty (Gardiner, Ramponi & Richardson-Klavehn, 1998). A simple solution proposed by Gardiner et al., (1998) is to include a third Guess response that filters guessed responses, thereby providing more accurate estimates of familiarity and recollection.

A third process estimation procedure which has had considerable impact on recent models of episodic memory is the analysis of Receiver Operating Characteristics (ROCs). Within recognition studies, ROC curves are obtained by plotting Hits and False Alarms as a function of response confidence [i.e., rating an item from 1 (sure new) to 6 (sure old)]. ROCs are particularly useful because there is a direct relationship between the shape of the ROC and the contribution of recollection and familiarity. In essence, familiarity is expected to result in an ROC that represents an inverse U shape (i.e., curvilinear – because familiarity is modelled as a continuous process that contributes to recognition at all confidence levels), and is symmetrical (i.e., because the familiarity distribution of both old and new items have equal variance). Recollection, by contrast, is characterized as a probabilistic threshold process and is associated only with high confidence judgments. The contribution of recollection will increase the Hit rate for only the highest confidence level, shifting the confidence point upwards in ROC space. An increase in the contribution of recollection will therefore make the ROC more linear and asymmetrical. It should be noted that during item recognition, familiarity and recollection will both contribute to performance and the ROC is observed as being curvilinear and asymmetrical.

The ROC method provides some clear advantages over other process estimation methods. First, the ROC graph provides a relatively clear representation of memory performance over several levels of confidence. A researcher who is familiar with ROCs is therefore able to interpret a complex dataset relatively quickly. In addition, ROCs can be analyzed using a variety of different models with various parameters. Not only does this allow old datasets to be reanalyzed and reinterpreted with more up-to-date models (see Slotnick & Dodson, 2005), it also allows for the comparison of different models using statistical techniques such as regression or goodness-of-fit (see Yonelinas & Parks, 2007). Although the ability to fit the ROCs to different models is an advantage, it can also be a limitation. Estimating different processes from ROCs, for example, is highly model specific, in that the estimates are derived from the underlying assumptions of the specific model being fitted (Wixted, 2007; Parks and Yonelinas, 2007). Furthermore, the use of subjective confidence ratings can also be problematic, because the confidence rating scale can be used by participants in different ways. Some participants, for example, will not spread their responses across the various confidence ratings and instead may rely on a particular response level to make the majority of their responses. This problem can be avoided to a certain extent by increasing trials numbers and emphasizing the use of the whole scale (Yonelinas & Parks, 2007).

1.3.3. Process purity

From the preceding sections it should be clear that attempting to design a task that isolates the contribution of familiarity and recollection is extremely challenging, with each method carrying both strengths and weaknesses. In theory, the principle of pure insertion (Dondors, 1868) suggests that the subtraction of two experimental conditions will reveal a single process of interest (for further discussion of this issue see Chapter 3 which considers the same logic underlying interpretation of ERPs). In practice, however, memory is relatively complex and performance on any given task will potentially involve the engagement of different memory systems and processes making process purity (i.e., isolation of a single process) extremely difficult.

Designing a task that isolates a specific process is also confounded by the fact that, on any given recognition task, retrieval is likely to be supported by both explicit and implicit processes. This interaction between explicit and implicit memory is actually accounted for by some dual process models. For example, whilst familiarity and implicit memory are considered completely independent (i.e., Tulving, 1985), other models propose that familiarity is supported by – or equivalent to – specific implicit processes (i.e., Mandler, 1986; Jacoby & Dallas, 1991). Repetition priming (i.e., increasing perceptual fluency of an item), in particular, has been shown to increase the estimates of familiarity (Henson, Shallice & Dolan, 2000; Logan, 1990). However, several studies of amnesic patients demonstrating preserved repetition priming but impaired familiarity (Knowlton & Squire, 1999, Hamann & Squire, 1997), indicate that both processes are independent. Despite the dissociation between familiarity and implicit priming, however, the evidence does not exclude the possibility that familiarity and implicit priming may share a common set of underlying cognitive processes. Regardless, whilst it may never be possible to completely isolate familiarity or recollection, methods for estimating the contribution of each retrieval process still provide a valuable tool for exploring episodic memory, even though they cannot be considered process pure.

1.4. Evidence supporting the separation of familiarity and recollection

A wealth of evidence has accumulated which supports the distinction between familiarity and recollection. Although this evidence has been discussed in detail elsewhere (see Yonelinas, 2002), this section first briefly reviews the evidence that supports a functional separation of familiarity and recollection, before outlining evidence that indicates familiarity and recollection are supported by distinct neural substrates.

1.4.1. Functional differences between familiarity and recollection

From a behavioral level of analysis, familiarity and recollection have been shown to function in different ways. First, recollection has been shown to be impaired to a greater extent than familiarity when attention is divided at study. Craik et al., (1996), for instance, found that dividing attention at encoding impaired performance on recall tests (believed to be heavily dependent on recollection) to a greater extent than recognition (supported by both recollection and familiarity), indicating that recollection relies more upon attentional processes than familiarity. Furthermore, studies employing alternative methods such as process-dissociation and Remember/Know procedures typically converge to support the finding that although recollection and familiarity are affected by divided attention at study and test, recollection is disrupted to a greater extent (Gardiner & Parkin, 1990; Yonelinas, 2001; Mangels, Picton & Craik, 2001; Troyer et al., 1999; Skinner & Fernandez, 2007; although see Naveh-Benjamin et al., 2014, for an alternative account when employing incidental and intentional tests). In addition, results from studies employing response deadline procedures also demonstrate that estimates of recollection, but not familiarity, increase under non-speeded conditions but are significantly reduced when speeded judgments are required (Benjamin & Craik, 2001; Savauge, Beer & Eichenbaum, 2010; although see Dewhurst, Holmes & Brandt, 2006). Finally, studies manipulating the level of processing reveal that recollection rather than familiarity increases when 'deep' (i.e., greater semantic processing) encoding is encouraged compared to 'shallow' (perceptual) encoding (Wagner et al., 1997; Rajaram, 1993, Gallo et al., 2008).

The alternative dissociation, whereby a manipulation has a greater effect on familiarity rather than recollection, has also been extensively reported. First, studies that manipulate the study-test modality of stimuli, for example, have been shown to have a greater impact on familiarity compared to recollection (Toth, 1996; Gregg & Gardiner, 1994). A study carried out by Gregg and Gardiner (1994), for example, demonstrated that changing the modality of words between study and test reduced the proportion of 'Know' responses compared to 'Remember' responses, particularly when encoding instructions emphasized the perceptual features of the word. Second, in line with Signal Detection Theory, instructions that encourage participants to relax their response criterion (i.e., encourage participants to accept more items as being studied) has been shown to increase the estimates of familiarity, whilst recollection estimates are not affected (Gardiner & Gregg, 1997; Postma, 1999; Strack & Foerster, 1995; Yonelinas, 2001). Lastly, interference effects and short study-test delays have also been shown to reduce the contribution of familiarity, whereas recollection remains constant (for a review see Sadeh et al., 2014). By comparison, response deadline procedures that requires responses within 1sec (see section 1.31.) spare familiarity but reduce the contribution of recollection. Collectively, results from a range of studies suggest that the temporal characteristics of familiarity and recollection are distinct – i.e., familiarity operates quicker than recollection, but recollection may occur across a longer period of time than familiarity.

1.4.2. Neural substrates of familiarity and recollection

Although many regions of the brain may support episodic memory, the Medial Temporal Lobes (MTL) have received the most attention and are generally considered the locus of long-term memory. The MTL is comprised of the amygdala, hippocampus and surrounding hippocampal regions including the perirhinal, parahippocampal and entrohinal cortex. The hippocampus was identified as being critical to long-term memory in a seminal case study by Scoville and Milner (1957). In this particular case study, it was found that patient H.M. suffered severe anterograde amnesia (i.e., an inability to form memories of everyday events) following surgery removing much of his hippocampus, amygdala and uncus. Although later MRI scans of H.M.'s medial temporal lobe revealed that regions other than the hippocampus were also damaged (Corkin et al, 1997), more recent cases of patients with more localized hippocampal damage have supported the initial insights of Scoville and Milner (see Spiers et al., 2001).

In a review of animal lesion, immediate early gene and neuronal recording studies of rats and monkeys, Brown and Aggelton (2001) concluded that the hippocampus is critical to relational and spatial information, whereas the perirhinal cortex supports the retrieval of object based information. Based on the assumption that different types of information are supported by distinct retrieval processes during recognition, the data presented by Brown and Aggelton (2001) support the view that the hippocampus is critical to recollection, and the perirhinal cortex is critical to familiarity. Below, we review the evidence from neuropsychological and neuroimaging studies that support this neural dissociation.

A large proportion of the evidence that familiarity and recollection are supported by different neural substrates comes from case studies of amnesic patients. Severe damage to the hippocampus and the surrounding temporal lobe, for example, has been associated with deficits in recognition, suggesting that these areas are critical to supporting episodic memory (Vargha-Khadem et al., 1997; Mayes, 2002; Holdstock et al., 2000; Aggelton et al., 2000, 2005; Hayes, Salat & Verfaellie, 2012; Park et al., 2014; for a review see Eichenbaum, Yonelinas & Raganath, 2007). Evidence that the hippocampus is specifically related to recollection is supported by a number of studies that examine patients who have developed memory loss following transient cerebral hypoxia. To be clear, postmortem and structural imaging scans confirm that mild hypoxia is associated with neuronal loss largely confined to the hippocampus (Hopkins et al., 1995; Zola-Morgan et al., 1986; Rempel-Clower et al., 1996). Studies examining hypoxic patients have reported a disproportionate impairment in relational compared to item recognition (Giovanello et al., 2003; Holdstock et al., 2005; Mayes et al., 2002), and selective reductions in estimates of familiarity whereas estimates of recollection were relatively unimpaired (Yonelinas et al., 2002). Although impaired familiarity and spared recollection is less often observed than the reverse pattern, a recent study by Bowles et al., (2007) found that a patient with selective damage to the perirhinal cortex exhibited impairment to familiarity but spared recollection, supporting the view that the perirhinal cortex for critical to familiarity. More generally however, amnesic patients often exhibit damage to both the hippocampus and surrounding cortical structures, leading to deficits in both familiarity and recollection.

Although there is considerable evidence from amnesic studies supporting the neural dissociation of familiarity and recollection, results to date are by no means conclusive. To be clear, the highly plastic nature of the brain means that after a particularly extended period of time, performance on certain tasks may be compensated for by alternative neural regions (Poldrack, 2000). In practice, this means that there will be a certain ambiguity when comparing performance on a task between amnesic and healthy controls. In addition, there is an inherent difficulty in characterizing the extent of neural damage which is limited by the spatial resolution of structural imaging technology. Given the relatively close proximity of structures within the MTL, for example, identifying specific regions is currently pushing the limits of the spatial resolution of modern structural imaging technology (Eichenbaum et al., 2007). Observed cognitive impairment therefore may actually be associated with more widespread damage than can currently be detected. Regardless, the evidence from clinical studies has had immense value in identifying the neural substrates that play an important role in familiarity and recollection. Given the limitations of neuropsychological research, however, it is important to examine the converging evidence from neuroimaging data from healthy populations.

Neuroimaging data provides an alternative source of evidence supporting the anatomical dissociation between familiarity and recollection. Two methods that are often employed are functional Magnetic Resonance Imaging (fMRI) and Event Related Potentials (ERPs). ERPs provide specific information about the time course of neural events by measuring changes in electrical potential from the scalp. ERPs have high temporal resolution but poor spatial resolution meaning that the method says very little about the underlying neuroanatomical substrates of familiarity and recollection. Regardless, ERPs have shown that familiarity and recollection differ qualitatively with regards to their time-course and scalp distribution (for a comprehensive review of ERPs and recognition see Chapter 3 & 4). Alternatively, fMRI detects hemodynamic blood flow in the brain. In contrast to ERPs, the fMRI method has poor temporal resolution because it can take up to several seconds to detect hemodynamic changes in blood flow. Despite its poor temporal resolution, the fMRI method has excellent spatial resolution, making this method ideal for identifying the underlying neural substrates of familiarity and recollection.

Consistent with the evidence from amnesic studies described previously, fMRI studies have consistently detected increased activity in the hippocampus both at encoding and retrieval that is correlated with recollection but not familiarity of items during retrieval (Davachi et al., 2003; Kirwan & Stark, 2004; Stark & Squire, 2000; Cansino et al., 2002; Yonelinas et al., 2005; Hannula et al., 2013). A similar but less robust pattern of results is also observed for the parahippocampal cortex for both encoding and retrieval (see Diana, Yonelinas & Raganath, 2007 for a review). In addition, fMRI studies have also demonstrated that perirhinal activity at encoding is (more closely) correlated with familiarity estimates, but not recollection estimates at retrieval (Haskins et al., 2008; Uncapher et al., 2006; Henson et al., 1999), whilst reduced perirhinal activity is found when comparing items that elicit familiarity compared to items that are later forgotten (Weis et al., 2004). In addition, Ford et al., (2012) have also demonstrated that retrieval of compound words (i.e., item information) was associated with increased perirhinal activity compared to the retrieval of unrelated word pairs (i.e., associative information), which was instead associated with increased activity in the left hippocampus.

The evidence reviewed above is consistent with the dual process view that the hippocampus and parahippocampal regions support recollection and the perirhinal cortex supports familiarity. The dual process perspective of MTL function, however, is far from a commonly held perspective (even among those who ascribe to a dual process framework). Instead, critics have argued that a simple one-to-one mapping of the hippocampus to recollection is not well supported by existing data (Manns et al., 2003; Wixted et al., 2006). Similar arguments have also been made with regards to the mapping of familiarity and the perirhinal cortex, with some studies demonstrating that the perirhinal cortex is sensitive to the retrieval of associative information (Eldrige et al., 2005; Staresina & Divachi, 2008; Kirwan & Stark, 2004: although for an alternative account see Diana et al., 2008). Single process accounts of neural imaging data, for instance, argue that fMRI studies confound familiarity and recollection with variation in memory strength (Wixted & Squire, 2011). To be clear, according to this view, the presence or absence of hippocampal activity simply reflects whether the memory being retrieved is associated with stronger or weaker memories, rather than qualitatively distinct types of memories (Wixted et al., 2010). In a recent source study conducted by

Wais, Squire and Wixted (2010) fMRI was used to measure hippocampal activity at retrieval after equating memory strength for source correct and source incorrect trials. Memory strength was equated by only focusing on old/new trials that received the highest confidence rating, regardless of source accuracy. The data revealed that hippocampal activity was elevated for both source correct and source incorrect trials, suggesting that the hippocampus was involved for both familiarity and recollection (although the single process account is hotly disputed by other researchers including Diana & Ranganath, 2011; Staresina et al., 2013; and Montaldi & Mayes, 2010).

1.5. Summary

From the review above it should have become clear that memory is not a unitary system, but comprises a complex interaction between different systems, sub-systems and processes. This thesis is primarily concerned with episodic memory, which is a specific sub-system of long-term, declarative memory. Episodic memory is typically tested using recognition tasks and attempts to explain performance can be generally classed according to two competing theories. Single process accounts, for example, suggest that episodic retrieval is supported by a single strength based process, whereas dual process accounts suggests that retrieval is supported by two functionally independent retrieval processes known as familiarity and recollection. Although the debate between single process and dual process models is unresolved, current evidence strongly supports the distinction between a continuous familiarity process and a thresholded recollection process.

The main aim of the current thesis is to test two important predictions of familiarity and recollection made by dual process theory. The first prediction is that recollection is a probabilistic threshold process distinct from a continuous familiarity process. Secondly, the prediction that familiarity can, under certain circumstances, support associative retrieval of novel information will be tested. In the following chapters these separate predictions will be explored in more detail (Chapter 2) before discussing the ERP method (Chapter 3) and reviewing how ERPs have been used to investigate recognition (Chapter 4).

Chapter 2

Associative Recognition Memory

The purpose of the previous chapter was to introduce episodic memory, outlining current theories of how memory is structured, conceptualised and measured, with particular emphasis on dual process accounts of episodic recognition. The current chapter expands on the previous introduction, focusing on how the nature of information affects memory. Recognition of item information, for example, entails retrieval of a single stimulus, whereas associative recognition requires one to place that item in context: remembering the spatial, temporal and other contextual details that bring the item to mind. As made clear in the previous chapter, although there is agreement among single and dual process accounts that familiarity reflects a variable ‘memory strength’ signal, accounts disagree about the functional nature of recollection. The current chapter begins by describing why an understanding of associative recognition[1] is important, before reviewing the thresholded and continuous accounts of recollection during associative and source recognition tasks. The chapter ends by discussing the evidence of specific circumstances that allow familiarity to contribute to successful associative recognition.

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[1] In the current chapter reference will be made to associative recognition, which refers to the retrieval of associative information. Associative recognition should not, however, be confounded with associative recognition tasks, because source memory tasks also provide a measure of associative retrieval. To be clear, the term associative recognition will be used to refer to the retrieval of associative information (measured by both associative recognition and source memory tasks).

2.1. The importance of associative recognition

Associations are not directly observed, but are inferred from the tendency for one item to bring to mind another. Associations that automatically come to mind, such as fountain and pen, or jam and jar, will typically have been reinforced over long periods of time. Associations, however, can also be formed between unrelated items after a single exposure. In essence, when a pair of items are attended to in close proximity (such as the name of your new teacher, or that your car is parked next to the yellow caravan) that association is stored temporarily in memory. Often, such new associations are only held in mind for the purpose of a short-term goal, for example, locating where your car is parked. In some circumstances, however, new associations can be encoded sufficiently enough after a single exposure as to be recognised over a longer period of time. The ability to encode, store and retrieve novel associations after a single exposure is referred to as episodic associative memory (Hattori & Hagiwara, 1996). Episodic associations are important to our knowledge of self by allowing us to remember events in our lives which are comprised of individually related elements and our position within them. In addition, without the ability to form new associations we would be stuck in the present, unable to form new episodic memories making, making normal everyday life impossible.

Importantly, recollection (and therefore memory for episodic associations) is particularly vulnerable to mental decline caused by ageing (for a review see Koen & Yonelinas, 2014), disease and disorders including Alzheimer’s (Naveh-Benjamin, 2000; Healy et al., 2005), and schizophrenia (Heckers et al., 1998; Sponheim et al., 2004). Specific recollection impairment can be devastating, and developing behavioural interventions aimed at mediating age-related cognitive decline will be critical, particularly in the context of an ageing population. These behavioural interventions can be improved by accurately characterising the function of recollection at both a behavioural and neural level. To this end, one particular aim of the current thesis will be to better characterise the functional nature of the underlying neural signal of recollection (explored in more detail in Chapter 4). First, however, this chapter will set the thesis in context, by first reviewing the relevant behavioural evidence which has attempted to characterise recollection at a behavioural level, before reviewing evidence suggesting that under certain circumstances associative recognition may also be supported by familiarity.

2.2. The functional nature of recollection

2.2.1. Recollection is thresholded

Although many dual process models have been proposed (for a review see Yonelinas, 2002), the current chapter will elaborate upon the Dual Process Signal Detection (DPSD) model (briefly discussed in Chapter 1) because it is currently being extensively applied to neuroimaging and neuropsychological studies. One core assumption of the DPSD model is that recollection and familiarity differ in the type of information they provide (Yonelinas et al., 2010). Familiarity is assumed to reflect the assessment of quantitative memory strength in line with signal detection theory. Recollection, by contrast, reflects thresholded retrieval of qualitative information about a previous event in a probabilistic fashion – i.e., recollection can either succeed or fail. Recollection is not accurately characterised by signal detection because individuals do not recollect information about every studied event. For example, on some trials recollection strength will not exceed a threshold and will fail to provide any evidence that will support successful discrimination. In its simplest form, the DPSD model has two parameters: d´ which describes the distance of memory strength distributions for both familiar and unstudied items and p(R) which describes the probability of recollecting an item.

One advantage of the DPSD model is that it can account for performance on source and associative recognition tasks (both of which require the retrieval of episodic associative information). To be clear, source tasks require participants to retrieve the source that was associated with an item at encoding (e.g., was the voice male or female?). Associative recognition tasks require participants to indicate whether a pair of items were associated with each other at encoding (e.g., was Dog and Cigar studied together?). Both source and associative tasks differ from item recognition because both tasks are believed to be supported primarily by recollection. Familiarity observed in both source and associative tasks is expected to be less diagnostic in supporting successful discrimination, because all test items have been studied; leading to a greater reliance on recollection (although see Section 2.3. for potential circumstances that allow familiarity to contribute to associative and source retrieval).

Behavioural evidence supporting a recollection threshold comes primarily from ROC studies (see Chapter 1 for more detail). To briefly reiterate, the shape of ROCs (which are derived from confidence judgements made during a recognition memory task) indicate whether performance relied on either recollection or familiarity. For example, because familiarity is a continuous process it will contribute to all levels of confidence, producing an ROC that is curvilinear and asymmetrical. By contrast, recollection will contribute to the highest confidence level (because only items that have exceeded a thresholded will be recollected), and will increase the hit rate, pushing the overall ROC up; producing an ROC that is more linear and asymmetrical. Thus, under conditions where recollection is believed to be the dominant process contributing to retrieval (e.g., source and associative tasks) the resulting ROC should be more linear than a signal detection account would predict. Yonelinas (1997) initially confirmed this prediction by comparing performance between item and associative recognition tasks. Analysis of ROCs for each task revealed that associative performance produced very linear ROCs, but item recognition ROCs were more curvilinear. In a follow up study, Yonelinas (1999) also observed more linear ROCs during a source memory task (whereby participants had to identify if a word was presented on either the left or right hand of the screen), consistent with the view that source retrieval relies heavily on recollection. The linear and curvilinear pattern of ROCs has now been replicated numerous times (for a review see Yonelinas and Parks, 2007) and has even been demonstrated across species (Sauvage et al., 2007).

2.2.2. Recollection is a continuous process

Although the DPSD model has been used extensively in behavioural, neuroimaging and neuropsychological studies, the assumption that recollection operates in a thresholded fashion has been challenged. Critics argue against a probabilistic all-or-none threshold, instead insisting that recollection should be modelled as a continuous process that always returns some information from memory (Rotello et al., 2005; Wixted, 2007; Slotnick, 2013; Starns & Ratcliff, 2014). For example, the Unequal Variance Signal

Detection (UVSD) model (Green & Swets, 1966; Wixted, 2007) assumes that memory strength decisions are based on a single memory strength signal with old and new item strength values forming Guassian distributions (i.e., strength for studied items will on average be stronger than new items). Critically, the UVSD model predicts that not only do strength distributions differ in their means, but also in variance – with strength for studied items leading to greater variance than new items. The UVSD model has therefore been relatively successful in accounting for studies demonstrating that variance in studied item strength is often greater than new item variance (Glanzer & Adams, 1990; Hirshman & Master, 1997; Yonelinas, 1994; Wixted, Mickes & Wais, 2007), although the model is less successful in specifying the cause of the observed difference in variance (see Koen & Yonelinas, 2010).

One particular problem for the traditional UVSD account is the considerable evidence from recognition paradigms demonstrating that recognition performance cannot be adequately accounted for by a single signal of memory strength (see Section 1.2.1). In a recent revision of the UVSD model, however, Wixted (2007) has suggested that the memory strength signal reflects the summed contribution of multiple memory signals (i.e., familiarity and recollection). To be clear, both familiarity and recollection are viewed as being continuous processes with their own strength parameters and variance ratios but aggregate together to support retrieval. The revised UVSD model is still consistent with a single process account because recognition is supported by the overall memory signal (comprising of the summed contribution of familiarity and recollection). By acknowledging the existence of familiarity and recollection, however, the revised UVSD model is considered to advance traditional single process models because it can theoretically account for both behavioural and neural evidence supporting the presence of multiple memory signals.

The core difference between the DPSD and UVSD models is the assumption that recollection is either a thresholded (i.e., all-or-none) process or a continuous process (i.e., ranging from strong recollection to weak recollection). Evidence that recollection may be continuous has been provided by studies demonstrating curvilinear ROCs in both associative and source tasks, as opposed to the more linear ROCs predicted by the DPSD model. For example, Mickes et al., (2010) presented unrelated word pairs either once (associatively weak) or five times (associatively strong) at study. Results from an associative recognition task revealed that strongly associated pairs exhibited greater curvilinear ROCs compared to weak pairs, as well as exhibiting a greater proportion of Remember responses (taken as evidence of increased recollection). In addition, Slotnick and Dodson (2005) also found evidence of curvilinear ROCs during a source memory task, particularly when noisy trials (i.e., guess trials) were excluded. From the UVSD perspective, curvilinear ROCs observed during associative and source tasks provide strong evidence in favour of a continuous recollection process.

The evidence of curvilinear ROCs during associative and source tasks (believed to be reliant on recollection) appears to be inconsistent with the assumptions underlying the DPSD model. Recently, however, proponents of the DPSD model have clarified that their argument for a threshold has been misunderstood, leading to much confusion in the literature. Originally, Yonelinas (1994) proposed that recollection was ‘all-or-none’; although recent revisions by Yonelinas and colleagues have clarified that the term ‘all-or-none' simply means that recollection can sometimes fail. In essence, Yonelinas and colleagues agree that recollection can appear graded overall because participants can recollect different amounts of information about a previous episode. However, recollection operates in an all-or-none fashion for any element of a previous episode that is being tested during a recognition task (Parks & Yonelinas, 2007; Yonelinas et al., 2010). Thus, recollection of a retrieval cue can fail on a sub-set of trials.

Although the more nuanced description of recollection can account for the variation in recollection strength, it is incompatible with the formal DPSD model. To be clear, variation in recollection cannot be captured by a high threshold model that characterises recollection as all-or-none. One particular problem for the DPSD account is that the model was originally developed to account for ROC data with only a small number of response confidence levels (usually around 6). The use of a small number of confidence levels means that participants are more likely to assign recollected trials with the highest confidence rating. Theoretically, studies that employ a larger array of confidence ratings should allow participants to dissociate strong from weak recollection. This prediction was recently confirmed when Mickes, Wais and Wixted (2009) carried out a source task using a 20 point confidence scale, and encouraged participants to spread their responses. The results revealed curvilinear ROC for source correct trials that were consistent with a continuous recollection signal.

In defence of the DPSD account, evidence of curvilinear ROCs during an associative or source memory task does not necessarily provide evidence against the DPSD model. The argument provided by single process theorists is that source tests provide a process pure measure of recollection, and since recollection is assumed to be thresholded, source ROCs should be perfectly linear. In practice, however, source and associative tasks are not process pure, because there are certain circumstances in which familiarity can support associative and source recognition (see Section 2.3 for more detail).

To date, the debate between the thresholded and continuous models of recollection is still fiercely contested (Koen et al., 2013; Slotnick, 2013). One reason why the debate still remains to be settled is because the data used to support either account is dependent on use of ROCs which can be used to argue for either a thresholded or continuous process (Wixted, 2007; Yonelinas & Parks, 2007). Furthermore, ROCs do not provide a direct measure of memory because confidence ratings are a subjective measure of memory strength. As such, confidence may be influenced by a number of other non-mnemonic factors such as fatigue or mood which may possibly make the shape of the ROC appear less linear and incompatible with a threshold (see Broder & Shutz, 2009). For these reasons, recent attempts to resolve the debate about whether recollection is thresholded or continuous have moved away from relying on ROC procedures by employing a more direct and objective assessment of memory strength.

2.2.3. Recollection may be some-or-none

In a recent study by Harlow and Donaldson (2013), memory strength was assessed during a novel source task by measuring positional response accuracy rather than relying on subjective confidence. At study, participants were shown a marked location around a circle, followed by a single word. During the test block, participants were shown previously studied words and were required to recollect the paired location around the circle; allowing for the precision of the source response to be measured. Importantly, both threshold and continuous accounts of recollection predict different error distributions.

According to a continuous model, retrieval should always produce some information from memory, with a greater likelihood of recollecting and greater frequency of responses around the target location (see Figure 2.1, right). Importantly, the distribution of errors should monotonically decrease from the target, with decreasing likelihood of recollection and thus fewer responses from the target. However, a threshold model predicts that successful recollection can fail to provide any information from memory, resulting in a distribution whereby responses cluster close to the target (high strength recollected trials), mixed with sub-thresholded guesses (see Figure 2.1, left). According to the threshold model, guesses will be made in the absence of any retrieved information and responses will therefore be randomly distributed relative to the target. Consequently, the overall distribution will exhibit a pattern of responses that cluster closely to the target, decaying rapidly but stabilizing to an asymptote that is greater than zero. In short, continuous models predict that guesses are based on weak recollection (and should therefore be non-random), but threshold models predict that guesses are based on the absence of any recollection (and therefore randomly distributed). The results of Harlow and Donaldson (2013) revealed that the threshold model provided a significantly better fit to the response pattern than the continuous model – i.e., the continuous model underestimated the proportion of highly accurate responses and highly inaccurate responses (see Chapter 6 for more detail).

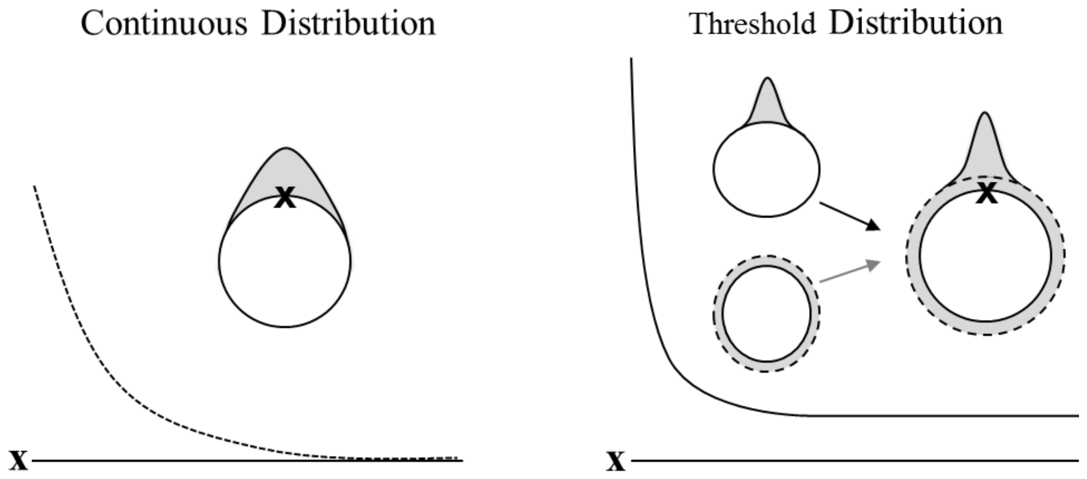

Figure 2.1: Predicted distribution of errors for both a threshold (left) and continuous (right) accounts of recollection.

Harlow and Donaldson (2013) also investigated whether the threshold could have been introduced at encoding rather than retrieval (i.e., the encoding threshold account proposed by DeCarlo, 2003; Slotnick & Dodson, 2005). To test between encoding and retrieval thresholds, encoding conditions were identical, but the retrieval duration between study and test was varied (i.e., short and long delays). If an encoding threshold account was accurate, then it was expected that the frequency of above-threshold responses and overall precision (i.e., mean error) would not differ between short and long delays. Contrary to an encoding threshold, the data revealed significantly reduced frequency of above-threshold responses and less precision after the longer delay, consistent with a retrieval threshold. The change in precision over retrieval delay was, however, also inconsistent with an all-or-none account. Instead, Harlow and Donaldson (2013) concluded that recollection reflected a some-or-none process where recollection can fail to return any information from memory (i.e., thresholded) but is variable when successful.

Although the results of the novel source task developed by Harlow and Donaldson (2013) demonstrate that behaviourally recollection is thresholded and variable, the data says nothing about the underlying neural mechanism supporting recollection. To be clear, even if recollection is thresholded behaviourally, from a theoretical perspective it is nonetheless reasonable to propose that the behavioural outcome stems from a neural process which is itself continuous. For example, although studies employing old/new or Remember/Know tasks demonstrate a thresholded signal (Yonelinas et al., 1998), analysis of neural data suggests that recollection may operate in a continuous fashion (Woodruff, Hayama & Rugg, 2006). In short, the demonstration of a behavioural threshold does not necessarily imply a neural threshold. The current thesis attempts to resolve the issue of whether the neural signal of recollection is also thresholded by replicating the novel source paradigm designed by Harlow and Donaldson (2013), and using Event Related Potentials (ERPs) to index recollection. A more detailed discussion of the neural correlate of recollection, as well as the specific aims of the current thesis, is provided in Chapter 4.

2.3. Can familiarity support associative recognition?

Given that recollection has been shown to fail on a sub-set of trials, the question arises as to whether other retrieval processes may contribute to associative retrieval. Traditionally, the DPSD model assumed recollection was essential for the retrieval of source and associative recognition. However, in light of evidence indicating that ROCs during source and recognition tasks were sometimes curvilinear, a new prediction was proposed that under specific circumstances, familiarity could contribute to successful associative recognition (thereby accounting for the observed curvilinear ROCs).

Developing a proper understanding of the conditions that allow familiarity to contribute to successful associative retrieval has been the focus of recent behavioural, neuroimaging and patient studies. In addition, considering the vulnerability of recollection to cognitive decline, the possibility of successful associative recognition in the absence of recollection also has important practical implications for those with selective recollection deficits. The aim of the current section is to provide a review of the evidence supporting the assumption that familiarity can contribute to successful associative recognition; whilst also highlighting the need for further investigation.

2.3.1. Unitization

From a dual process perspective, unitization is arguably the most promising and well researched candidate for explaining the observed curvilinear ROCs during associative and source retrieval tasks. Defined in the late 1980's, unitization involves the encoding of previously separate units of information into a single configuration (Graf and Schacter, 1989). Importantly, unitization refers to the creation of a novel configuration – for example, the words 'FACE' and 'BOOK' both have their own distinct properties but can be combined to form a single item with a shared meaning (i.e., 'FACEBOOK'). A unitized item is therefore constructed from two or more independent units of information; allows for the acquisition of rigid associative information after a single exposure (Rhodes and Donaldson, 2008; Bader et al., 2010) and results in poorer discrimination performance and reduced familiarity for item recognition (Haskins et al., 2008; Pilgrim, Murray & Donaldson, 2012). Additionally, the new novel item does not necessarily have to be associatively or semantically related to its component parts (as in 'FACEBOOK') or even have to be a word (i.e., unitization has been demonstrated with non-lexical stimuli: see Yonelinas et al., 1999; Diana et al., 2008). Most importantly, because item recognition is assumed to be supported by familiarity, a unitized configuration can engender a sense of familiarity for the whole at retrieval.

2.3.2. How can associative information become unitized?

Unitization of associative information can be encouraged in a number of different ways. First, however, it is important to note that unitization has been argued to be a continuous variable in which two stimuli can vary in the level to which they have become unitized. Although it is difficult to determine if two stimuli have become unitized, experimental conditions or materials can be manipulated in such a way as to make unitization more or less likely to have occurred (Quamme et al., 2007; Yonelinas et al., 2010). The lexical manipulation, for example, requires participants to encode unrelated word pairs as compound words (e.g., VEGETABLE-BIBLE: A reference book for gardeners). Here, the shared meaning serves to combine both items into a single representation, allowing the discrimination of intact and recombined pairs to be supported by familiarity. The compound method can be contrasted with a sentence frame method, whereby the separate meaning of each word is maintained (e.g., VEGETABLE-BIBLE: The ___ was thrown near to the ___). For the sentence frame method, the separate meanings are related by association, and familiarity should be less likely to contribute to their retrieval. Mental imagery has also been used to manipulate unitization. Mental imagery can be used to encourage unitization by asking participants to either imagine unrelated words interacting together (thereby creating a single unitized representation). To discourage unitization, participants are asked to imagine words separately.

Importantly, because there is currently no way of determining if pairs have become unitized on individual trials, manipulations of unitization should not be treated as being process pure. To be clear, although the instructions are designed to manipulate the level of unitization, it is likely that some pairs within the non-unitized condition may be perceived as being unitized, resulting in the contribution of familiarity. On average, however, the estimates of familiarity when unitization is discouraged should be considerably less than is observed when participants are encouraged to unitize pairs.

2.3.3. Unitization carries costs and benefits

One particular problem when interpreting unitization is the use of circular logic. To be clear, familiarity provides evidence of unitization, but unitization is used as an explanation for observed familiarity. In an attempt to address this circularity, Mayes et al., (2007) suggested that unitization could be defined by demonstrating measurable costs as well as benefits to memory. Specifically, unitization should increase to the extent that item memory is strengthened for an associated pair but correspondingly weakened for the individual components. Mayes et al., (2007) prediction was tested by Haskins et al., (2008) by reversing the order of components of novel compound words (e.g. VEGETABLE-BIBLE at study would become BIBLE-VEGETABLE at test). The results revealed that under unitization instructions, discrimination performance was significantly poorer for reversed compared to intact pairs, but performance was equivalent between intact and reversed pairs under non-unitization instructions. However, as no estimates of recollection and familiarity were measured, the poorer discrimination performance for unitized pairs is impossible to attribute to a reduction in familiarity.

In a later study, Pilgrim, Murray and Donaldson (2012) measured the contribution of familiarity and recollection during an item recognition task. At study, word pairs were either encoded with item or interactive mental imagery. During the test phase, participants were required to discriminate between words that were previously presented as word pairs at study and new words. The contribution of familiarity and recollection was measured by analysing their respective neural correlates (see Chapter 3 & 4 for more detail). The results revealed that the ERP correlate of familiarity was significantly reduced when instructions encouraged unitization compared to non-unitization instructions. By contrast, the neural correlate of recollection did not differ between conditions, indicating a selective modulation of familiarity. Collectively, the evidence from both Haskins et al., (2008) and Pilgrim et al., (2012) is consistent with the view that unitization carries costs, at least when encoding occurs in interactive mental imagery or compound definitions.

2.3.4. Behavioural evidence for unitization

A vast majority of the behavioural evidence supporting unitization comes from studies examining ROCs. As described earlier, the DPSD model interprets curvilinear ROCs during associative and source tasks as reflecting familiarity, rather than a continuous recollection signal. The increased curvilinearity, for example, has been observed during associative recognition of face stimuli. Yonelinas et al., (1999) asked participants to study line drawings of upright and inverted faces. At test, both upright and inverted faces were either shown intact from study, or were rearranged (i.e., the facial outline and internal features such as eyes, nose and mouth, were recombined). The results revealed that associative ROCs were more curvilinear for faces presented upright, but more linear when inverted. Yonelinas et al., (1999) concluded that upright faces are encoded and retrieved as a single unitized configuration, whereas inverted faces are encoded as separate associated features. Importantly, the results also demonstrated that unitization was not limited to lexical stimuli, but could be encouraged to occur across stimulus materials.

Evidence of unitization has also come from source memory tasks. For example, Diana et al., (2008) used mental imagery to encourage unitization of object/colour associations. Here, unitization was encouraged by asking participants to imagine the object in the colour presented (e.g., the RHINO was GREEN because it was sick), and discouraged unitization by imagining the object and colour as separate entities (e.g., the RHINO stood by the GREEN dollar bill). Consistent with the findings from Yonelinas et al., (1999), familiarity estimates derived from ROC analysis were greater in the unitized condition compared to the non-unitized condition, suggesting that familiarity was able to support correct source judgements.

2.3.5. Unitization and the neural substrates of familiarity

Investigating conditions that allow familiarity to contribute to successful associative recognition is also of practical importance, given the vulnerability of recollection to ageing, disease and disorder. Importantly, there is some evidence from unitization studies demonstrating preserved associative recognition in the absence of recollection. In two separate associative recognition studies, for example, amnesic patients exhibited better than chance performance for pre-existing compound words (i.e., ‘blackbird’ or ‘fireman,’ Giovanello, Keane & Verfaellie, 2006) and completely unrelated word pairs that were encoded with compound definitions (i.e., Quamme et al., 2007). Critically, the associative recognition performance in both studies was related to increased estimates of familiarity (e.g., increased Know responses observed by Giovanllo et al., 2007; and familiarity estimates derived from ROC analysis by Quamme et al., 2007), suggesting unitization may provide a powerful method for improving associative recognition among those with recollection deficits.

The observation of preserved associative recognition among amnesic patients also has important implications for our present understanding of how familiarity and recollection are supported by the Medial Temporal Lobe (MTL). To reiterate from Chapter 1, specific neurobiological models (i.e. Aggleton & Brown, 2006; Eichenbaum Otto & Cohen, 1994) highlight the dissociation of familiarity and recollection within MTL. According to these models, the hippocampus is responsible for the associative binding of item information with the contextual information associated with that item. By contrast, the individual features that comprise an item are believed to be supported by subcortical structures and in particular the Perirhinal Cortex (PRc).

To account for the preserved associative recognition among amnesic patients, another more recent neurobiological model has been proposed. The Binding of Items and Context (BIC) model (Eichenbaum et al., 2007; Diana et al., 2007) implicates three main substructures within the MTL, each responsible for the storage and retrieval of different types of information (rather than simple one-to-one mapping of recollection and familiarity). According to the BIC model the perirhinal cortex (PRc) receives and stores information about items that are to-be-remembered, whereas the para-hippocampal cortex (PHc) is responsible for information about the spatial context in which items are encountered. Item and context information is then bound within the hippocampus. The BIC model is based on the core assumptions of the DPSD model and is consistent in explaining data linking recollection with the hippocampus (Yonelinas, 2001; Brown & Aggleton, 2001, Diana et al., 2007; Norman and O'Reilly, 2003). In addition, the PHc is also believed to be critical for recollection, since it is responsible for context information. By contrast, the PRc which is responsible for item information should be capable of supporting familiarity in the absence of recollection.

The BIC model is important because it is able to account for unitization. For example, the preserved associative recognition demonstrated by amnesic patients can be accounted for because retrieval of item information is supported by the PRc; so long as items are sufficiently unitized. With regards to healthy participants, this prediction has been supported by fMRI research. Haskins et al. (2008), for example, showed that novel word pairings unitized using compound definitions resulted in an increase in activity within the PRc at study, compared to word pairs encoded using sentence frames. In a later study, Ford et al. (2010) observed activity in the PRc also increased at test as a function of unitization, further validating the BIC model.

Staresina and Davachi (2010), however, maintain that the function of the PRc remains unclear; reflecting either the processing of conceptually novel object information, or the fusion of components into a single entity. In order to clarify the function of the PRc, Staresina and Davachi (2010) attempted to investigate unitization of real object information by providing images of objects that were either intact or fragmented. Participants were asked to unitize these images by forming a single mental image of the objects with an associated colour. It was predicted that dividing the objects into various numbered fragments would vary the demand on unitization – i.e., a smaller number of fragments would be more easily unitized than a larger number of fragments. The results revealed that successful recognition of the object and colour information was highly correlated with PRc activation at encoding. The results, however, also showed that the posterior visual cortical region, but not PRc, was sensitive to levels of fragmentation. According to Staresina and Davachi (2010), object unitization may occur at processing stages 'downstream' from processing related to the PRc. The Staresina and Davachi study, however, conceptualised unitization as creating a perceptually intact object, as opposed to the creation of a novel conceptual representation. Currently it is unclear wither the PRc is modulated in a similar manner by perceptual and conceptual demands.

The effects of unitization have also been examined in animal studies[2]. For example, Sauvage et al., (2007) examined unitization using rats, predicting that hippocampally lesioned rats (resulting in severely impaired recollection) would rely on familiarity to make successful associative recognition judgements. Stimuli consisted of household odours (including lemon, thyme and cumin) mixed into a digging medium (woodchip, beads or sand). Results from adapted ROC analysis showed that lesioned rats, compared to healthy controls, demonstrated significantly reduced estimates of recollection but increased estimates of familiarity. The results also revealed that no overall performance differences were observed between the two groups, suggesting that controls and lesioned rats performed the experimental task with similar levels of associative

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[2] Animal studies have the advantage of allowing one to selectively lesion parts of the animal brain in a systematic way to investigate neural function.

recognition, albeit using different strategies. Sauvage et al., (2007) noted that their results do not provide direct evidence that the increase in familiarity observed for lesioned rats was a result of an increased tendency to unitize odour and medium (i.e., lemon-smelling wood chip), although the results are consistent with fMRI studies demonstrating similarly preserved associative recognition in patients with selective lesions to the hippocampus (Quamme et al., 2007; Giovanello et al., 2006).

2.3.6. The domain-dichotomy hypothesis

Importantly, unitization may not provide the only explanation of preserved associative recognition exhibited by those with recollection deficits. According to the domain-dichotomy hypothesis (Mayes et al., 2007), the relationship between pairs of items determines the contribution of familiarity and recognition during retrieval. Preserved retrieval of item, intra-item (integrated features of a single stimulus) and within-domain inter-item (e.g., face-face, word-word pairs) associative information has been observed when no attempt has been made to manipulate unitization. However, those same patients demonstrate impaired between-domain (e.g., face-word) associative recognition (Vargha-Khadem et al., 1997; Mayes et al., 2004). These findings have led some to suggest that although unitization may occur under limited circumstances, it is unlikely to provide a general explanation of familiarity during associative recognition (Mayes et al., 2010). According to Mayes et al., (2007) and Montaldi and Mayes (2010), within-domain associations will be represented by overlapping populations of neurons within the PRc, where cortical circuits form representations that can then be used to discriminate familiar from unfamiliar stimuli. In contrast, between domain associations do not converge until the hippocampus, where they are bound by pattern-separating algorithms and require recollection to be retrieved as a pair. The neuropsychological evidence providing support for domain dichotomy theory should be treated with caution because no attempt was made to prevent participants from unitizing information (Quamme et al., 2007).

Similarly, behavioural support for the domain dichotomy theory with healthy participants is mixed. For example, Bastin et al., (2010) observed greater reliance on familiarity for within-domain (face-face) pairs compared to between-domain (face-name) pairs. However, another study by Harlow et al., (2010) found that between-domain pairs elicited greater discrimination accuracy and higher levels of familiarity than within-domain pairs. A possible explanation put forth by Harlow et al., (2010) is that between-domain pairs were more robustly unitized than within-domain pairs. Without any manipulation of unitization, however, it is unclear whether or not unitization is more likely to occur for one domain over another, although evidence from source recognition experiments suggests that unitization can occur between stimulus domains (see Diana et al., 2008). Regardless, it is clear from the Harlow et al., (2010) study that the way stimuli are combined can influence the contribution of familiarity, suggesting that encoding strategy rather than stimulus similarity is more important for encouraging familiarity.

2.3.7. Current issues with unitization research

Although more direct experimental questions will be made explicit in Chapter 4, it is worth reviewing here the main issues with the current unitization literature. For example, it is clear that the majority of the evidence in support of unitization is dependent on the DPSD interpretation of ROCs. To be clear, unitization has been critical for the DPSD model to account for curvilinear ROCs within associative and source memory tasks. This is problematic, given that the DPSD model is likely to be updated or abandoned in favour of a more accurate model, which could force a revision of unitization research. In addition, the reliance on ROC data is also problematic, given the highly model specific nature of interpreting ROCs. As mentioned earlier, curvilinear ROCs observed for associative and source recognition tasks have been interpreted as reflecting a continuous recollection signal rather than familiarity. For example, in the Mickes et al. (2010) study described in Section 2.2.2., stimuli repeated multiple times increased the curvilinearity of the ROC and increased the proportion of ‘Remember’ (indicating an increase in recollection) responses. By contrast, unitization was ruled out because the proportion of Know responses (i.e., familiarity) did not differ between stimulus repetitions. It is important to note, however, that Mickes et al., (2010) did not directly manipulate unitization and therefore their study cannot definitively rule out a unitization account of the observed curvilinear ROCs. Instead, the Mickes et al., (2010) study demonstrates the problem with relying on curvilinear ROCs to support unitization. In order to resolve this issue, Parks and Yonelinas (2007) have suggested that the complex relationship between recollection and familiarity must be demonstrated by other methods of analysis and tasks.

In the current thesis, we provide an alternative assessment of unitization that does not rely on ROC analysis – namely, by investigating the neural correlates of familiarity and recollection. If familiarity can be encouraged for novel associations, a selective modulation of the neural correlate of familiarity would be predicted in the absence of any significant change in the neural correlate of recollection. Of course, investigating unitization using the neural correlate of familiarity is also open to the circularity problem posed in Section 2.3.4. To this end, we only employ methods for manipulating unitization that have previously been demonstrated to carry costs – i.e., the mental imagery and lexical manipulations. In Chapter 4, we come back to unitization by reviewing the current ERP literature and highlighting where there is need for further investigation.

2.4. Summary

This chapter has described what is currently known about the contribution of recollection and familiarity towards successful associative retrieval. First, the chapter began by arguing that associative recognition memory is important to understanding episodic memory and more specifically, the memory deficits caused by cognitive decline. Traditionally, retrieval of associative information is believed to be heavily dependent on recollection, although exactly how recollection operates has been a source of controversy. The second part of this chapter discussed in detail the debate surrounding whether recollection should be characterised as a thresholded or continuous process, with recent evidence suggesting that a more nuanced some-or-none account may be more accurate. According to the some-or-none account, recollection can fail on a sub-set of trials (i.e., is thresholded) but is variable when successful. Lastly, this chapter discussed the evidence supporting the view that familiarity may contribute to successful associative recognition when individual items become unitized.

The overall goal of the current thesis is to provide a more accurate understanding of how recollection and familiarity contribute to the retrieval of associative information. Firstly, the thesis will use ERPs to investigate whether the underlying neural signal supporting recollection is also thresholded by replicating the novel source paradigm developed by Harlow and Donaldson (2013). Secondly, ERPs will be used to investigate whether unitization allows familiarity to contribute to the retrieval of novel associations, thereby providing alternative evidence beyond ROC studies. Before discussing the precise experimental chapters, the thesis will first describe the ERP method (Chapter 3) before reviewing studies that employ ERPs to investigate episodic recognition (Chapter 4).

Chapter 3

Event Related Potentials (ERPs)

The purpose of this chapter is to provide a general overview of Event-Related Potentials (ERPs) from the level of a single neuron to the common procedures used to extract and analyse electrical activity across the scalp. The chapter will also cover a range of topics involved in collecting and understanding ERPs, including the recording, processing and interpretation of ERP signals. The overall aim is to demonstrate the advantages and limitations of using ERPs to investigate particular questions concerning cognitive neuroscience. First, however, we begin by providing an operational definition of ERPs.

An ERP is the averaged neural response to a specific set of external or internal events (e.g., stimuli, responses or decisions). ERPs are derived from the electroencephalogram (EEG), which is measured by placing an active and ground electrode on the scalp, allowing changes in electrical potential to be recorded over time. Since the neural activity associated with specific cognitive events is initially embedded within the global EEG signal (Dawson, 1947), specific data averaging procedures are employed to extract the signal of interest. The averaging procedure operates by first dividing the EEG into epochs (segments of EEG over a certain time period) time locked to the onset of an event. Averaging over many trials reduces any EEG activity not related to the signal being studied (see section 2.3.1 for more detail). Grand average ERPs are then formed by averaging ERPs elicited by a particular stimulus across participants, thereby reducing individual participant variation and enabling examination of common neural activity.

ERPs are an incredibly useful tool for investigating cognitive processes and provide a continuous and non-invasive measure of neural processing. Typically, ERPs are recorded using stimulus locking, revealing the activity elicited by the initial onset of the stimulus, the response to the stimulus and any post response activity. ERPs are considered the ‘gold standard’ for high temporal resolution imaging providing information about neural events on a millisecond by millisecond basis. The high temporal resolution obtained by ERPs offer a clear advantage over alternative non-invasive neuroimaging techniques such as functional Magnetic Resonance Imaging (fMRI) or Positron Emission Topography (PET) that measure changes in the haemodynamic response (lasting over several seconds). In common with other neuroimaging methods, ERPs are not suitable for answering all questions concerning neural processes. Identifying the exact source of neural activity within the brain, for example, is not possible due to the poor spatial resolution of the ERP method. To fully appreciate the advantages and limitations of interpreting ERP data, a clear understanding of the neural origins of the ERP signal is required.

3.1. The neural origin of ERPs

Neuroscience is a specific branch of biological science concerned with investigating the fundamental properties of the nervous system. According to the ‘neural doctrine’ (Cajal, 1909), the neuron is considered the basic structural and functional unit of the central nervous system. The basic structure of the neuron comprises a cell body (or soma) dendrites and an axon (see Figure 3.1). The cell body is where protein synthesis occurs and contains the nucleus of the cell. The dendrites are filaments that arise from the cell body and branch out many times, allowing for the reception of thousands of electrical inputs from other neighbouring neurons. The axon, by contrast, is a single projection that extends from the cell body and is responsible for carrying nerve signals away from the cell body.

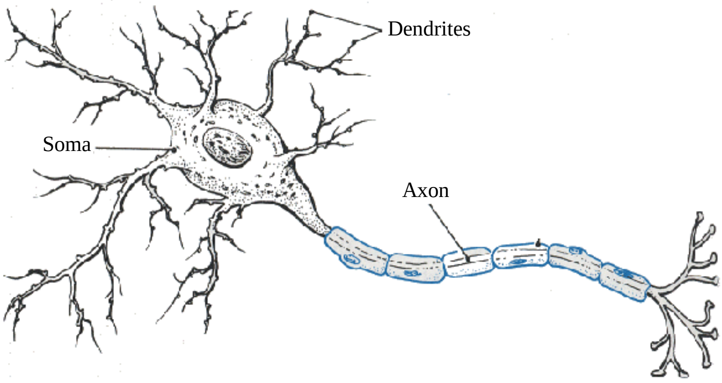

Figure 3.1: Structure of a neuron with the soma (cell body), dendrites and axon (adapted from Carlson, 1992).

Although the primary form of communication between neurons is through action potentials, these signals are almost impossible to detect using scalp electrodes. Instead, the source of the electroencephalogram originates from Post-Synaptic Potentials (PSPs). PSPs occur when neurotransmitters are released from the synapse of the presynaptic neuron and bind to receptors on the postsynaptic terminal. This neurotransmission causes ion channels on the postsynaptic cell membrane to open or close, resulting in a continuous change in the potential across the cell membrane. PSPs typically last hundreds of milliseconds and are confined to the dendrites and the cell body. When a PSP occurs within a single neuron, the difference in electrical potential between the dendrites and cell body generates a tiny electrical dipole (i.e., an oriented flow of current). Detecting the electrical activity generated by a single neuron is impossible using scalp electrodes; it is only the fact that PSPs summate that allows them to be measured from a distance. For PSPs to summate thousands of dipoles must be activated at the same time and share a similar spatial orientation (known as an open field: see Figure 3.2). Open field configurations exist where neurons are organised into layers such as the cerebral cortex, whereby neurons share the same orientation, perpendicular to the cortical surface (Ruggs & Coles, 1995). By contrast, neurons in other parts of the brain, such as sub-cortical structures, do not share a similar spatial orientation (i.e., a closed field: see Figure 3.2) and therefore the positivity/negativity of a dendrite may be aligned with the positivity/negativity of cell body of a neighbouring neuron making it impossible to detect activity from distant recording electrodes.

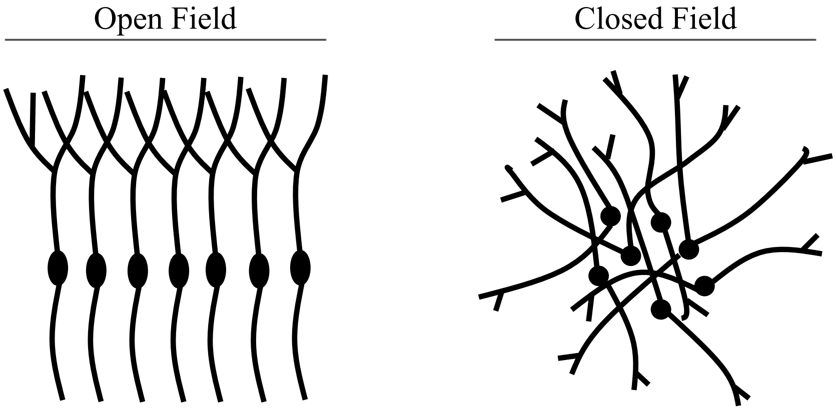

Figure 3.2: An example of the different spatial configuration of neurons, illustrating open (left) and closed (right) fields (adapted from Allison, Wood & McCarthy, 1986).

There are certain caveats about the position and orientation of dipoles that must be considered when recording from scalp electrodes. First, a lack of any significant ERP differences between experimental conditions does not necessarily imply an absence in differential processing within the brain. Any differential neural activity between conditions could be generated by populations of neurons with a closed field and therefore undetectable using scalp electrodes. Additionally, the observed spread of voltages across the scalp depends on both the position and orientation of the generator dipoles within the cortex, as well as the shape and levels of resistance of the different constituents of the head (including the brain, meninges and skull). When dipoles are embedded within a conductive medium such as the brain, the electrical current will spread out until it reaches the surface. Although the brain and meninges are excellent conductors of electricity, the skull is not. Consequently, the voltage field will spread laterally when deflecting off the base of the skull making it relatively difficult to ascertain the neural generator of the observed EEG signal from the scalp. To be clear, ERPs generated by one part of the brain may lead to substantial voltages recorded at different locations on the scalp, weakening the ability to make inferences about the number and location of specific neural generators responsible for the scalp recorded signal (Coles, 1998; for more detail see Section 3.4.2).

3.2. Recording ERP data

3.2.1. Active electrode

Voltage refers to the potential for electrical charges to move between two locations, and EEG is measured as voltage between two electrodes. The EEG is a fluctuating electrical potential on the scalp detected by surface recording electrodes. Changes in voltage are always measured by recording between an active and reference electrode, plotted as a function of time. Each active electrode will produce a separate waveform, typically plotted with time on the X axis and voltage on the Y axis (see Figure 3.3). The waveform consists of a mixture of brain activity (signal) between the active and reference electrode, but also includes non-neural background activity commonly referred to as noise. To isolate noise, a third ground electrode is used during EEG recording. To demonstrate: an active electrode (Active) is placed on the site of interest, a reference electrode (Reference) is placed on a selected location on the scalp and a ground electrode (Ground) is placed on another location (usually the head). Activity from these electrodes is then recorded by a differential amplifier, magnifying the difference in activation between the pairs of electrodes [(Active-Ground) - (Reference-Ground)]. Activity measured by the ground electrode will be removed by the subtraction, leaving only the voltage between the two scalp electrodes of interest.

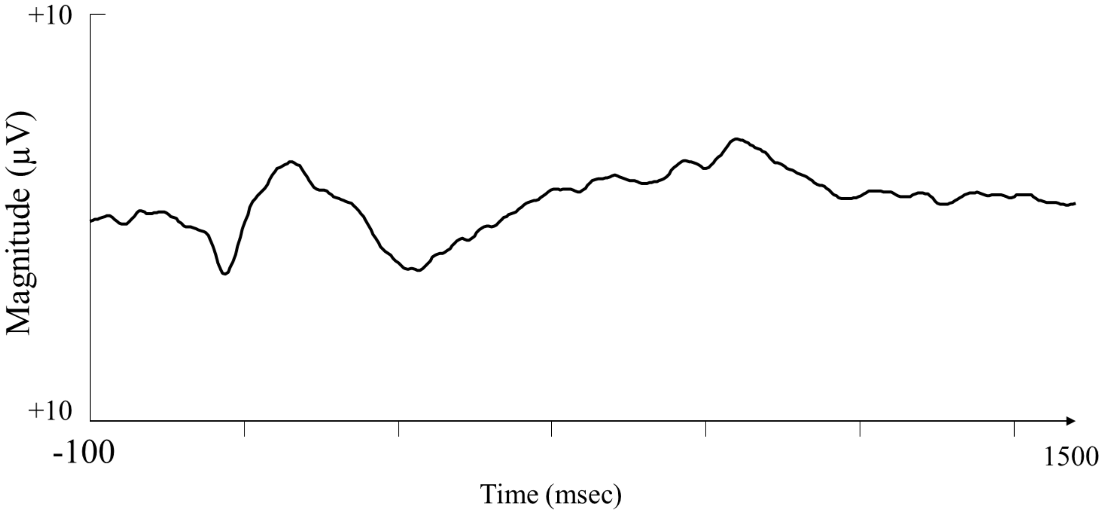

Figure 3.3: Illustration of an ERP waveform at a single electrode. Time is plotted on the X axis, while voltage is plotted on the Y axis.

During typical ERP experiments, voltages are recorded at different locations using multiple active electrodes. The most common and widely adopted arrangement and naming classification for scalp electrodes is the International 10-20 system (Jaspers, 1958; see Figure 3.4). The International 10-20 system recommends that electrodes are placed at 10 and 20 per cent points along the lines of latitude and longitude across the scalp. The system is based on the assumption that the skull is symmetrical and has the advantage of exploiting certain features of the skull (including the nasion & inion) to position electrodes over the scalp. Each electrode name begins with 1-2 letters denoting a general brain region (FP = Frontal Polar, F = Frontal, FC = Frontal Central, C = Central, CP = Central Parietal, P = Parietal, O = Occipital and T = Temporal). Every name ends with a number indicating the distance from the midline; with odd numbers for the left hemisphere, even numbers across the right hemisphere and Z (zero) for midline electrodes. Across laboratories the number of electrodes used during recording is variable. Depending on the effects being investigated, relatively few electrodes will be sufficient, while other effects may require high density arrays – i.e., typically comprising of 256 electrodes. Although a larger number of electrodes will result in greater spatial resolution, the methods of applying high density arrays may result in poorer signal quality and lower statistical power (Kappenman & Luck, 2011). In the current thesis, an intermediate number of electrodes (64) was used throughout.

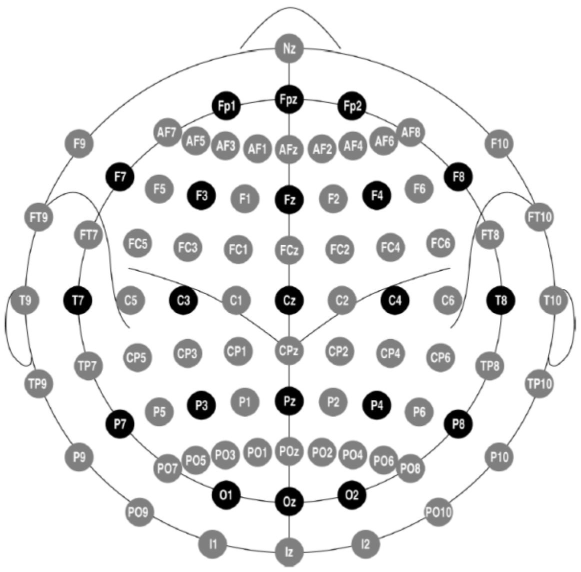

Figure 3.4: The International 10-20 system: position of electrodes placed across the scalp. The nose indicates the front of the head. Black circles show the original 10-20 system and the grey circles show the positions introduced with the 10/10 system (adapted from Oostenveld & Praamstra, 2001).

3.2.2. Reference electrodes

The EEG signal recorded at any particular location will reflect the electrical activity from both the active and reference electrodes. The activity detected by the reference will therefore contribute equally to all of the active electrodes. The reference electrode should ideally be placed on a neutral site that does not bias one hemisphere over another. Many locations of the human body serve this function including the tip of the nose or toe, the mastoid bones and the ear lobes, but no one location is more neutral than any other. One key consideration needs to be that the site selected is comfortable for the participant; moreover, the choice of reference must be consistent across experiments/laboratories to facilitate comparison of ERP data.

Of the many potential reference sites available, the mastoid (the bony protrusion behind the ear) is the most common. To avoid any hemispherical bias a ‘linked mastoid’ is typically used, whereby recordings are taken from the left mastoid electrode and averaged offline with the right mastoid. The linked mastoid prevents particular problems of physically linking both reference electrodes during recording. If impedances, for example, were to vary between physical linked mastoids during recording, the linked reference would become hemispherically asymmetrical as the flow of electricity would move towards the electrode with the lowest impedance (Miller et al., 1991). Although the linked mastoid is the most common method of referencing it is worth noting that there are other options such as the averaged reference, and selection of an appropriate reference site is still a common source of contention among researchers (Dien, 1998). To facilitate comparison with other ERP studies regarding episodic memory, however, the linked mastoid reference is adopted throughout this thesis.

3.2.3. Amplifying, filtering and digitising the signal

Before the EEG signal is processed the recorded potentials must first be amplified, digitised and filtered. To allow analogue to digital conversion the signal for each electrode is amplified by a separate EEG recording channel and the amplifier gain (amplification factor) is adjusted to encompass the entire range of the analogue-to-digital (A/D) converter. Although amplification of the signal prevents the loss of information during digitisation, care must be taken when amplifying the signal, because any amplified voltage that exceeds the A/D converter range can lead to signal saturation. The saturation of the signal may also occur with slow, systematic changes in electrode impedance (e.g., as is caused by increased temperature in the recording chamber) resulting in voltage ‘drift’. To control for large drift in voltage, high pass filters are applied during EEG recording that attenuate low-frequencies and pass high frequencies, serving to maintain the amplified signal within the input range of the A/D converter.

The amplified and filtered data is digitised and stored as a series of discrete time points called samples. The sampling period is the amount of time between consecutive samples (e.g., 4ms) and the sampling rate is the number of samples taken per second – typically ranging from 200-250Hz. According to the Nyquist theorem, all information in an analogue signal can be captured digitally if the sampling rate is at least twice as great as the highest frequency in the signal (see Figure 3.5: right panel). An insufficient sampling rate may cause aliasing, whereby high frequencies appear as artefactual low frequencies in the digitised waveform (see Figure 3.5: left panel). Most modern amplifiers include low-pass filters that attenuate high frequency signals before digitisation, thereby avoiding sampling artefacts. Nonetheless, the subsequent EEG data will still comprise many other sources of noise as well as the signal of interest. To isolate this signal associated with specific cognitive processes, further off-line processing is required.

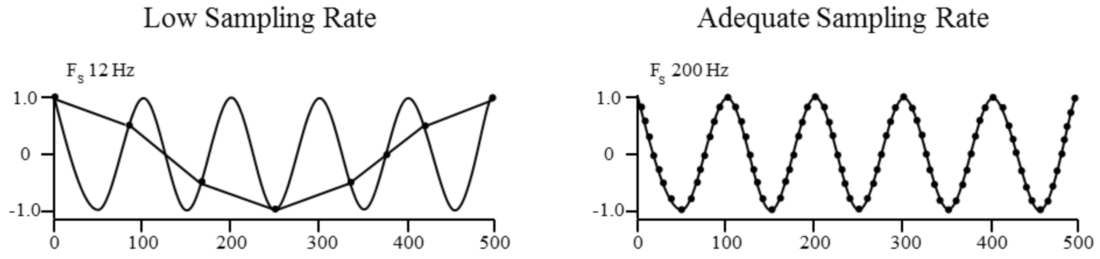

Figure 3.5: The diagram illustrates results the effects of different sampling rates during analogue-to-digital conversation. The left side panel represent the effect of aliasing due to low sampling, whilst the right side panel demonstrate the effect of selecting an appropriate sampling rate.

3.3. Data processing: From EEG to ERP

Recorded EEG comprises a mixture of the specific neural signals of interest and noise (i.e., general background EEG). Sources of EEG noise include artefacts associated with the eye balls (i.e., ocular artefacts), voltage drift and muscle activity, all of which must be minimised if the ERP signal of interest is to be clearly identified. The ERP signal is often very small and is easily overshadowed by larger changes in voltage generated by other concurrent brain activity and EEG artefacts. For this simple reason it is necessary to employ signal processing techniques to extract the signal from the background noise.

3.3.1. Averaging

As previously discussed in the introduction to this chapter, the ERP signal is extracted from the general EEG recording by averaging together EEG epochs time-locked to specific events of interest. There are, however, important implications of averaging that must be taken into consideration. Averaging assumes that the ERP signal has stable characteristics such as identical waveform morphology, amplitude and latency across trials. The signal of interest is generally very small compared to the background noise and as a result EEG typically has a poor Signal to Noise Ratio (SNR). When the time-locked event of interest is more highly correlated with the neural signal of interest than with the background noise, averaging will attenuate the noise and retain the signal; thereby improving the SNR. In principle, the SNR increases as the square root of the number of trials averaged together (Perry, 1966). Consistent with many modern memory studies, this thesis required at least 16 good trials from each participant per condition to form an ERP, and any participant who did not provide 16 trials was excluded from the overall analysis.

Often neural activity is not perfectly correlated with the event of interest. In practice ERPs very rarely demonstrate stable characteristics across individual trials and the same cognitive process may not be engaged to the same degree for every trial. This problem can be moderated by simultaneously gathering behavioural responses and using these to exclude trials with incorrect responses. Even for the remaining correct trials, however, changes due to fatigue, boredom or lapses in attention will also introduce variance during the recording session. It is important to consider these problems when designing ERP experiments and interpreting results and as a result it is widely considered good practice to limit the amount of time an experiment takes to complete as well as providing opportunities to take breaks.

Variability can also be introduced with temporal differences between trials. The epochs used to form ERPs are generally time-locked to a particular event of interest, such as the onset of a stimulus, to ensure that the cognitive process under examination is present in each trial. The amplitude peak associated with a particular cognitive process may, however, occur at different times across trials. When this ‘latency jitter’ occurs, the averaged signal will display a wider temporal distribution and smaller peak amplitude compared to the peaks elicited by individual trials (Rugg and Coles, 1995: see Figure 3.6). To mitigate latency jitter, area amplitude measures can be used which are less susceptible to latency variability (although amplitude may still be reduced). The area under an averaged ERP component, for example, is equivalent to the average area of ERP components from individual trials. Area based measures, such as the mean voltage deflection over a particular time interval, are therefore almost always superior to peak-based measures. When using area based measures, however, it can be difficult selecting the time interval that accurately captures the component of interest, especially in the context of distinct but overlapping components.

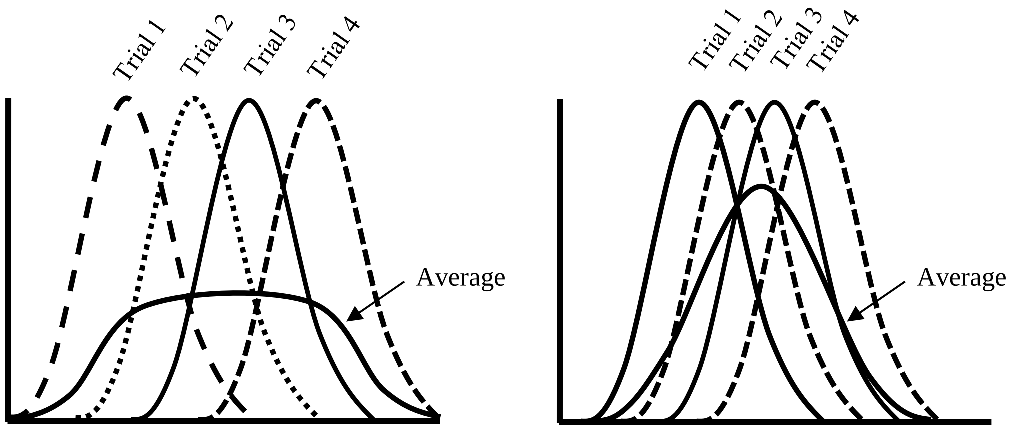

Figure 3.6: The diagram illustrates the effect of latency jitter. Each panel shows individual trials and an averaged waveform. Although the same individual trial waveforms are illustrated in the left and right panels, the effect of latency jitter is illustrated in the left panel, distorting the peak amplitude of the average waveform (adapted from Luck, 2005).

In practice, many sources of noise do correlate with the event of interest and will not be attenuated to the same degree by averaging. Participants may blink or move their eyes, for example, every time a stimulus is presented. Any systematic sources of noise should ideally be identified, and compensated for, when designing an experiment or directly removed from the recorded data. There are multiple methods, for instance, that can be used to eliminate or compensate for noise associated with eye movements and blinks (discussed in detail in the following section). In general, an ERP component should be viewed as a record of all electrical activity correlated with an event and must be interpreted within this context.

3.3.2. Ocular artefacts

One of the most common and systematic sources of noise contained in the EEG are generated by eye blinks and eye movements. Ocular artefacts can occur from muscle movements caused by eye blinks, but may also arise from the electrical gradient of the eye, which is positive at the front and negative at the back. As a result, eye movements can heavily distort EEG recordings. Both eye blinks and eye movements produce relatively large changes in potential at the scalp that can often mask smaller changes related to neural activity – especially at anterior scalp locations. Eye movements are typically measured with Electro-OculoGram (EOG). The EOG records differences in electrical potential between electrodes placed above and below one eye (Vertical EOG or VEOG) and between electrodes on the outer canthi to the left of the left eye and right of the right eye (Horizontal EOG, or HEOG).

There are three main methods of accounting for and removing ocular artefacts. First, one may limit the amount and severity of eye movements during the critical epochs by asking participants to constrain their blinks to set gaps between trials. Although effective, this method is often difficult for certain populations of participants including the elderly, the young and those who wear contact lenses. Additionally, asking participants to monitor their eye movements may introduce a secondary cognitive load that could potentially influence the EEG recording (Verleger, 1991). A much more common approach is to control eye movements indirectly by focusing the participants gaze onto the centre of the screen during critical epochs (using fixation crosses) and presenting stimuli on the screen within the focal area.

Secondly, researchers can identify and discard contaminated trials with excessive eye movements. Those trials that remain should then be free of ocular artefacts without introducing physical or cognitive noise associated with asking participants to monitor and suppress their own eye blinks/movements. One particular disadvantage of this approach, however, is the possibility of eliminating a large number of trials, which may severely reduce the overall power to detect a significant effect. Another issue is the relative difficulty in identifying excessive eye movements in every trial, resulting in a reduced and unknown contamination of the signal in the remainder of the trials.

The third and more common method is to correct for ocular artefacts rather than reject them. This approach allows for the retention of trials that contained ocular artefacts rather than rejecting trials. The method also avoids the issues associated with the requirement to suppress eye blinks/movements as previously discussed; for these reasons, the correction method is implemented in the current thesis. To be more specific, the correction procedure employed in this thesis applied a modelling technique that computes a regression coefficient for each electrode, allowing for a percentage of EOG activity to then be subtracted from every electrode. In most cases the subtraction will be more pronounced over the anterior scalp locations and less so across the central and parietal scalp areas. One potential limitation, however, is that eye electrodes detect neural activity (recorded from ocular electrodes) and subtraction of this mixed signal may lead to elimination of genuine effects. It is therefore important to take into consideration the advantages and disadvantages of each method for reducing and compensating for ocular artefacts when designing and implementing ERP experiments.

3.3.3. Saturation, voltage drift and additional artefacts

In addition to ocular artefacts, noise from other sources can also lead to contamination of the EEG recording. Slow voltage drifts in the signal, for example, are caused by changes in skin impedance brought about by rising temperatures in the recording chamber and slight changes in electrode position as a result of participant movement. It is important to bring down impedances before the experiment begins and to ensure that the participant remains as still as possible. Although high pass filters applied during recording go some way to attenuate these voltage drifts, they may still be evident in the recorded data. Voltage drift can be so large as to mask the effects of interest or even cause the signal to saturate by exceeding the input range of the digitiser. Although there are several methods of detecting drift, the current thesis uses a drift algorithm that identifies and eliminates any epochs in which one or more active electrode varied in amplitude by 75µV between the first and last data-point, over a period of 2000ms.

More high frequency sources of noise can be introduced by muscle activity, tension or surrounding electrical equipment. As with low frequency noise, the effects of high frequency noise can be reduced with low pass filters. Additionally, averaging techniques used to form ERPs are also effective in reducing the effects of high frequency noise. In some instances, however, the effects of high frequency noise still remain and it is important, as was done in the current thesis, to visually inspect the recorded EEG data for excessive muscle movement and reject contaminated epochs where necessary.

Visually inspecting the to-be-averaged epochs for other sources of noise such as signal saturation or recording artefacts is an effective way of eliminating additional noise from the data. Commonly, however, a final artefact rejection procedure is typically applied before averaging which systematically examines epochs of interest for large artefacts. For instance, epochs containing any active electrode that deviated by more than a pre-defined amount, at any particular time during the epoch, will be rejected prior to forming ERPs.

3.4. Interpreting ERPs

Once the signal of interest has been extracted and artefacts have been minimised, the resulting waveform must be interpreted within the context of the initial experimental hypothesis. Interpreting ERP waveforms in terms of the functional properties of an underlying cognitive process is fraught with difficulty, but done correctly, ERPs can provide invaluable insight. In the next section, the problems of interpreting ERPs are outlined and potential solutions are described. What emerges is a complex picture of what can and cannot be inferred from ERP data.

3.4.1. ERP components

Very broadly, an ERP component can be defined as a voltage deflection produced when a specific neural process occurs within a particular region of the brain (Luck, 2005). An ERP ‘component’ is therefore defined as part of the waveform with a specific scalp distribution, reflecting the activity of a distinct underlying neural population, with a specific relationship to experimental variables, indicating a particular cognitive function related to the activity of the distinct neural population (Donchin, Ritter & McCallum, 1978). There are three general categories of ERP components, including: i) exogenous components – early sensory activity generated by the presence of a stimulus; ii) endogenous components – reflecting task dependent neural processes, and iii) motor components – activity generated by the preparation and execution of a motor response. Although ERP components can be systematically defined and categorised, in practice, identifying them is often less than straightforward.

Identification of ERP components was originally based on the polarity and latency of particular peaks evident in the average ERP waveform. Characterising an ERP component in terms of the particular peaks contained in an averaged waveform was, however, found to be unreliable because it is unclear whether the peak reflects the activity of a single component or the summation of several components. To demonstrate, the P300 (the P indicating a positive polarity and 300 describing when the peak is maximal) elicited by unpredictable events was later found to be the sum of the P3a and P3b components – each with their own distinct timing and scalp distribution (Comerchero & Polich, 1999). Similarly, defining a peak in terms of polarity is also problematic, because polarity will manifest as either a positive or negative deflection depending on what end of the dipole is being measured. A component defined in terms of polarity could therefore be positive or negative depending on the relative position of the active electrode. Polarity is also influenced by other known factors, such as the location of the reference electrode and unknown factors including the particular cell location where neurotransmission is occurring and whether neurotransmission is excitatory or inhibitory. Although identifying ERP components in terms of peaks is still practised, ERP research on the whole has tended to shift away from this approach.

A more common approach, and the one adopted in this thesis, is to isolate ERP components using the subtraction method. An ERP component can be defined as the difference in activity between the ERPs elicited by two carefully selected experimental conditions; the resulting difference is typically referred to as an 'effect.' The subtraction isolates the cognitive component of interest while minimising the contribution of other components that are common to both conditions. During recognition memory paradigms, in theory, identification of an encountered stimulus will engage attentional, perceptual and many other processes, as well as those directly involved in recognition. These overlapping processes may be accounted for by comparing the ERP elicited by correctly identifying an encountered stimulus to the ERP elicited by a baseline condition (this is typically an unstudied item during recognition studies). The baseline must be selected such that it will engage many of the same processes as the target, but not the critical process of interest, and is therefore an effective way of isolating the activity related to successfully recognising a target stimulus. Subtraction therefore provides a functional definition of a component as it is based only on the relationship between experimental variables.

There are, however, two important caveats to consider when using subtraction waveforms. First, the subtraction approach assumes that cognitive processes are additive and no not interact – i.e. the pure insertion principle (Donders, 1968). In reality, however, the principle of pure insertion is likely to be violated when the latency of a shared cognitive process is altered when additional processes are engaged in one condition. Importantly, however, violation of the pure insertion principle is not specific to ERP research and can occur in other neuroimaging techniques as well as behavioural methods (see Friston et al, 1996). Secondly, difference waveforms contain more noise and will have a lower signal-to-noise ratio than those of the constituent ERP waveforms. If the two ERP waveforms included in the subtraction have similar noise levels, the noise in the difference wave will be doubled (Luck, 2005). Regardless, so long as the ERP experiment is designed with care, both valid and reliable conclusions about specific cognitive processes can still be made (Picton et al, 2000).

In this thesis, the subtraction approach was adopted to measure the components of interest. Furthermore, the ERP effects were quantified by averaging the mean amplitude differences between ERP waveforms over specific latency periods consistent with the approach used in previous research in the area of memory.

3.4.2. Making inferences from ERPs

Once an ERP effect or component has been isolated from the general EEG recording it must then be interpreted. ERPs generally allow for three different types of inferences to be made about underlying cognitive processes; their timing, functional equivalence and degree of engagement. These three types of inferences are based on ERP differences in time course, scalp distribution and amplitude, respectively. Such inferences are made based on the assumption that invariant patterns of neuronal activity are correlated with a specific cognitive process. Importantly, since ERP data is inherently correlational in nature, one cannot infer that the neuronal activity is necessarily critical for the process to occur. Instead, differences in ERP effects or components indicate differential engagement of cognitive processes.

3.4.2.1. Inferences from latency

The high temporal resolution of ERPs, relative to other neuroimaging techniques, makes ERPs especially sensitive to changes in the time course of specific cognitive processes. One particularly powerful temporal measure is on-set latency. The onset latency can be measured by comparing two waveforms elicited by different conditions. The point in time when the waveforms begin to diverge can then be used as a measure of when the brain is able to distinguish between experimental conditions. One main advantage of using this approach is that it is component-independent – in other words, it is the difference between waveforms that is critical, regardless of the specific component driving the effect. The relationship between the temporal properties of an ERP effect and the underlying neural process is, however, far from simple.

One limitation of making inferences from latency information is that any ERP difference can only be treated as an upper bound on the time that cognitive processes begin to diverge. The specific point in time when ERP waveforms begin to diverge does not necessarily reveal when experimental conditions were initially distinguished at a neural level. To be clear, it is entirely plausible that early downstream processes (associated with neural activity that is not visible from the scalp) distinguished between the experimental conditions long before the ERP was sensitive enough to detect a difference. ERPs can therefore not be used to claim that an effect occurred at a particular time; simply that a difference was evident by that time.

3.4.2.2. Inferences from scalp topography

ERP effects can also be interpreted in terms of the voltage distribution across the scalp. If differences in the experimental effect reveal distinct topographic distributions across the scalp (provided the effect is significant after rescaling: as described below, see McCarthy and Wood, 1985), then it can be assumed that different neural generators - or at the very least differential engagement of a common set of generators - are responsible. The inverse problem, however, prevents specific identification of the cause of different scalp topographies. A specific scalp topography, for example, could be generated by either a relatively small number of focal dipoles or by a very large and widely distributed number of dipoles. The inverse problem means that it is mathematically impossible to ascertain the correct source of electrical activity, given that a single scalp distribution can arise from an infinite number of dipole configurations (Helmholtz, 1853). Although the inverse problem rules out any concrete conclusions about exactly what neural generators are responsible for a given ERP effect or component, differences in topographical distribution nonetheless definitively indicate the engagement of partially non-overlapping neural populations.

3.4.2.3. Inferences from source location

As previously discussed, the inverse problem severely limits the ability to identify the neural generators responsible for the electrical activity measured from the scalp. Although problematic, some attempts have been made to identify the source of neural activity recorded from the scalp (e.g., Koles, 1998; Ventouras et al., 2010; Mosher & Leahy, 1998). Source localisation algorithms are perhaps the most common method for attempting to identify the source of neural generators. These algorithms are mathematical models that attempt to satisfy a number of constraints (including the ability to reproduce the original scalp distribution), in order to estimate the likely source of the observed neural activity. A correct model may not always provide a perfect fit to the data because the noise inherent in the EEG signal will to some degree distort the observed distribution. Additionally, any model that correctly fits the observed distribution will be only one possible solution among many internal configurations that could also be responsible, (i.e., as per the inverse problem). Thus, to more precisely localise the source, additional external constraints may be added to these models, such as specifying a particular spatial location on the cortical surface based on structural imaging data. Spatial constraints of this type should be viewed with caution, however, because not all activity detected by EEG is generated from the cortex. Although these algorithms allow researchers to interpret ERP effects (and components) in terms of their neural origin, they are often difficult to implement, complex in terms of the number of constraints that need to be satisfied, and prone to type 1 errors. Consequently, it is imprudent to rely on ERPs alone to address questions concerning the neuroanatomical generators of electrical activity.

3.4.2.4. Inferences from amplitude

Functional differences between experimental conditions can also be derived in terms of amplitude, even in the absence of any significant differences in scalp topography or timing. Amplitude differences between experimental conditions are typically interpreted as a quantitative difference in the engagement of a particular cognitive process. To be clear, amplitude differences can be used to infer that a particular cognitive process is engaged to a greater degree in one condition than another. Making an inference based on amplitude, however, should be interpreted with caution. For instance, changes in the engagement of a cognitive process across conditions must only be made when no measurable differences in scalp topography are observable; since qualitative differences in the distribution of ERPs reflect the operation of different cognitive processes across conditions.

Changes in amplitude elicited between experimental conditions can also occur in the absence of any change in signal strength of the underlying neural activity. For example, in practice, it is often difficult to distinguish whether difference in amplitude reflect differential engagement of the underlying cognitive process(es) or variation in the proportion of trials carrying an effect of constant amplitude (Wilding, 2000; Otten & Rugg, 2005; see Chapter 7). Differences in the proportion of trials carrying the signal suggest that variation in amplitude does not indicate that strength of an underlying cognitive process across conditions, but instead reflect variation in the probability of its engagement. Take for instance, the ERP left parietal old/new effect which is believed to reflect recollection of a previous study episode. During a source task one must recollect not only the target item but also the context within which the item was studied. ERP results from source memory paradigms often reveal greater amplitudes for the left parietal old/new effect for items with correctly identified sources compared to incorrectly identified sources (see Vilberg & Rugg, 2007; Wilding & Rugg, 1997; Wilding, 2000). Critically, however, the observed change in amplitude cannot simply be assumed to reflect greater strength in the cognitive processes that support recollection, given that the same strength could be evident for source correct and incorrect trials, with the difference being driven by the change in the proportion of trials that contain the signal. Despite clear differences in the theoretical conclusions that follow from these two possible interpretations, distinguishing between them presents a significant challenge to researchers (for unique solutions see Wilding, 2000, and Murray & Donaldson, in preparation). Thus, whilst differences in the amplitude of ERPs can be informative, it is important to rule out potential confounds that explain away the differences as an artefact of signal averaging.

3.5. Statistical analysis

The reliability of ERP differences is often characterised and assessed with inferential statistics (which is the approach adopted in this thesis). Within the ERP literature, the most common statistical technique for assessing the reliability of overall magnitude differences between ERPs is the repeated measures analysis of variance (ANOVA). In general, the ANOVA divides the variation contained in a data set into components related to the effect of interest (the difference in means between groups) and noise (within group variance), and tests whether the effect of interest can account for a significant amount of the variance. The ANOVA, however, is based on the assumption of sphericity; namely that all possible pairs of variables share equal variance. In practice ERP datasets routinely violate this assumption because nearby electrodes are almost always more correlated than distant electrodes. A common solution is to apply the Greenhouse-Geisser correction for non-sphericity (Jennings and Wood, 1976) which adjusts the increased probability of making a type 1 error (i.e., an incorrect rejection of the null hypothesis) by decreasing the degrees of freedom and increasing the p-value. The ANOVA therefore becomes more conservative.

Another feature of the ANOVA is that it calculates individual p-values for all factors which are entered into it. For the analysis of ERP data this can become a problem because the likelihood of detecting a significant effect will increase with the number of factors (i.e., increased family-wise error rate). In fact, with enough electrode sites, it is always possible to find a statistically significant difference between two conditions driven simply by random noise (Luck, 2005). Increases in the family-wise error rate can be avoided by collapsing irrelevant factors, and in ERP research this is achieved by dividing electrodes into factors that typically correspond to different spatial locations (i.e. frontal/central/parietal), hemispheres (left/right), and sites (superior/medial/inferior). Not only do these divided factors reduce the family-wise error rate, they also allow for better characterisation of the effects and guide follow up tests. In addition, it is also permissible to identify a component or effects of interest in advance, based on previous research, and compare magnitude differences only at specific relevant electrodes – providing an alternative way to minimise the family-wise error rate.

When significant amplitude differences are detected, it is initially unclear whether they arise from the greater engagement of an equivalent cognitive process or topographic differences caused by the engagement of distinct neural generators. Such uncertainty arises because changes in dipole strength are multiplicative – changes in electrical activity generated by a single neural generator contributes variably across electrodes – whereas the ANOVA is additive and assumes changes in voltage are constant across electrodes. To be clear, the ANOVA will account for any difference in scalp distribution as an interaction between effect and location, regardless of whether the difference is caused by changes in magnitude (i.e., implying a common neural generator) or differences in topography (i.e., qualitatively different neural generators).

To assess real differences in scalp distribution, the ERP data can be rescaled before a topographic analysis is conducted. Rescaling involves matching the absolute voltage across conditions, whilst preserving the pattern of electrical activity across the scalp. One common method of rescaling is known as the min/max method developed by McCarthy & Wood, (1985). This method finds the maximum and minimum voltage value in each condition across participants, subtracting the minimum from every data point, and dividing the resulting value by the difference between the maximum and minimum. After the values have been computed, the multiplicative effect of changes in the magnitude of effects is minimalized. Any significant interaction obtained with the rescaled data will therefore be due to a genuine qualitative difference in scalp topography indicating the contribution of distinct neural generators. The issue of normalisation is, however, still a source of much debate and many critics suggest that the min/max method can lead to an increase in the probability of making a type II error (Urbach & Kutas, 2006). Consequently, the dominant view within the literature is that rescaled data should only be used to confirm that differences in scalp topography are genuine and that all interpretations of the results should make reference to the original data set (Wilding, 2006). This latter approach is the one adopted in the current thesis.

3.6. Summary

The present chapter has provided a general overview of the ERP method, from the source that generates the EEG signal, to the formation and interpretation of ERP components. Relating cognitive processes to underlying neural activity is clearly complex and the limitations of the ERP approach constrain the inferences that can be made. Nonetheless, the high temporal resolution of ERPs tells a unique story about the function of cognitive processes, without having to rely on assumptions about the underlying neuroanatomical structures responsible. In short, ERPs enhance and compliment other neuroimaging techniques – such as fMRI – which are suitable for answering very different questions concerning cognition. Given that ERPs are a powerful tool for investigating cognition in general, the next chapter provides a more focused description of how ERP research has contributed to our understanding of episodic memory retrieval.

Chapter 4

ERPs and Recognition

Within the memory literature ERPs have been particularly useful for investigating encoding, retrieval and post-retrieval processing. In this thesis, only ERP effects associated with retrieval success during recognition tasks will be reviewed because they provide the most direct evidence in support of neural dissociations between familiarity and recollection. The current chapter will expand upon the introduction set out in Chapters 1 and 2 by providing a selective review of the ERP evidence supporting the existence of qualitatively distinct ERP correlates of familiarity and recollection. The chapter begins by discussing the basic pattern of ERP old/new effects observed during recognition tasks, before reviewing the evidence establishing the neural correlate of recollection, and the more contentious evidence establishing the neural correlate of familiarity. Both recollection and familiarity sections will end with a discussion of the topics that are addressed in the current thesis.

4.1. The ERP old/new effect

As reviewed in Chapter 1, episodic retrieval has generally been investigated using study-test recognition tasks. To briefly reiterate, recognition tasks require participants to study lists of items and at test a mixture of studied (i.e., ‘old’) and unstudied (i.e., ‘new) items are shown. Participants are required to judge whether items have been shown previously (i.e., by making an old response) or are new to the task (i.e., by making a new response). ERPs are analyzed by contrasting neural activity elicited by correctly identified old responses (Hits) and correctly identified new responses (Correct Rejections). Typically, neural activity elicited by Hits is more positive going than that elicited by Correct Rejections, with the difference in waveforms diverging around 300ms post-stimulus onset and lasting until around 800ms. Comparison of neural activity elicited by Hits and Correct Rejections has revealed two reliable effects with distinct latency periods and scalp locations that been associated with the contribution of independent retrieval processes.

Early observations of neural activity observed during successful episodic retrieval interpreted ERP old/new effects as reflecting a single memory process (Sanquist et al., 1980; Warren, 1980). Today, the existence of two qualitatively distinct ERP old/new effects is interpreted as supporting the dual process account of episodic memory[1]. In this Chapter, evidence supporting the existence of these two ERP old/new effects is reviewed, beginning with the old/new effect associated with recollection and followed by old/new effect associated with familiarity. At the end of the recollection section the functional nature of the underlying neural mechanism supporting recollection will be considered, making clear reference to the specific questions posed in experimental Chapters 6 and 7. At the end of the familiarity section, a review the current ERP evidence attempting to clarify the circumstances that allow familiarity to contribute towards successful associative recognition will be described, making clear the questions addressed in Chapters 8, 9 and 10.

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[1] It should be acknowledged that the two ERP old/new effects described in this thesis belong to a larger family of old/new effects that have been identified (including the early frontal parietal effect, late posterior negativity, and late right frontal effect). However, as this thesis was concerned primarily with those effects that have been extensively linked to familiarity and recollection, the evidence in support of these other effects will not be reported.

1.2. Left Parietal old/new effect and recollection

The ERP correlate of recollection is known as the Left Parietal old/new effect (see Figure 4.1), characterized by a greater positivity for Hits compared to Correct Rejections, occurring around 500ms post stimulus onset and maximal over parietal electrodes, often largest over the left hemisphere. There is general consensus that the Left Parietal old/new effect reflects processing related to, or depending, upon recollection (Rugg et al., 1998; Donaldson & Rugg, 1998; for reviews see both Curran, Tepe & Piatt, 2006; Wilding & Ranganath, 2011). The Left Parietal effect is functionally and topographically dissociated from other posterior effects that occur within the same latency period and are sensitive to either response confidence or stimulus probability (Curran, 2004; Woodruff et al., 2006; Herron et al., 2004). Importantly, the effect does not always exhibit a left sided asymmetry (see Mecklinger, 2000) and has been found to be elicited by a number of different stimulus materials such as words, pictures and faces (see Ranganath & Paller, 2000; Guillaume & Tiberghien, 2001; Johansson, Mecklinger & Treese, 2004; Mackenzie & Donaldson, 2009; Curran & Cleary, 2003).

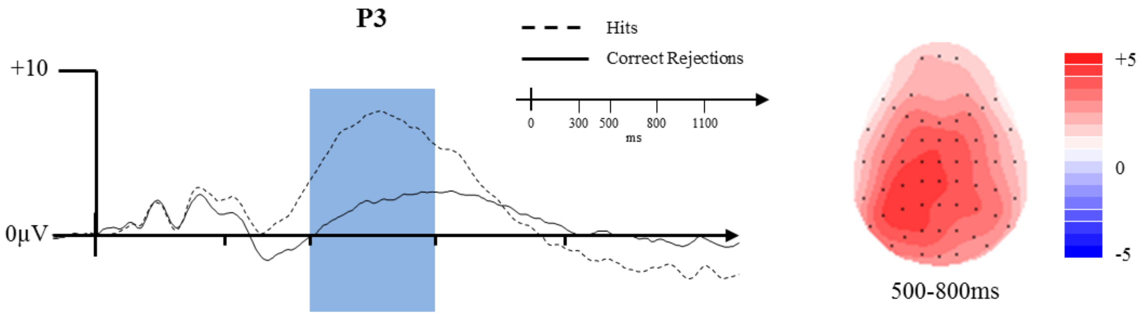

Figure 4.1: Illustration of the Left Parietal old/new effect (adapted from Chapter 7). On the left side are the waveforms for correctly identified old word pairs (Hits: dashed line) and correctly identified new word pairs (Correct Rejection: solid black line) at electrode P3. The blue bar captures the 500-800ms time window. The scalp topography Hits-Correct Rejections is illustrated on the right (the front of the head is pointed upwards) showing the distribution of the Left Parietal old/new effect. The scale bar represents the voltage range (µV).

The Left Parietal old/new effect was originally interpreted as reflecting a simple repetition effect (Doyle & Rugg, 1998). The repetition interpretation, however, was firmly ruled out when it was observed that the Left Parietal effect was not observed for previously studied items erroneously identified as new (i.e., Misses), or for new items misidentified as old (i.e., False Alarms). Both these observations suggest that the Left Parietal effect is neither an index of stimulus repetition, nor the subjective belief that an item had been previously studied. By contrast, the Left Parietal old/new effect is now believed to be associated with successful retrieval of previously studied information. The evidence establishing the Left Parietal old/new effect as a neural correlate of recollection will be reviewed in the next section, followed by a discussion of the potential neural substrate and functional nature of the Left Parietal old/new effect.

Early evidence that the Left Parietal old/new effect is related to recollection was derived from studies implementing the Remember/Know procedure. To briefly reiterate from Chapter 1, the Remember/Know task is a process estimation method that derives estimates of recollection and familiarity from subjective introspection. Participants must decide if their decision to respond to an item as being old was based on the conscious retrieval of contextual information about an event (resulting in a feeling of recollection indexed by a 'Remember' response) or retrieval based on the absence of contextual information (resulting in a feeling of familiarity indexed by a Know response). Although the Remember/Know task is subjective and may only provide a very simple estimate of recollection and familiarity, the ability to separate ERPs *ad hoc* based on Remember and Know judgments has proved particularly useful for investigating retrieval related neural activity.

Studies examining recognition of words using the Remember/Know paradigm have observed Left Parietal old/new effects for both Remember and Know responses, although the size of the Left Parietal effect is significantly larger for Remember responses (Smith, 1993; Duzel et al., 1997; Mark & Rugg, 1998; Trott et al., 1999). In addition to words, the Left Parietal old/new effect has also been observed for pictures, suggesting that the effect is not material specific. In one particular study employing pictures, Vilburg, Moosavi and Rugg (2006) had participants learn pairs of pictures at study and presented a mixture of previously studied and unstudied single pictures at test. The recognition task required participants to make one of four possible judgments: New responses when the picture was new or unknown; Know responses when the participant could recognize the picture but could not recollect any details of the prior study episode; R1 responses when details about the prior study episode could be recollected by not the associated picture; and R2 responses when the associated picture could be remembered. The Left Parietal effect was modulated by the amount of information recollected – i.e., the magnitude of old/new effects was significantly larger for R2 responses compared to R1 responses, whilst both were larger than Know responses. Consistent with a recollection account, ERP studies have demonstrated that the Left Parietal old/new effect is larger for Remember responses compared to Know responses and scales with the amount of information retrieved.

As previously discussed in Chapters 1 and 2, source memory tasks have been also been used to isolate the contribution of recollection, because participants must successfully recollect the associative details of a prior study episode to make a correct judgment (although for circumstances whereby familiarity may also contribute to source retrieval see Diana et al., 2008). Consistent with behavioral pattern of recollection, ERP studies employing source memory tasks reveal that the Left Parietal effect is modulated by source accuracy (Wilding, Doyle & Rugg, 1995; Wilding & Rugg, 1996; Senkfor & Van Patten, 1998; Wilding, 2000; Cansino et al., 2012). Wilding and Rugg (1996), for instance, required participants to make old/new judgments to words, and if old to recall if the word was spoken in a male or female voice. The ERP results showed that the Left Parietal old/new effect was largest for source correct judgments and smaller for source incorrect judgments, consistent with the view that the Left Parietal old/new effect is modulated by the amount of information recollected (although for an alternative explanation see Section 4.2.3).

Similar to source memory tasks, additional evidence supporting the relationship between the Left Parietal effect and recollection has come from ERP studies of associative recognition. To reiterate from Chapter 1, associative recognition typically requires participants to discriminate between pairs of items that maintain their relationship between study and test, and rearranged pairs in which previously studied items form new pairings at test. The associative test therefore requires retrieval of the association rather than the items *per se* (because all items presented at test were presented at study and will share the same level of familiarity). ERP studies of associative recognition tasks have generally demonstrated that retrieval of intact pairs elicits larger Left Parietal effects compared to rearranged pairs when new pairs are used as a baseline (Rugg et al., 1996; Donaldson & Rugg, 1998; Opitz & Cornell, 2006).

If the Left Parietal old/new effect does index recollection, then it follows that the Left Parietal effect should be sensitive to response confidence. To be clear, according to some dual process models familiarity is a continuous variable and will contribute to all levels of confidence, whereas recollection should only contribute to high confidence ratings (Yonelinas, 1999). An ERP study carried out by Woodruff et al., (2006) tested this assumption with regards to the neural correlate of recollection using a modified Remember/Know procedure constructed by Yonelinas et al., (2005). At study participants were required to make animacy judgments (e.g., is the object alive?) about presented words. During the test phase, participants were shown old and new words and were required to respond with a Remember judgment if they could recollect specific contextual information about the prior study episode, or when failing to recollect contextual information to respond either Confident old, Unconfident old, Unconfident new, Confident new (reflecting variation in familiarity). Only Remember responses elicited a significant Left Parietal old/new effects; the ERP effect was absent for comparisons of varying confidence – a result that is consistent with the assumption that recollection should only be sensitive to trials that were recollected, rather than variations in familiarity strength (as per the Dual Process Signal Detection model: Yonelinas, 1999).

The studies discussed so far have interpreted the Left Parietal old/new effect as an index of recollection – in line with a dual process perspective. Alternatively, ERP old/new effects have also been interpreted from a single process perspective, with different ERP old/new effects reflecting processes related to memory strength and decision making. Finnigan et al., (2002), for example, observed a 300-500ms old/new effect over parietal electrodes which varied with presentation frequency and was interpreted as reflecting changes in memory strength. By contrast, a later 500-800ms parietal effect was modulated by recognition accuracy and so was interpreted as reflecting decision making processes. The single process interpretation, however, is difficult to reconcile with ERP studies examining confidence ratings. To be clear, if the Left Parietal old/new effect reflects decision making processes then the effect should be observed for both studied and unstudied items. Evidence from ERP studies employing confidence ratings, however, observe Left Parietal old/new effects for studied but not new items (Woodruff et al., 2006; Curran, 2004), supporting the recollection as opposed to decision making hypothesis of the Left Parietal old/new effect.

Further evidence supporting the recollection account of the Left Parietal old/new effect comes from studies demonstrating that the Left Parietal old/new effect is modulated by many of the same behavioral manipulations of recollection. Curran (2004), for example, required participants to learn words, with either full or divided attention. In this study attention was divided by having participants learn single words whilst at the same time listening to spoken numbers and responding when three consecutive odd numbers were heard. At test, participants were required to discriminate between old (learnt under full or divided attention) and new words. A Remember/Know task was also administered to gather behavioral estimates of recollection and familiarity. The results confirmed that the proportion of Remember responses and the size of the Left Parietal effect were both significantly reduced for divided attention compared to full attention, suggesting that recollection was impaired at both a behavioral and neural level of analysis. In addition to the divided attention manipulation, the Left Parietal old/new effect has also been shown to be sensitive to levels of processing manipulations (Rugg et al., 1998), and is reduced in magnitude when specific amnesic drugs designed to impair recollection are administered to healthy controls (Curran et al., 2006).

4.2.1. Neural basis of the Left Parietal old/new effect

The evidence presented in the previous section suggests that much is known about the circumstances that modulate the Left Parietal old/new effect. In addition, there has also been significant interest in identifying the precise neural generators of the Left Parietal effect. Although source localization techniques have been unsuccessful in identifying these neural substrates, evidence from neuropsychological and neuroimaging studies have been more illuminating. To briefly reiterate from Chapter 1, behavioral studies of amnesic patients have provided strong evidence that declarative memory is supported by the Medial Temporal Lobes (MTL) and the Hippocampus. Several ERP studies of amnesic patients have shown that patients with MTL lesions and selective Hippocampal damage exhibit either reduced or absent Left Parietal old/new effects (Düzel, et al., 2001; Mecklinger et al., 1998; Wolk et al., 2013; Hoppstadter et al., 2013). Evidence from amnesic studies need to be interpreted with caution, however, as it is unclear whether the lesion is located at the source of the neural generator responsible for the observed ERP effect, or alternatively affects neural connections feeding into the neural generator. As made clear in Chapter 3, it is unlikely that activity generated from structures deep in the brain will contribute to the electrical potential detected from the scalp.

The neural activity detected from the scalp is instead much more likely to be generated by areas of the cortex relatively close to the skull (Wilding & Ranganath, 2011). Some have argued, for example, that there are strong functional parallels between the Left Parietal old/new effect and the inferior parietal cortex identified by fMRI studies of recollection (Vilberg & Rugg, 2009; Wagner et al., 2005; Simons & Mayes, 2008)[2]. Similar to the Left Parietal effect, old/new activity in the inferior parietal cortex is greater for Remember than Know responses (Henson et al., 1999; Eldridge et al., 2000; Wheeler & Buckner, 2004), is associated with accurate source responses (Cansino et al., 2002; Dobbins et al., 2003), and is also sensitive to the amount of information recollected (Vilberg & Rugg, 2009; for a review see Wagner et al., 2005). Evidence of both hippocampal (i.e., from studies of amnesic patients) and parietal cortical activity relating to the Left Parietal old/new effect are not incompatible but most likely reflect the projections between the MTL structures and the parietal cortex (see Kobayashi & Amaral, 2003) suggesting that recollection involve the interactions between the hippocampus and cortical networks (Norman & O'Reilly, 2003).

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[2] To date, it is impossible to identify the generators of the Left Parietal old/new effect to the same inferior parietal regions identified by fMRI. Regardless, Vilberg & Rugg (2008) have argued that the functional parallels between the two effects are persuasive enough to imply that the Left Parietal old/new effect is a neural correlate of the hemodynamic activity detected by fMRI.

4.2.2. The functional significance of the Left Parietal old/new effect

The evidence so far described has supported the association between the Left Parietal old/new effect and recollection. Although a clearer understanding of the neural substrates underlying the Left Parietal old/new effect is beginning to emerge, how these neural mechanisms operate is currently unclear. As reviewed in Chapter 2, there is considerable debate about whether the behavioral expression of recollection is thresholded (i.e., according to dual process theories) or continuous (i.e., single process theory), with recent evidence suggesting that recollection may be more accurately modelled as a some-or-none process (i.e., recollection can fail but is variable when successful). Importantly, because recollection interpreted from a behavioral level of analysis will reflect the summed contribution of many different underlying processes, this data cannot say anything about the function of recollection from a neural level of analysis. Within the electrophysiological and neuroimaging literature, the evidence indicates that the Left Parietal old/new effect may operate in a graded fashion (perhaps reflecting a continuous process), although currently an all-or-none threshold account cannot be firmly ruled out. This section will review the evidence and theoretical explanations concerning the functional nature of the Left Parietal old/new effect, before discussing the interpretational issues inherent in many of the studies supporting a graded account. The section will conclude with the specific questions concerning the functional nature of the Left Parietal old/new effect that will be addressed in the current thesis.

According to one theoretical account from the neuroimaging literature, the Left Parietal old/new effect reflects the active maintenance of stored information in working memory

(Vilberg & Rugg, 2007, 2008), akin to Baddeley’s (2000) episodic buffer. By this perspective, the parietal region supports the representation or maintenance of retrieved episodic information in a form that is accessible to decision making processes. The episodic buffer account of Left Parietal function is supported by carefully designed experiments demonstrating that the magnitude of the effect is modulated by the amount of information retrieved. As previously described, Vilberg et al., (2006) found that the magnitude of the Left Parietal old/new effect was sensitive to participant’s perception of the amount of information recollected – i.e., the magnitude of the effect was largest for R1 (recollected) responses and smaller than R2 (partial recollection) responses. The graded signal of the Left Parietal old/new effect was corroborated by a follow up study whereby the left inferior parietal cortex was also observed to be sensitive to the amount of information recollected (Vilberg & Rugg, 2008). In essence, evidence that the Left Parietal old/new effect and left inferior parietal cortex are sensitive to the amount of information recollected appears to be inconsistent with an all-or-none threshold account (Vilberg et al., 2006; Woodruff et al., 2006; Wilding, 2000).

The finding that damage to the parietal cortex often does not result in explicit impairment of episodic retrieval, however, is difficult to reconcile with the episodic buffer hypothesis (Simons et al., 2008; Yasuda et al., 1997). Alternative theories of parietal activity suggest that the parietal region plays an indirect role in recollection. The Attention-to-Memory model proposed by Cabeza et al., (2008, 2011) explains parietal activation as reflecting attentional processes that supplement retrieval. By this perspective, the parietal cortex does not hold the contents of retrieval, but instead re-directs attention from a retrieval cue to the contents of retrieval (held in the MTL). The Attention-to-Memory model has the advantage of accounting for evidence in which parietal cortical lesions do not result in any explicit deficits to episodic memory. It follows, however, that re-directed attention should operate in all-or-none thresholded fashion (i.e., attention is either successfully re-directed or it is not). This account is therefore at odds with the majority of ERP studies reporting a graded Left Parietal old/new effect.

One particular reason why the function of the Left Parietal old/new effect (and by extension the parietal cortex) remains unresolved is that many of the studies reporting a graded account stem from source memory paradigms (although see Villberg & Rugg, 2006). Wilding (2000) has noted that a graded Left Parietal old/new effect may simply reflect a data averaging artefact. To be clear, a graded signal may arise from the averaging of trials with and without recollection. By this account, the smaller magnitude of Left Parietal old/new effect for source incorrect trials could equally reflect accurate recognition driven by acontextual familiarity or ‘lucky’ guesses. In essence, the observed Left Parietal old/new effects will appear graded, even if the underlying neural signal is thresholded.

In the current thesis, the novel source task designed by Harlow and Donaldson (2013) is employed, allowing the Left Parietal old/new effect to be examined within a continuous rather than a binary forced choice task. By analyzing trials associated with positional response accuracy, we avoid the problems with analyzing source correct and source incorrect judgments. The continuous task also allows us to ask whether the Left Parietal old/new effect is sensitive to the precision of recollected information, rather than the amount of information retrieved (see Chapter 6). A graded Left Parietal old/new effect would lend further support to the argument that parietal activity reflects processes that act upon the neural representation of recollected information (as per the episodic buffer account). By contrast a thresholded pattern would be more consistent with the Attention-to-Memory account. In Chapter 7 we propose an alternative pattern to the graded and all-or-none thresholded accounts – namely, that the Left Parietal effect may operate in a some-or-none fashion. To be clear, rather than defining the Left Parietal old/new effect as either graded or thresholded, it is theoretically possible that the Left Parietal effect may scale with precision when recollection is successful, but be absent when recollection fails. Demonstrating that the Left Parietal effect operates in a some-or-none fashion would provide further support for recent behavioral evidence that recollection is both variable and thresholded.

4.3. The Mid-Frontal old/new effect and familiarity

To date, there is a considerable body of research supporting the existence of two temporally and topographically distinct ERP old/new effects that are believed to reflect recollection and familiarity. The preceding section explored the evidence that the Left Parietal old/new effect indexes recollection. By contrast, a second early occurring frontal old/new effect is believed to be associated with familiarity. The early occurring effect is characterized by more positive going activity elicited by Hits compared to Correct Rejections, maximal between 300-500ms post stimulus onset with a bilateral distribution over the frontal electrodes.

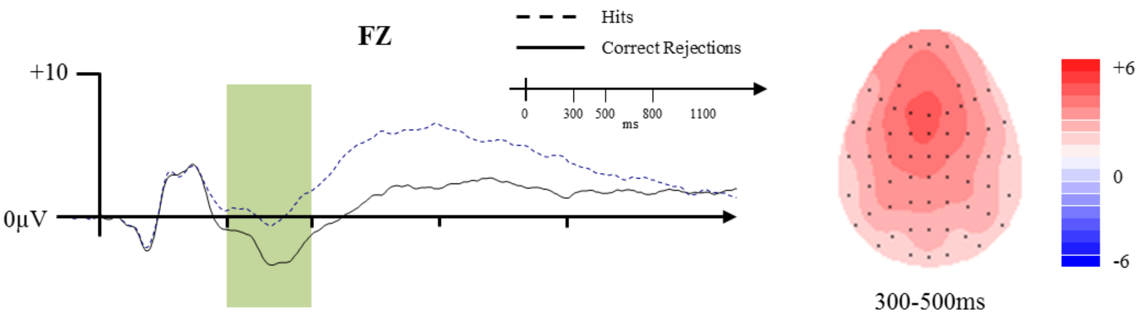

Figure 4.2: Illustration of the Mid-Frontal old/new effect (adapted from Chapter 9). On the left side are the waveforms for Hits (dashed line) and Correct Rejections (solid black line) at electrode FZ. The green bar captures the 300-500ms time window. The scalp topography is illustrated on the right (the front of the head is pointed upwards) showing the distribution of the Mid-Frontal old/new effect. The scale bar represents the voltage range (μV).

Although there is general consensus that the Left Parietal old/new effect reflects recollection, the association between the Mid-Frontal old/new effect[3] and familiarity is more contentious. Ambiguity surrounding the Mid-Frontal old/new effect in part stems from the lack of any precise definition of familiarity among dual process models. As discussed in Chapter 1, familiarity has been defined as reflecting the assessment of lexical node activation strength (Atkinson & Juola, 1973, 1974), assessment of perceptual fluency (Jacoby & Dallas, 1991), assessment of item activation (Mandler, 1980), or assessment of quantitative memory strength (Yonelinas, 1994). Since there is no general consensus about the functional characteristics of familiarity, it appears unlikely that a precise neural correlate of familiarity will be agreed upon. In addition, the ambiguity surrounding the Mid-Frontal old/new effect also stems from the deductive reasoning employed in many ERP studies, rather than direct manipulation of retrieval processes. To be clear, demonstrating that the Mid-Frontal old/new effect is not affected by manipulations of recollection does not necessarily imply that the effect

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[3] The 300-500ms Mid-Frontal old/new effect is also known as the FN400 (Curran, 2000, 2004), medial frontal (Friedman and Johnson, 2000) and early frontal (Mecklinger, 2000) old/new effect.

is associated with familiarity (Paller et al., 2007). It is therefore possible that given new information the interpretation of the Mid-Frontal old/new effect may change in the future. With this qualification in mind, the next section will review the evidence supporting the association between the Mid-Frontal old/new effect and familiarity.

Duzel et al., (1997) initially observed that specific ERP effects with qualitatively different scalp topographies were correlated with ‘Remember’ and ‘Know’ responses. In a later study, Rugg et al., (1998) reported separate old/new effects that could be dissociated with a levels of processing manipulation (Craik & Lockhart, 1972; Craik & Tulving, 1975). Rugg et al., (1998) had participants perform either a ‘deep’ (generating sentences) or ‘shallow’ (alphabetic judgment) encoding task before taking part in a standard recognition test. Analysis of ERPs revealed a parietal old/new effect that was larger following deeply encoded words between 500-800ms post stimulus onset, and an earlier 300-500ms bilateral frontal old/new effect that was insensitive to depth of processing. Rugg et al., (1998) suggested that the observed Mid-Frontal old/new effect was related to familiarity because the behavioral data had shown that only recollection, and not familiarity, was sensitive to depth of processing manipulations. Importantly, neither the Duzel et al., (1997) nor Rugg et al., (1998) studies were initially set out to investigate the Mid-Frontal old/new effect, and therefore these early observations provided relatively weak evidence supporting the association between the Mid-Frontal old/new effect and familiarity.

More direct investigation of the Mid-Frontal old/new effect has come from studies attempting to dissociate familiarity and recollection by comparing lure items that are similar but not identical to previously studied items[4]. Initially, Curran (2000) used plurality reversed words as lures (i.e., Cat presented at study would be presented as Cats at test) to investigate the Mid-Frontal old/new effect. Curran hypothesized that recollection was required to discriminate between studied and plurality reversed lures (resulting in a difference in parietal old/new activity). By contrast, both studied and plurality reversed lures would be more familiar than new words resulting in similar Mid-Frontal old/new effects elicited by correctly identified studied words and falsely recognized similar lures (i.e., False Alarms). Analysis of the ERP effects confirmed Curran's predictions, revealing that parietal old/new effects were only present when words maintained their plurality, whereas the Mid-Frontal old/new effect was equivalent for correctly identified studied words and falsely identified lures. In a later experiment, Curran & Cleary (2003) attempted to replicate the earlier study by Curran (2000) but this time comparing studied pictures, mirror reversed lures and unstudied pictures. The Mid-Frontal old/new effect was equivalent for both studied and falsely recognized mirror reversed lures, but the parietal old/new effect was only observed for studied pictures. The finding from Curran and Cleary (2003) is important in demonstrating that the Mid-Frontal old/new effect is not limited to lexical material (although the effect may be different for faces: see Mackenzie & Donaldson, 2009).

The data presented by Curran (2000) and Curran and Cleary (2003) also has important implications for different functional accounts of familiarity. The perceptual account of familiarity proposed by Jacoby and Dallas (1981), for instance, is difficult to reconcile

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[4] The dissociation of familiarity and recollection by comparing studied, lure and new items is based on the assumptions of global matching models of memory (Murdock, 1982; Hintzman, 1988; Norman & O'Reilly, 2003). To be clear, familiarity reflects the global assessment of the similarity between study and test items, therefore similar lures are expected to elicit familiarity.

with the finding that that mirror reversed pictures did not result in a reduction in magnitude of the Mid-Frontal old/new effect. Alternatively, a conceptual (i.e., semantic) account of familiarity would be consistent with observed pattern of Mid-Frontal old/new effects found by Curran and Clearly (2003). To investigate the influence of conceptual processing on the Mid-Frontal old/new effect, Nessler, Penny and Mecklinger (2001) implemented a DRM false memory paradigm.[5] When encoding was focused on the conceptual similarity of words, analysis of ERPs at retrieval found that the Mid-Frontal old/new effect was equivalent in magnitude between true and false recognition of conceptually similar lures. When encoding was focused on item information, however, no Mid-Frontal old/new effect was found for falsely recognized lures. In a follow up study, Nessler and Mecklinger (2003) observed a Mid-Frontal old/new effect for falsely recognized lures after a 40 second delay, but not after an 80 second delay, suggesting that familiarity for lures declines with delay (although see Wolk et al., 2006, who found no difference between delays). Collectively, the results suggest that conceptual similarity enhances familiarity in a similar fashion to manipulations of physical similarity observed by Curran (2000) and Curran and Cleary (2003).

Further evidence supporting the familiarity account of the Mid-Frontal old/new effect comes from studies examining ERPs as a function of response confidence. Under the assumption that familiarity is defined by both single and dual process theories as a variable signal of memory strength, then the Mid-Frontal old/new effect should vary

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[5] The DRM paradigm (Deese, 1959; Roediger & McDermott, 1995) requires participants to learn a series of semantically related words (e.g., wolf, fox, meat, bone, kennel) at study and a test are presented with previously studied words and non-studied themed words (similar lures: e.g., dog). DRM studies demonstrate that similar lures are incorrectly identified as being recognized as often as correctly identified studied words.

over different response confidence levels. As mentioned earlier, Woodruff et al., (2006) had participants study words and in a later test make a five-way response. Although the Left Parietal effect was only reliable for items attracting a Remember response, the Mid-Frontal old/new activity increased in magnitude from confident new responses to confident old responses. A graded Mid-Frontal old/new effect was also observed by Azimian-Faridani and Wilding (2006), who directly manipulated familiarity by altering the response criterion set by participants. This was achieved by encouraging participants to respond old when they were confident that the word was old (conservative response bias) or respond new when they were confident the word was new (liberal response bias). According to the experimental prediction, those trials with conservative response bias would require a greater level of familiarity compared to those trials with a liberal response bias. Consistent with the prediction that the Mid-Frontal effect reflects familiarity, ERP activity for correct judgments varied according to response confidence – i.e., being more positive over mid-frontal electrodes for the conservative compared to the liberal condition. In summary, both the results of Woodruff et al., (2006) and Azimian-Faridani and Wilding (2006) demonstrate that the Mid-Frontal old/new effect scales with response confidence and is consistent with a continuous familiarity signal.

4.2.1. Neural basis of the Mid-Frontal old/new effect

Further evidence in support of the link between familiarity and the Mid-Frontal old/new effect comes from studies of amnesic patients with impaired recollection but spared recognition. Duzel et al., (2001) have demonstrated, for example, that amnesic patients and control subjects both elicit reliable Mid-Frontal old/new effects, but only controls elicit significant Left Parietal old/new effects. A similar pattern of results has also been demonstrated with Alzheimer's patients, who exhibit impaired recollection but spared familiarity. A study carried out by Tendolkar et al., (1999) comparing source memory for Alzheimer's patients and healthy controls, observed above chance item recognition across groups but found that only control groups exhibited accurate source judgments (requiring recollection) and reliable Left Parietal old/new effects. The Mid-Frontal old/new effect, by comparison, was observed for both amnesic and control groups, indicating that familiarity was intact.

Further evidence supporting the familiarity account comes from single and multi-cell recording studies of primates, which have found familiarity sensitive neural populations in the prefrontal cortex (Xiang & Brown, 2004). The role of the prefrontal cortex is also bolstered by fMRI studies demonstrating that familiarity strength modulates activity in the lateral prefrontal cortex in human populations (Yonelinas et al., 2005). Collectively, the evidence appears to support the idea that the prefrontal cortex is involved in processing related to familiarity and that this activity may be the neural source of the Mid-Frontal old/new effect (although caution should always be exercised when inferring neural generators from scalp topographies: see Chapter 3).

4.3.2. Alternative accounts of the Mid-Frontal old/new effect

Although the evidence relating the Mid-Frontal old/new effect to familiarity appears compelling, this association has not been unchallenged. One alternative hypothesis that has received considerable attention is the conceptual priming account, which interprets the Mid-Frontal old/new effect as a frontally distributed N400 (i.e., a neural correlate of conceptual priming). Olichney et al., (2000), in particular, have argued that a conceptual priming account can explain some of the memory data described in the previous section if it is assumed that repetition of studied items at test is sufficient to result in conceptual priming (see also Yovel & Paller, 2004). In addition to the views of Olichney et al., (2000), others suggest that conceptual priming may instead support familiarity, or that familiarity and conceptual priming share some of the same underlying cognitive processes (Wang, Ranganath & Yonelinas, 2014).

One potential problem for the conceptual priming account is that observed Mid-Frontal old/new effects are present for apparently meaningless stimuli. Curran et al., (2002), for example, examined ERP correlates during recognition and categorization tasks employing novel stimuli known as ‘blobs.’ The results revealed reliable Mid-Frontal old/new effects during successful recognition of blobs, suggesting that familiarity was able to contribute to the retrieval for meaningless objects. In this particular study, however, participants were required to undergo extensive training in order to learn several families of blobs prior to the recognition test. It is possible that the training session allowed participants to assign meaning to these novel objects and could therefore have been coded into semantic memory. However, in support of the interpretation favored by Curran et al., (2000), a study carried out by Groh-Bordin et al., (2006) found reliable Mid-Frontal old/new effects for novel lines drawings that were only presented once at study. Collectively, both Curran et al., (2000) and Groh-Bordin et al., (2006) suggest that the Mid-Frontal old/new effects can be elicited by stimuli without any pre-existing conceptual meaning (but see Yovel & Paller, 2007).

In light of evidence demonstrating that perceptual features of test stimuli modulate the Mid-Frontal old/new effect, Rugg and Curran (2007) argue that the conceptual priming account may be too simplistic. To be clear, the magnitude of the Mid-Frontal old/new effect has been found to be modulated by perceptual changes to stimuli between study and test – i.e., the magnitude of the effect is reduced when perceptual features are altered between study and test phases (Groh-Bordin et al., 2005, 2006; Ecker et al., 2007). The conceptual priming account is difficult to reconcile with these findings because perceptual manipulations (so long as they do not alter the meaning of the item) should have little effect on conceptual priming. The sensitivity of the Mid-Frontal old/new effect to meaningless stimuli and perceptual manipulations indicate that the effect is not limited to conceptual processing.

Finally, evidence from studies attempting to dissociate familiarity and conceptual priming also appear to challenge a pure priming account of the Mid-Frontal old/new effect. Recently, Bridger et al., (2012) carried out an experiment whereby a semantic priming paradigm served as the study phase to a surprise old/new recognition test. During the semantic priming task, participants were required to make valence judgments about single words that were either preceded by semantically related or unrelated primes. Comparison of ERPs to semantically related versus unrelated words revealed a significant N400 effect with a central-parietal maximum between 300-500ms post stimulus onset. By contrast, ERPs elicited by Hits and Correct Rejections during the old/new recognition task revealed a significant old/new difference across Mid-Frontal electrodes between 300-500ms, which was qualitatively distinct from the N400 observed in the semantic priming task. The results support the view that the Mid-Frontal old/new effect and the N400 conceptual priming effect are qualitatively dissociable – although as the different ERP effects were measured at encoding and retrieval the data does not definitively rule out the possibility that conceptual priming may contribute to the Mid-Frontal old/new effect observed at test.

In short, there is sufficient evidence to suggest that a purely conceptual priming account of the Mid-Frontal old/new effect is unlikely given it’s sensitivity to perceptual manipulations and it’s dissociation from ERP effects that are typically associated with semantic priming. Instead, this thesis adopts the view that Mid-Frontal old/new effect reflects episodic recognition because the familiarity account can arguably accommodate a larger proportion of the data than either a purely perceptual or conceptual priming account. Given that the current thesis is primarily concerned with testing the predictions of dual process theory, an interpretation of the Mid-Frontal old/new effect as reflecting familiarity is adopted throughout (although the conceptual priming account is explored in a subsidiary analysis in Chapter 10).

4.3.2. Unitization and the Mid-Frontal old/new effect

As made clear in Chapter 2, if recollection can fail on a subset of trials, then it is important to identify circumstances that may allow familiarity to contribute to successful associative retrieval. Currently, unitization appears to be the strongest candidate for encouraging familiarity during associative retrieval, although current evidence in support of unitization has relied heavily on ROC data. ERPs arguably provide a more objective assessment of familiarity, and are at least not dependent on subjective confidence ratings. Current examination of unitization using ERPs has been limited; sometimes revealing a pattern of old/new effects inconsistent with the neural correlates of either recollection or familiarity. Critically, observed Mid-Frontal old/new effects have only been observed when unitization has been manipulated using word pairs sharing a conceptual relationship, and it is currently unclear whether the Mid-Frontal old/new effect can be modulated with novel associations (as per the definition of unitization proposed by the Dual Process Signal Detection model). Below, we review the current ERP evidence of unitization and highlight the need for further investigation.

Initially, Rhodes and Donaldson (2007) used ERPs to test the prediction that unitization may encourage familiarity during associative recognition. Rhodes and Donaldson (2007) demonstrated that familiarity supported associative retrieval of word pairs sharing particular relationships. Participants studied either word pairs sharing either an associative relationship (traffic-jam), associative and semantic relationship (lemon-orange) or only a semantic relationship (violin-guitar) and were asked to discriminate between intact, recombined and new word pairs. Results revealed that the early mid-frontal old/new effect was engaged only during retrieval for word pairs sharing an associative relationship, whereas the Left Parietal old/new effect was invariant to relationship type. Rhodes and Donaldson (2007) concluded that only associatively related word pairs were perceived as being unitized and could therefore be supported by familiarity during retrieval. In this particular study, however, no attempt was made to manipulate unitization, and the results therefore only provided indirect evidence in support of the unitization hypothesis.

In a later study, Rhodes and Donaldson (2008) directly manipulated unitization by employing different encoding instructions. In the unitization condition, participants were encouraged to imagine either associative or semantically related pairs interacting together (i.e., interactive imagery). By contrast, the non-unitized condition encouraged participants to create separate mental images of each word in a pair (i.e., item imagery)[6]. During the test phase, participants were required to make intact/recombined/new judgments. Although associatively related pairs did not receive any benefit from instructions encouraging unitization, improved discrimination and faster response times were observed for semantically related pairs encoded with interactive as opposed to single item imagery. Similar to the behavioral results, analysis of the ERP data revealed equivalent Mid-Frontal old/new effects observed for associatively related pairs (regardless of encoding task) and semantically related pairs encoded with interactive imagery. By contrast, semantically related pairs encoded with item imagery resulted in a significantly reduced Mid-Frontal old/new effect. Importantly, the magnitude of the Left Parietal old/new effect was equivalent across encoding conditions and relationship type – indicating that recollection was not sensitive to unitization instructions.

Rhodes and Donaldson (2008) concluded word pairs sharing an associative relationship are already perceived as being unitized and do not therefore receive any benefit from encoding instructions that encourage unitization. Semantically related pairs, by contrast, are not perceived as being unitized and thus do receive a benefit from unitization instructions resulting in increased familiarity, as indexed by an enhanced Mid-Frontal old/new effect, and improved behavioral performance.

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[6] The mental imagery manipulation was chosen because previous behavioral evidence had demonstrated that interactive imagery (i.e., imaging two objects interacting together) compared to single item imagery (i.e., imaging objects separately) improved both recall (Bower, 1970) and recognition performance (McGee, 1980).

One potential problem with both of the Rhodes and Donaldson (2007, 2008) studies was the encoding and retrieval of related word pairs, which may have resulted in pre-experimental conceptual knowledge contributing to familiarity-based recognition. To be clear, to the extent that pre-existing relationships are already represented in memory, related word pairs may be treated as single items rather than pairs of items (akin to the compound words such as blackbird which would be considered a single item). To date, only one other ERP study has attempted to assess whether familiarity may contribute to associative retrieval of novel information. Bader et al., (2010) manipulated unitization of unrelated word pairs by encouraging unitization using compound definitions (i.e., BIBLE/GARDEN: A reference book for gardeners) and discouraging unitization using sentence frames (i.e., BIBLE/GARDEN: The __ was left in the __). The results of this study, however, were difficult to reconcile with unitization given the lack of any difference in discrimination performance, or observed Mid-Frontal old/new effect and Left Parietal old/new effects. Instead, a parietally focused old/new effect between 350 and 500ms was observed for compound definitions and a broad effect old/new effect was found for sentence frames between 500-700ms. The absence of the standard old/new effects associated with either familiarity or recollection makes interpretation of the Bader et al., (2010) findings difficult. Currently, it is unclear whether or not completely unrelated word pairs encoded using unitizing instructions can modulate the Mid-Frontal old/new effect.

In general the results from the limited number of ERP studies investigating unitization are inconclusive. First, it is unclear whether unitization enhances familiarity for completely novel information. From a practical perspective, providing evidence of familiarity to successful retrieval of novel associations has important implications given the vulnerability of recollection to failure, particularly among patients with recollective deficits and the elderly. At a theoretical level, demonstrating that the Mid-Frontal old/new effect can be enhanced for unrelated unitized pairs would support the prediction made by the DPSD model that familiarity can support the learning of arbitrary associations. So far the only study that has attempted to examine the Mid-Frontal old/new effect for unrelated pairs failed to find evidence of a reliable Mid-Frontal or Left Parietal old/new effects (Bader et al., 2010). This raises the possibility that familiarity can only be encouraged for associations that already share a pre-existing conceptual representation – consistent with the Atkinson and Juola (1973, 1974) and Mandler (1980) accounts of familiarity. To this end, the aim of Chapter 8 is to address whether unitization can enhance familiarity for completely unrelated word pairs using the mental imagery paradigm employed by Rhodes and Donaldson (2007, 2008). Chapter 9 attempts to expand the circumstances that allow familiarity to contribute to novel associative retrieval by attempting to manipulate unitization using alternative encoding instructions (i.e., the lexical manipulation). Finally, Chapter 10 investigates whether the benefits of unitization (i.e., enhanced Mid-Frontal old/new effect and improved behavioral performance) is greater for either conceptually related, or unrelated, word pairs.

4.4. Summary of research aims

Overall, this thesis aims to clarify the contribution of retrieval processes to episodic memory. As outlined at the beginning of this chapter, ERPs provide an objective method for dissociating familiarity and recollection, allowing researchers to address specific questions regarding successful episodic retrieval without relying on subjective behavioral estimates (i.e., Remember/Know judgments or confidence ratings). As discussed in Chapter 2, the assumptions about recollection and familiarity made by current dual process models are highly reliant on the outcome of ROC studies, requiring the assumptions of dual process models to be supported by evidence from other domains (Yonelinas & Parks., 2007). The current thesis employs ERPs to address two main questions regarding the contribution of retrieval processes to episodic recognition:

1. What is the functional nature of the underlying neural mechanism supporting recollection?

2. Under what circumstances does familiarity contribute to successful retrieval of novel associations?

Chapter 5

General Method

This chapter describes the core methods used in the thesis, providing a general overview of the participants, stimulus materials, procedures, data processing and analyses. The procedures and stimulus materials for the continuous source and unitization tasks are described separately for clarity. Further details of experimental methods that deviate from the fundamental methods described in the current chapter are provided in the relevant experimental chapters.

5.1. Study participants

The experiments reported in this thesis were approved by the ethics committee at the University of Stirling. All participants were students from the University of Stirling. Participants were right-handed, British/Irish native English speakers with normal or corrected-to-normal vision, aged between 18-35 years with no history of dyslexia, neurological problems or brain injury. Participants were reimbursed at a rate of £7.50 per hour. Undergraduate psychology students were provided with the option of receiving two course credits for the first hour of the experiment as an alternative to the £7.50 of financial reimbursement. Participants were fully briefed on experimental tasks and ERP preparation before giving consent and were given verbal and written debriefing after the experiment.

5.2. Continuous source task

5.2.1. Stimuli

Chapter 6 consisted of 480 words selected from the MRC psycholinguistic database (www.psych.rl.ac.uk – Coltheart, 1981). The 480 words were divided into two sets (A and B) of 240 words and matched for word length (5-7 letters) imagability, concreteness and Kucera-Francis word frequency (reported in Table 5.1). Set A and set B were equally presented assigned as ‘old’ and ‘new’ across participants. Chapter 7 consisted of a subset of 240 words from the initial 480 words selected from Chapter 6. Words were selected based on low ratings of imagability and concreteness to discourage participants visualising each word as an object located in the paired location. By keeping imagability and concreteness ratings low we discouraged possible unitization of word/source associations that may have resulted in the added contribution of familiarity during retrieval. For the practice, 18 additional words were selected for Chapter 6, and from those, 9 were used in Chapter 7.

Target locations were identical to those selected by Harlow and Donaldson, (2013). The locations were presented on a grey circle, with a radius of 200 pixels, and marked by a black cross. The use of a circle meant that locations could be defined in degrees with 360 potential targets. From the 360 target locations, those that could be identified as distinguishable features of a circle (i.e., multiples of 45°) were removed. The mean distance between two adjacent targets (i.e., a distance corresponding to 1°) was 3.5 pixels. Within each study/test block a minimum distance of 10° (35 pixels along the circle arc) was maintained between each pair of targets.

	Word Length	**Familiarity**	**Imagability**	**Word Frequency**
Chapter 5 (Set A)	6 (1)	508 (56)	398 (69)	33 (31)
Chapter 5 (Set B)	6 (1)	502 (63)	405 (73)	36 (24)
Chapter 6	6 (1)	506 (65)	395 (75)	33 (32)

Table 5.1: Means (and standard deviation) of word length, familiarity, imagability and word frequency of words employed in Chapters 6 and 7. Set A and B refer to the separate word lists that are presented as either ‘old’ or ‘new’.

5.2.2. Procedure

The continuous source experiments were designed and run with E-Prime software (version 1.2, Psychology Software Tools Inc: www.pstnet.com). Stimuli were presented on a 19” flat screen computer monitor positioned exactly one meter away from the participant. Single words subtended a maximum horizontal visual angle of approximately 3.7˚ and maximum horizontal vertical angle of approximately .6˚. For the continuous source task participants used a combination of a PST serial response box and mouse to make responses.

Presented in Figure 5.1 is a general overview of the experimental procedure for the continuous source task. For detailed description of timings and deviations from the general procedure please see the relevant experimental chapters. Participants began every study trial with a fixation cross (+). The cross was followed by a blank screen after which a black cross located on a grey circle outline was shown. After another blank screen the target word was presented. Participant’s attention to the location was then tested by asking them to verify the (now hidden) location using the mouse. Responses within 20 pixels (~ 6º) from the target advanced participants to the next trial.

If the participant's response was over 20 pixels, the target location was presented again for 250ms and the verification task was repeated.

During test trials participants were presented with a fixation cross followed by blank screen. The target word from the previous study block was then shown followed by a blank screen. Participants were then presented with a grey circle outline and were asked to recall the paired location, then to move the mouse cursor to the remembered location and click the left mouse button. A red marker then appeared on the circle to indicate the chosen location. No response time limit was set and participants were free to change their decision. Participants finalized their response by pressing a button on the response box and initiating the next trial.

After the experiment was completed the precision of each test response was calculated, converting the screen co-ordinates selected by the participant into degrees: the remembered location was compared to the target location to provide the degree of error for that chosen location. To calculate response errors (Figure 5.1c) location responses at study and retrieval were converted from the co-ordinates selected using the mouse into an angle in degrees from the center of the circle. To ensure that the error statistic in angles was precise, response angles were compared to the corresponding target angles – themselves calculated from the pixel on which the target cross was centered.

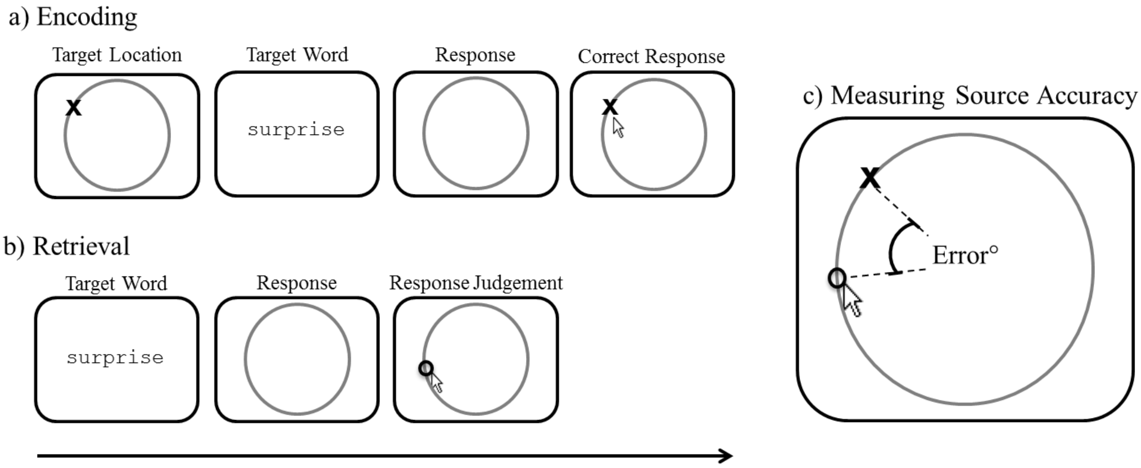

Figure 5.1: The continuous source task paradigm: a) illustrates the encoding phase whereby participants must remember each location/word pair and verify the recently studied target location; b) in the retrieval phase word cues are presented and the target location must be remembered; c) represents how the response error was calculated.

5.3. Unitization tasks

5.3.1. Stimuli

The experiment presented in Chapter 8 employed 1280 nouns and verbs selected from the MRC psycholinguistic database (Coltheart, 1981). The words formed 640 unrelated word pairs that were randomly allocated to two lists assigned to either the interactive mental imagery or item mental imagery conditions – counterbalanced across participants. The experiment presented in Chapter 10 employed a sub-set of 320 word pairs from those used in Chapter 8, along with a further 320 related word pairs constructed using additional words taken from the MRC psycholinguistic database. The experiment presented in Chapter 9 consisted of 880 words selected from those used in Chapter 8, and these were divided into two lists of 440 word pairs that were paired to facilitate the construction of meaningful sentence frames and compound definitions (see Chapter 9 for more details). All word pairs used in Chapters 8, 9 and 10 were matched across lists for familiarity, word length, imagability and Kucera-Francis word frequency (see Table 5.2), thereby ensuring that the unitization manipulation was the only independent variable.

	Len	Fam	Img	Freq	Sem	Ass
Chapter 8 List 1	5 (1)	523(44)	528 (45)	62 (72)	.06 (.06)	0 (0)
Chapter 8 List 2	5 (1)	530(40)	530 (46)	68 (69)	.06 (.06)	0 (0)
Chapter 9 List 1	5 (1)	522(44)	530 (44)	60 (70)	.06 (.06)	0 (0)
Chapter 9 List 2	5 (1)	530(41)	530 (47)	67 (66)	.06 (.06)	0 (0)
Chapter 10 Related List 1	5 (1)	536(47)	520 (50)	66 (84)	.04 (.03)	0 (0)
Chapter 10 Related List 2	6 (1)	532(47)	524 (44)	63 (68)	.04 (.03)	0 (0)
Chapter 10 Unrelated List 1	5 (1)	519(40)	519 (40)	60 (64)	.33 (.21)	.18 (.15)
Chapter 10 Unrelated List 2	5 (1)	516(42)	520 (51)	60 (72)	.34 (.21)	.18 (.14)

Table 5.2: Reported are means (and standard deviations) of word length (Len), familiarity (Fam), imagability (Img), frequency (Freq), semantic similarity (Sem) and associative strength (Ass). List 1 and 2 refer to the counterbalanced lists that are presented under instructions to either encourage or discourage unitization (see Section 5.3.1).

To ensure that words within a pair were either related or unrelated they were first visually inspected and then submitted to further analysis. Semantic relatedness was checked using the Latent Semantic Analysis (LSA: www.lsa.colorado.edu) database. The LSA is a mathematical/statistical technique for extracting and representing the similarity of meanings of words and passages through analysis of large text. Semantic similarity was checked by means of a pair-wise comparison function with a General-Reading up-to-1st-year-in-college database. The means and standard deviations of semantic similarity scores are presented in Table 5.2. In addition, associative strength within word pairs was also checked using the Edinburgh Association Thesaurus (EAT: Kiss et al., 1973). The EAT is a word production norm indexing the degree of associative strength between words in terms of the probability of participants who called to mind the second word as a first response to the presentation of the first. The mean and standard deviation scores of associative strength are again presented in Table 5.2.

5.3.2. Procedure

All Unitization experiments were designed and run on E-Prime software (Version 1.2, Psychology Software Tools Inc: www.pstnet.com) and responses were made using a PST Serial Response box. Word pairs were presented in white against a black background, using lower-case 18 point Courier New font. At the viewing distance of 97cm, the stimuli subtended a maximum horizontal visual angle of approximately 3.7°, and a maximum visual angle of approximately 1.4°.

Although two separate Unitization tasks were used throughout the thesis, a general overview is provided in this section. Specific procedural details such as timings are provided in the appropriate experimental chapters. Prior to each unitization task participants were required to complete a practice study and test block (using additional stimuli not employed in the actual experiment). Participants were provided with both verbal and written instructions prior to the beginning of the practice blocks. Participants who had completed the practice, but were still unsure were offered the opportunity to repeat both study and test practice blocks. For the experiments manipulating unitization through mental imagery (i.e. Chapters 8 and 10), the experimenter asked for examples of the mental images created by participants to verify that they had understood the experimental demands.

Example study and test trials used in the unitization tasks are shown in Figure 5.2. Study trials began with a fixation cross presented in the center of the screen in order to both focus the participant's attention and to indicate the imminent presentation of the study stimulus (i.e., either a word pair or word pair and sentence frame/compound definition). The fixation cross was followed by a blank screen after which the stimulus was presented. Each stimulus was presented with enough time for the participant to complete the task (as verified by either previous literature or pilot experiments). Study trials ended with a blank screen before the fixation cross was presented again indicating the onset of a new study trial.

Across all unitization experiments the test block directly followed on from the preceding study block. Test trials began with a central fixation cross followed by a blank screen. Stimuli were then presented on the screen, at which point participants were required to make a response. Participants were required to make a three-way Intact/Recombined/New response while the word pair was presented on the screen or shortly after during a blank screen. Responses were made using the index, middle and ring fingers of the right hand - corresponding to the second, third and fourth response buttons (of a five button response box). The mapping of Intact and New responses to the second and fourth buttons was counterbalanced across participants. After a response was made (or response time window elapsed) a blank screen was presented followed by the fixation cross indicating the next test trial.

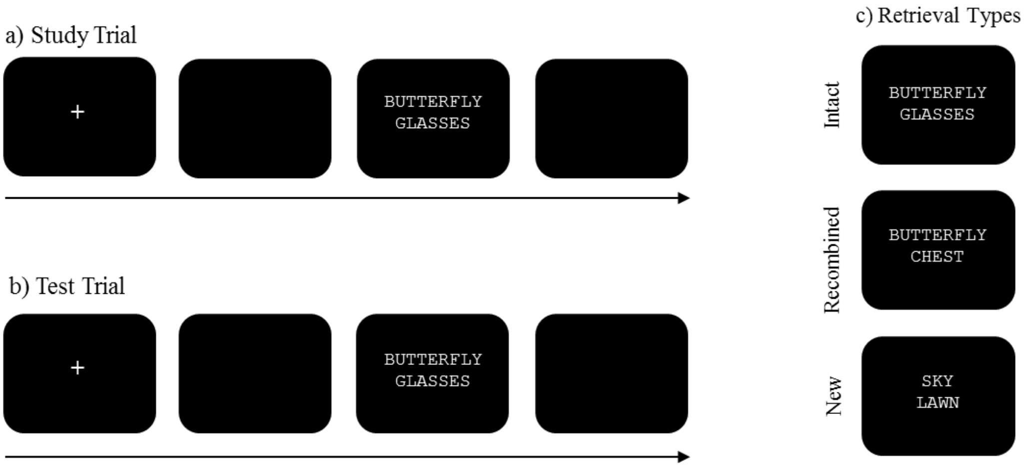

Figure 5.2: Unitization task paradigm: a) illustrates the study phase whereby participants must encode each word pair as per encoding instruction (i.e. unitization/non-unitization instruction); b) in the test phase the participant must discriminate between previously studied word pairs (intact), word pairs presented in a different pairing from study (recombined) and unstudied word pairs (new) - see c).

5.4. Data processing and analysis

5.4.1. Measuring discrimination accuracy

Discrimination accuracy is reported for all experimental tasks that required discrimination between previously studied and unstudied stimuli. Estimates of discrimination accuracy were calculated using the two-high threshold model (Snodgrass & Corwin, 1988). The discrimination index (Pr = Hits - False Alarms) was used to correct discrimination scores for lucky guesses. Although the discrimination index proposed by Snodgrass and Corwin, (1988) is applied routinely in the recognition literature, the index breaks down under certain circumstances. For instance, where a participant makes no errors, the two-high threshold model becomes undefined for hit rates of 1.0 or false alarm rates of 0 because the corresponding z scores are infinite (Snodgrass & Corwin, 1988). As a correction for values of 1 and 0, Snodgrass and Corwin, (1988) proposed that both the hit rate (number of hits + .5/number of old items

+1) and false alarm rate (number of false alarms +.5/number of new items +1) are routinely adjusted. This transformation has been applied with hit rates and false alarm values of 1 and 0 throughout the current thesis.

Importantly, studies of discrimination accuracy typically employ a measure of response bias (see Section 1.2.1. for more detail) to determine if participants are making conservative or liberal response judgements. In the current thesis however, the Unitization tasks employed required participants to make a three-way discrimination response between Intact, Recombined and New word pairs, a procedure identical to other ERP associative recognition studies (i.e., Bader et al., 2010; Rhodes & Donaldson., 2007, 2008). The inclusion of a Recombined response is important to ensure that participants do not identify an Intact pair based on the recognition of a single item – instead, the presence of Recombined items forces the participant to retrieve the association between pairs to make a successful judgement. The inclusion of a three-way response, however, makes the task inherently ambiguous with regards to response bias (which only accounts for bias between old and new responses). To date, the problem of accounting for response bias during a three-way decision task has not been resolved and it is therefore not included in the thesis. Regardless, the exclusion of a response bias measure does not have any direct bearing on the principle concern of the current thesis – to demonstrate difference in discrimination accuracy between Intact and New pairs between Unitized and Non Unitized tasks.

The three-way associative discrimination task employed in the current thesis is also distinct from previous behavioural associative recognition tasks that require participants to discriminate Intact from Recombined pairs. The inclusion of a third response will therefore make discrimination on any one trial more uncertain. Consequently, the results from the current experiments may not be directly comparable to behavioural studies employing a more simplified binary judgment. Employing 'New' pairs does, however, facilitate comparison with old/new effects strongly associated with recollection and familiarity (as outlined in Chapter 4). To ensure that discrimination accuracy accurately reflected the ERP Hit-Correct Rejection comparison, we treated Recombined responses as Hits; resulting in two types of false alarm (i.e., to Intact and Recombined pairs: identical to the procedure employed by Rhodes & Donaldson, 2008). Discrimination accuracy was therefore calculated separately for Intact and Recombined pairs. Although we accept that Recombined pairs can be treated as Correct Rejections, treating them as Hits allowed us separately analyse Intact/Correct Rejection discrimination that was of primary interest in the current thesis.

5.4.2. ERP data acquisition

EEG was measured at the scalp using 62 silver/silver chloride electrodes embedded in an elasticated cap (Neuromedical supplies: www.neuro.com) in accordance with an extended version of Jasper's (1958) International 10/20 system: (FP1, FPZ, FP2, AF3, AF4, F7, F5, F3, F1, FZ, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCZ, FC2, FC4, FC6, FT8, T7, C5, C3, C1, CZ, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPZ, CP2, CP4, CP6, TP8, P7, P5, P3, P1, PZ, P2, P4, P6, P8, PO7, PO5, PO3, POZ, PO4, PO6, PO8, CB1, O1, OZ, O2, CB2). The ground electrode GND was positioned midway between AF3 and AF4. During recording, each electrode was referenced to an additional electrode midway between CZ and CPZ. All channels were re-referenced offline to a virtual mastoid that was calculated by averaging the signal from electrodes located on the left and right mastoids. Vertical and horizontal EOG was recorded from bipolar pairs of electrodes placed above and below the left eye, and on the outer canthi. Electrode impedance was kept below 2kΩ. EEG and EOG data were amplified with a band pass filter of 0.1 – 40Hz, digitized by a 16 bit analogue to digital converter at a sampling rate of 250Hz and recorded on a desktop computer using Neuroscan Aquire software (Version 4.3). EEG data were processed using Neuroscan Edit (version 4.3).

The raw EEG was inspected and segments of data including high levels of noise (i.e. artefacts including excessive muscle movements) were removed. An ocular artefact reduction procedure was applied to reduce the effects of eye blinks: 32 optimal blinks from each participant were selected to estimate the individuals blink pattern and remove the contribution of the average blink from all channels. The EEG data was then epoched and time-locked to stimulus presentation at test using a 2040ms time window (starting with a 104ms pre-stimulus baseline). Epochs were rejected if they had a drift from baseline exceeding ±75 µV, or where the signal change exceeded ±100 µV. Averaged ERPs were then formed from correct responses and the data was baseline corrected and smoothed with a 5-point kernel. To ensure a good signal-to-noise ratio a minimum of 16 artefact-free trials was required from each participant, in each of the critical response conditions. The mean numbers of trials contributing to the grand average ERPs are described in the relevant experimental sections.

5.4.3. ERP analysis

In the current thesis, ERP ‘effects’ correlated with successful memory retrieval were of primary interest. For Chapters 6, 8, 9 and 10, memory retrieval was analyzed by comparing the difference in magnitude between ERP waveforms elicited by Hits (correctly identified ‘old’ items) and Correct Rejections (correctly identified ‘new’ items). Initial analysis focused on the 300-500ms and 500-800ms time windows; typically found to capture the neural correlates of familiarity and recollection respectively. To characterize the neural correlates of successful memory retrieval, mean amplitudes were calculated over the duration of each time-window for different electrodes and submitted to repeated measures ANOVA. In order to reliably capture the topography of old/new effects, selection of the number and location of electrodes are described in each experimental chapter. Only significant effects involving retrieval are reported and the Greenhouse Geisser correction for non-sphericity was applied where appropriate. Topographical analyses were employed on re-scaled data using the Min-Max method described by Mccarthy & Wood, (1985).

Chapter 6

Investigating the Nature of the Neural Mechanism Supporting Recollection

Recollection is one of the defining features of human declarative memory, allowing events such as the birth of one's child to be vividly remembered years later, while details of yesterday's finance meeting are simply forgotten. Although much is known about the cognitive and neural basis of episodic memory, clarifying exactly how the process of recollection operates has proved difficult. The current chapter attempts to address one key question: does the neural mechanism underlying recollection operate in a graded or all-or-none fashion? Whilst graded and thresholded accounts of recollection have been extensively debated within the behavioural literature, to date relatively little progress has been made in characterizing the mechanism supporting recollection at a neural level of analysis. To be clear, although much is known about *which* structures support recollection, exactly *how* the neural mechanisms underlying recollection operate remains a matter of heated debated.

6.1. Introduction

Attempts to characterize recollection at a behavioural level of analysis as either thresholded or continuous have largely focused on the interpretation of memory-related confidence ratings (using Receive Operating Characteristics, or ROC curves). According to threshold theories (e.g., Yonelinas, 1994) recollection attempts may succeed or fail, such that information is only available from memory on some occasions (leading to linear ROC curves when response confidence is assessed). By contrast, continuous accounts (e.g., Mickes, Wais & Wixted, 2009; Green & Swets, 1996) predict that recollection attempts always return some information from memory, but the information varies in strength (leading to curvilinear confidence-based ROC curves). Within the behavioural memory literature the thresholded versus continuous model question remains hotly debated (e.g., Wixted, 2007; Yonelinas, 2002), with confidence ratings being used to support claims made by both sides (e.g., Mickes, Wixted & Wais, 2007; Yonelinas & Parks, 2007). However, because confidence and memory retrieval are not directly related (e.g., Bröder & Shutz, 2009; Malmberg, 2002; Grasha, 1970), confidence ratings do not discriminate clearly between threshold and continuous accounts of recollection.

One promising solution is to use an alternative measure of recollection developed by Harlow and Donaldson (2013), based on the objective measurement of response accuracy. During a novel source memory experiment, participants were asked to remember a series of locations marked around a circle – each paired with a single word (illustrated in Figure 6.2a). At test, participants were presented with each previously studied word and asked to recollect the paired location (Figure 6.2b), allowing the precision of source memory responses to be measured. As no old/new decision is required in this task it is unlikely that participants could respond on the basis of familiarity or implicit memory. Importantly, threshold and continuous models of recollection make entirely different predictions about performance.

The specific predictors clearly distinguish thresholded from continuous models. In essence, according to the continuous model, guesses are based on weak below-criteria retrieval signals (and therefore non-random), whereas according to threshold models guesses are based on the genuine absence of any retrieval signal (and therefore randomly distributed). Continuous models predict that retrieval always produces some information from memory, with a greater likelihood of recollecting and therefore a greater frequency of responding, closer to the target. Critically, responding should decrease rapidly away from the target, with decreasing likelihood of recollection, and therefore fewer responses far from the target (as illustrated in Figure 6.3, right inset panel). By contrast, threshold models predict that successful recollection does not always provide information from memory, hence recollection responses will cluster close to the target, mixed with a separate set of sub-thresholded guesses. In this case, guesses are made in the absence of any retrieval signal and responses will therefore be randomly distributed relative to the target, producing a raised plateau of responses far from the target (Figure 6.3, left inset panel).

In the case of Harlow and Donaldson (2013), analysis of memory accuracy data revealed that the threshold model was better able to account for the pattern of responses than a continuous model, providing novel behavioural evidence that recollection is thresholded. Although the results of Harlow and Donaldson (2013) were able to characterise recollection behaviourally, their data says nothing about the underlying neural mechanism supporting recollection. In the current experiment, we employ the same novel source task to investigate the nature of the Left Parietal old/new effect which is strongly associated with recollection (for more detail see Chapter 4).

Within the broader neuroimaging literature, evidence for parietal retrieval success effects has been interpreted in a number of different ways. For example, the attention-to-memory model (Cabeza et al., 2008; Wagner et al., 2005; Rugg & Henson, 2002) views parietal activity as a reflection of the reorienting of attention to recovered episodic information. Alternatively, the episodic buffer model (Vilberg & Rugg, 2008, 2009) relates Left Parietal effects to the on-line maintenance of episodic information within working memory. Equally, accumulator models (e.g., Wagner et al., 2005; Donaldson et al., 2010) characterise retrieval success as reflecting the accumulation of evidence in support of memory judgements. Typically these models are not designed to characterise the way in which the retrieval mechanisms operate; nonetheless, they often allow explicit predictions to be made. For example, episodic buffer models characterise the neural generators of parietal retrieval success effects as being graded, reflecting sensitivity to the amount of information retrieved (e.g., Vilberg, Mossavi & Rugg, 2006; Vilberg and Rugg, 2009). By contrast, the attention to memory account is typically characterised as inherently thresholded, because the orienting of attention is considered to occur in an all-or-none fashion (e.g., Ciaramelli et al., 2008; Vilberg & Rugg, 2009). The purpose of the current experiment is to ask whether the underlying neural correlate of recollection operates in a graded or all-or-none fashion. As well as characterising the processes underlying recollection, this experiment should also help to discriminate between these competing models of the parietal cortex's role in episodic memory.

One reason imaging studies have failed to discriminate between all-or-none and graded accounts is that much of the evidence stems from studies of source memory, using contrasts that carry an inherent interpretational problem. Source memory tasks are useful because they allow comparisons to be made between successful responses accompanied by either correct or incorrect source judgements. Although ERP source memory findings reveal changes in the size of retrieval success effects that appear to be graded (i.e., larger Left Parietal effects for correct than incorrect source judgments; cf. Wilding & Rugg, 1995; Senkfor & Van Petten, 1998; Wilding, 2000), the observed pattern may in fact reflect little more than a data averaging artefact. That is, variation in the size of the parietal effect could simply reflect the averaging together of trials with and without recollection. A change in the proportion of responses upon which recollection had occurred across source correct and source incorrect conditions would result in a graded average, even if the underlying neural signal associated with recollection was all-or-none (see Wilding, 2000, and Vilberg et al., 2006, for discussion of this problem).

In summary, the picture that emerges from the existing literature is a pattern of Left Parietal effects that appears to reflect a graded signal (when examined in typical source memory contrasts), but could equally reflect an underlying all-or-none signal. Here we use an alternative approach that avoids the interpretational problem associated with traditional source memory paradigms; instead we measure neural activity associated with recollection as a function of positional response accuracy, using the Harlow and Donaldson (2013) source memory test. This continuous task allows us to focus on Left Parietal old/new effects associated with trials receiving accurate recollection responses – avoiding the problems associated with comparison of source correct and source incorrect responses. The current study, however, adapts the original Harlow and Donaldson (2013) study by employing an old/new task – therefore allowing comparisons of Left Parietal old/new effects to be made with previous source experiments[1]. It is important to note that the introduction of a correct rejection baseline does inherently alter the nature of guess responses in this task. In the distractor-free version of the task, guesses can be considered entirely free of memory if recollection is all-or-none, because the behavioural measure of recollection only reveals the retrieval of criterial information relevant to the task at hand. By contrast, even under the all-or-none assumption, guesses would be expected to give rise to Left Parietal old/new effects, because the neural measure reveals the retrieval of any information (criterial or not), and relative to correct rejections, some recollection of information would be expected (even if this information does not support accurate responding). On this basis, guesses should elicit Left Parietal old/new effects regardless of whether recollection is graded or all-or-none.

Consistent with previous ERP studies demonstrating that the Left Parietal old/new effect is sensitive to the amount of recollection, continuous accounts predict that the Left Parietal old/new effect will vary in magnitude according to how precisely the target location is retrieved – i.e., the Left Parietal effect will be larger when recollection responses are more precise (see Figure 6.1, left panel). By contrast, if the Left Parietal old/new effect behaves in an all-or-none fashion, the magnitude of recollection should be equivalent for both high and low precision responses (and larger than that seen for guess responses, see Figure 6.1 right panel). To be clear, in light of the results of Harlow and Donaldson (2013) demonstrating variable recollection from a behavioural

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[1] Adapting the novel source task by adding an additional old/new decision allows comparisons to be made with previous source studies. The addition of an old/new decision, however, does not allow for a test between continuous and some-or-none accounts because, under these circumstances, similar patterns of Left Parietal effects are predicted. To be clear, both some-or-none and continuous accounts predict that Left Parietal activity will be present in variable amounts as precision increases (see Chapter 7 for a test between these two accounts). The current experiment therefore cannot test between the presence and absence of a threshold per se, but rather aims to differentiate between continuous and all-or-none accounts of Left Parietal activity.

level of analysis, a graded neural signal would imply that the underlying mechanism supporting recollection operates in a similar variable fashion. Alternatively, an all-or-none pattern would suggest that the neural and behavioural signals of recollection operate in different manners.

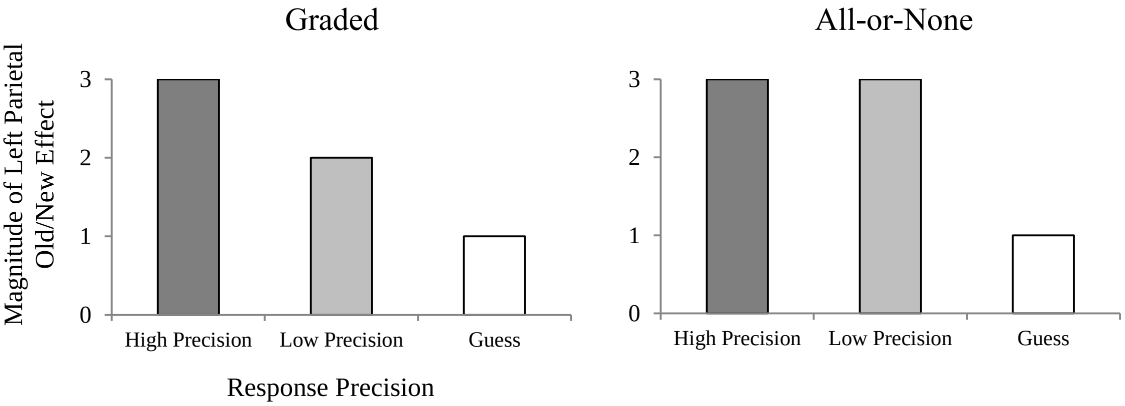

Figure 6.1: An illustration of the possible patterns of Left Parietal old/new effects. A Continuous account predicts a pattern of Left Parietal old/new effects that scale with precision. Alternatively, the All-or-None account predicts that trials that exceed a threshold will result in equal amounts of recollection.

6.2. Method

6.2.1. Participants

Thirty two University of Stirling students took part in the study. Data from two participants were excluded due to poor behavioural performance, and a further 8 were excluded due to an insufficient number of trials in at least one critical condition. The remaining 22 participants (11 female) had a mean age of 22 (range: 18 – 29).

6.2.2. Stimuli

The stimuli employed in the current experiment are identical to those described in the General Method (see Section 5.3.1). To reiterate in brief, 420 single nouns were randomly assigned to two lists (list 1 and list 2) of 240 words. These lists were matched for imagability, concreteness and word length. Both imagability and concreteness were kept low to prevent visualization of word/location associations which may encourage unitization. The presentation of lists as either 'old' or 'new' words was counterbalanced across participants. To be clear, list 1 words would be presented as 'old', and list 2 as 'new'. For the practice, an additional 18 words were employed; 8 as 'old' and 8 as 'new'. The target locations used during the source decision were identical to those described in the General Method (Section 5.3.1).

6.2.3. Procedure

The general experimental procedure is described in the General Method (see section 4.4.2). In the current experiment, participants began every study trial (see Figure 6.2a) by pressing a response button, which triggered the presentation of a fixation cross (+) for 2000ms. The cross was followed by a blank screen for 1000ms, after which a black cross located on a grey circle outline was shown for 2000ms. After a further 1000ms blank screen a word was presented for 2000ms. Participant's attention to the location was then tested by asking them to verify the (now hidden) location using the mouse. Responses within 20 pixels (~ 6º) from the target advanced participants to the next trial. If the participant's response was over 20 pixels away, the target location was presented again for 250ms and the verification task was repeated.

Every test trial (see Figure 6.2b), began with a fixation cross (500ms) followed by blank screen (500ms). A word from the previous study block was then shown (3000ms). Participants were given the entire length of time that the word was presented to make an ‘Old/New’ decision. Responses were made using buttons 1 and 5 on a 5 button response box and participants were instructed to use their index and ring finger of the right hand. The mapping of ‘Old’ and ‘New’ to buttons 1 and 5 was counterbalanced across participants. If the participant responded ‘New’, or time had elapsed, a blank screen was shown (1000ms) and the next trial began. If the participant responded ‘Old’, a grey circle outline was presented immediately after their response and participants were asked to recall the paired location by moving the mouse curser to the remembered location and clicking the left mouse button. A red marker then appeared on the circle to indicate the chosen location. No response time limit was set and participants were free to change their decision. Participants finalized their response with a button press, which initiated the next trial. After the experiment was completed the precision of each test response was calculated, converting the screen co-ordinates selected by the participant into degrees: the remembered location was compared to the target location to provide the degree of error for that chosen location.

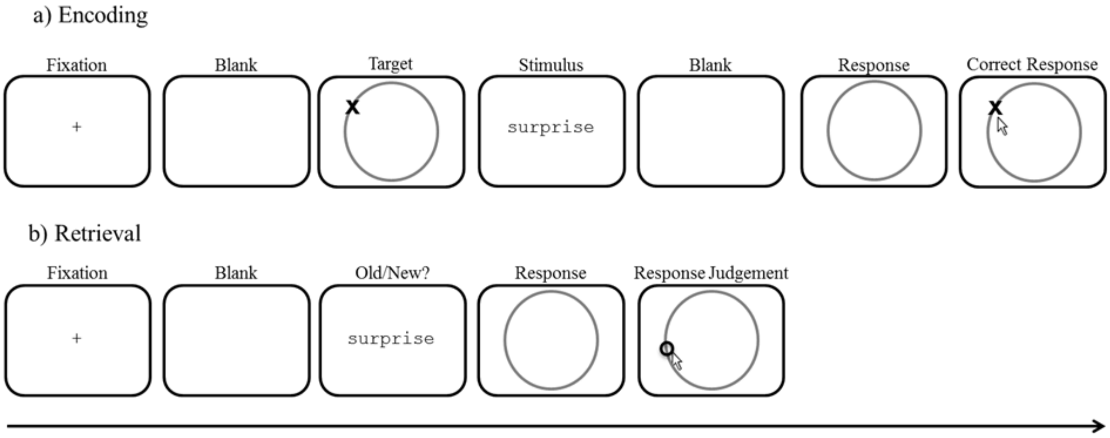

Figure 6.2: The source memory task. **a)** During encoding, participants were instructed to memorize words paired with locations, indicating the location after each trial to confirm attention. **b)** During retrieval, participants were required to discriminate between previously studied and new words. If an old response was given, participants were then required to recall the position using the mouse.

6.2.4. ERP Recording

The general ERP recording procedure was identical to that described in the General Method. ERPs were analysed by examining mean amplitudes (relative to the pre-stimulus baseline) during *a priori* defined time-windows, designed to capture the neural correlates of familiarity (300-500ms) and recollection (500-800ms). All ERP data analysis was carried out using repeated measures ANOVA (specific factors and levels are described where appropriate in the results) and were followed up with topographic analysis (as described in the General Method).

6.3. Results

6.3.1. Behaviour

Participants were able to successfully perform the Old/New discrimination task with a mean Hit rate of 65% (s.d. = 16%) and False Alarm rate of 7% (s.d. = 5%). Mean discrimination accuracy [pr = 58%, s.d. = 17%] was significantly above chance [t(21) = 2.25, $p < .05$]. Mean response time to Hits was 1140ms (s.d. = 232) and Correct Rejections was 1006ms (s.d. = 166).

To make sure stimuli were sufficiently attended to at encoding, participants were required to verify each location presented at study. The study revealed that participants were highly accurate at verifying the target location: analysis of participant's initial responses confirmed that 90% were within 10º of the target. More importantly, as would be expected, analysis of responses at test revealed a far lower level of accuracy: only 33% of responses were within 10º of the target. The overall pattern of test responses is shown in Figure 6.3. The data clearly suggest a threshold at retrieval – indicated by the raised level of responses at locations far from the target, which reflects a plateau of random guessing. As was observed previously by Harlow and Donaldson (2013), the pattern of responses at test exhibits a Cauchy distribution, with a greater frequency of very accurate and inaccurate responses than a Gaussian distribution can accommodate.

The data were analysed using the modelling procedures of Harlow and Donaldson (2013). To test whether the observed error distribution exhibited a threshold or continuous pattern, each participant's data was fitted to a threshold model with two free parameters: λ denoted the proportion of trials where recollection succeeded (larger values indicating more recollection); s denoted the spread of responses (larger values indicating greater mean error, i.e., less precision). To discriminate between the threshold and continuous accounts, we compared our model by either fixing the value of λ at 1 (such that all responses are based on some variable amount of recollection, consistent with a continuous pattern), or allowing λ to vary below 1 (such that recollection could completely fail on a subset of responses, consistent with a threshold pattern, and resulting in random guessing around the circle). To detect the existence of a threshold we conducted a likelihood ratio test[2]. By allowing λ to vary below 1 we significantly improved the likelihood of the observed data, compared to fixing λ at 1 [mean λ = .84, $\chi^2(22) = 2279.90$, $p<.001$]. The distribution of error responses was, therefore, more accurately modelled with a threshold.

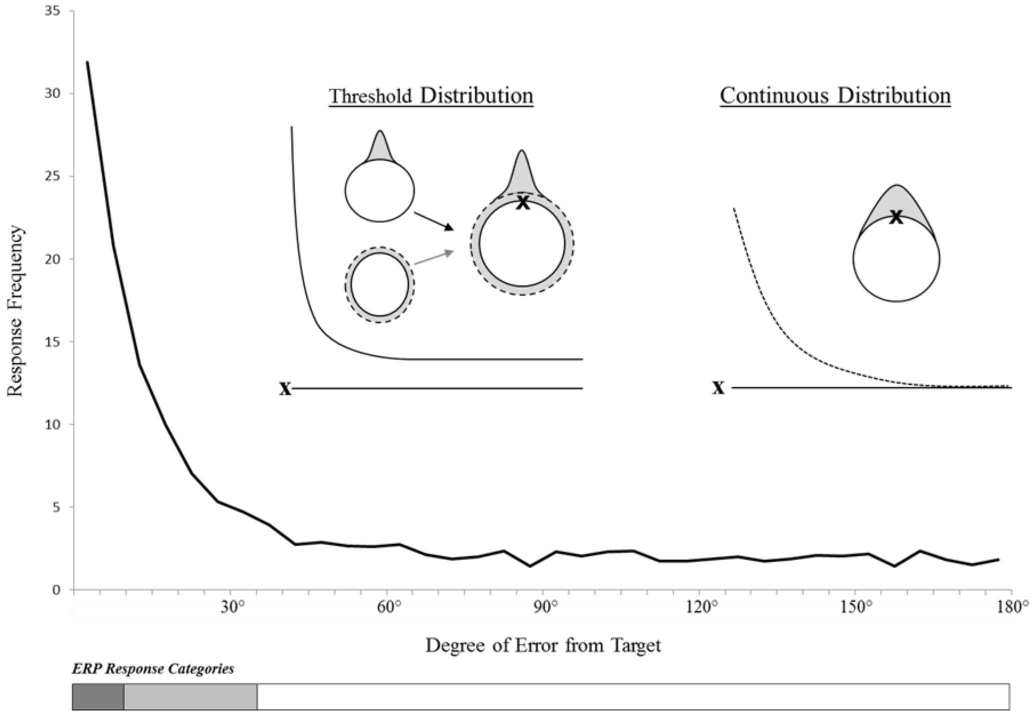

Figure 6.3: Observed error distribution. The data clearly shows that responses clustered around the target and also exhibited sub-threshold guessing (recollection failure). Inset is the distribution of errors predicted by both a Threshold and Continuous accounts. Below the error distribution is an illustration of the ERP Response Category bins, aimed at capturing High precision trials (<10°), Low precision responses (11>35°) and Guess responses (>36°).

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[2] The likelihood ratio test is a statistical test of the goodness of fit between two models. Typically, one model will be nested in another model with less parameters. In the current experiment, the Cauchy distribution has one extra parameter (e.g., shape parameter plus Guessing) than the Guassian distribution (e.g., containing only a shape parameter). The likelihood ratio test follows a chi-square distribution to determine if the difference between the two likelihood ratio scores (i.e., 2 [ln Cauchy - ln Guassian]) is statistically different.

Individual variability in responding was also examined, to assess the consistency of the response threshold across participants. Individual response profiles are shown in Figure 6.4. As is clear from the figure, the pattern of responses observed in the majority of participants is indicative of a threshold – matching the average data. For a small number of participants the pattern is less clear, exhibiting very precise responding with little guessing at all, or far greater guessing and a flatter profile of responses around the circle. Examination of the data revealed that the value of λ and s differed across participants (values ranged from .58 to .99 and 1.97 to 17.38 respectively) reflecting considerable variation in the rate and precision of recollection. Importantly, linear regression was conducted on each individual participant's data to determine the exact point participants began to guess – this was achieved by determining when the slope of the distribution curve became non-significant from 0. The range of thresholds across participants was dramatic (i.e., 14-110°), again reflecting the considerable variation in response accuracy among participants. Analysis of the overall distribution across all participants revealed that the mean threshold was at 60°.

6.3.2. Event Related Potentials

ERPs were formed for every participant by averaging EEG data recorded at test for Hits into three separate response categories, as well as forming Correct Rejection ERPs. The response categories were designed to capture ERP activity elicited by different rates of positional response accuracy (i.e., precision), whilst also providing sufficient trial numbers to form ERPs across participants: 'High Precision' ERPs were designed to capture only the most precise responses, defined as under 10º from the target location; 'Low Precision' ERPs captured less precise responses, ranging from 11º to 35º from target; ‘Guesses’ ERPs captured trials associated with guessing, ranging from 35° to 180°[3]. Finally, ‘Correct Rejection’ ERPs were formed from correctly identified new words (i.e., providing a comparison category that contains no memory signal that would be diagnostic of prior occurrence). The mapping of ERP response categories to the behavioural data is illustrated in Figure 6.2.

The experimental prediction that the Left Parietal old/new effect would be sensitive to precision was tested by averaging across Parietal and Centro-Parietal strings of electrodes (CP5/P5, CP3/P3, CP1/P1, CP6/P1, CP4/P4, CP2/P2: see Figure 6.5) and comparing activity elicited for correctly recollected, guessed and baseline responses. Initial ANOVAs were performed on each response category to test for within category old/new effects, with factors of Category (High, Low or Guess/Baseline), Hemisphere (Left/Right) and Site (Inferior/Middle/Superior) during the 500-800ms time window. The mean number of trials contributing to the grand averages are as follows: High precision response (42), Low precision response (40), Guess response (52), Correct Rejection (215). The outcomes of these analyses are described below, followed by subsidiary analysis as appropriate.

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[3] A further bin capturing trials with sub-thresholded guessing (i.e., over 90°) would have been preferable to examine ERPs to responses made on the other half of the circle – synonymous with an incorrect source judgment. Unfortunately, not enough trials from a sufficient number of participants were available to form ERPs to responses over 90° in the current experiment. In addition, an insufficient number of trials also prevented us from using the average 60° threshold.

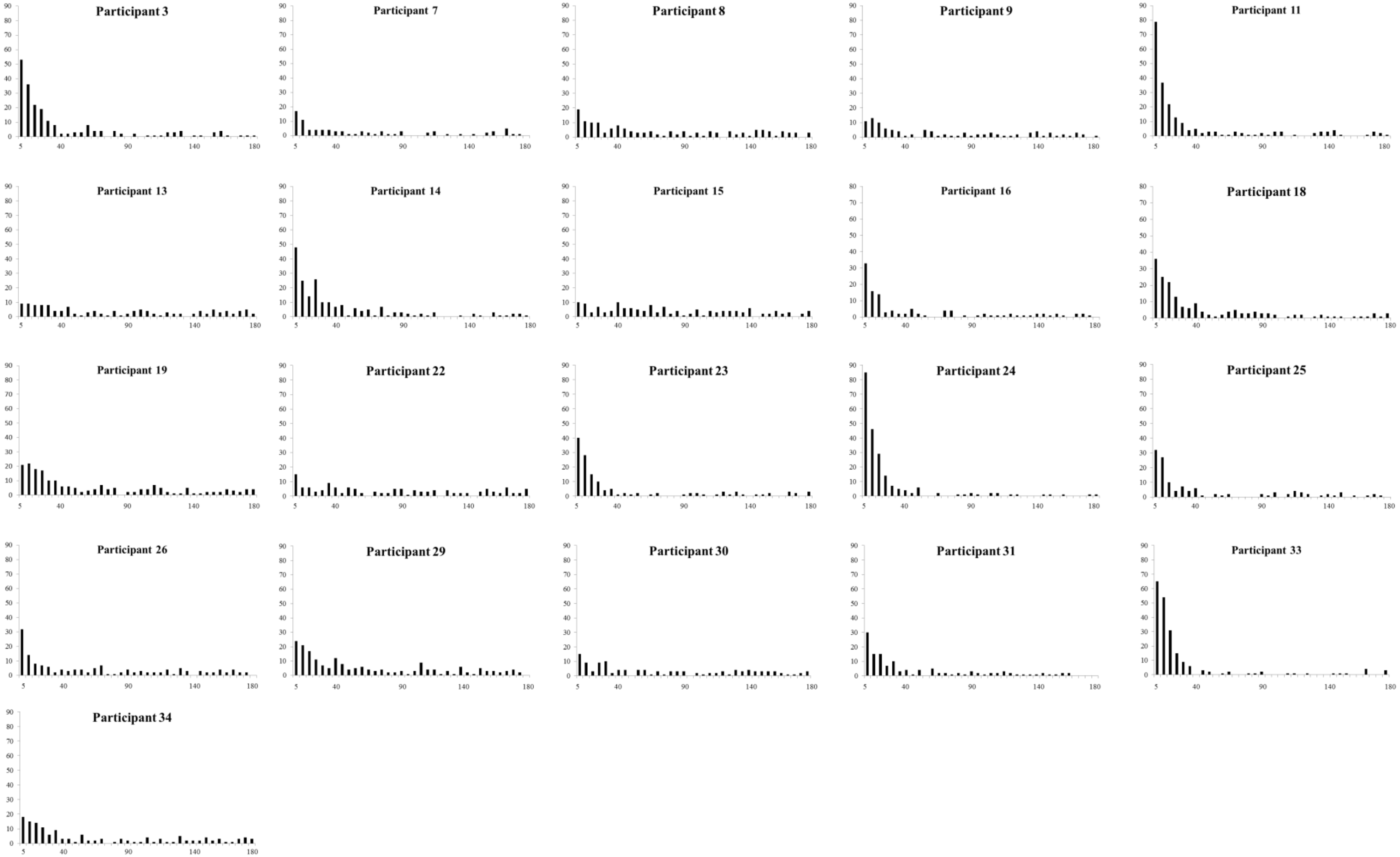

Figure 6.4: Individual response frequencies for all 22 participants. Error distance is displayed on the x axis and frequency (real counts) is displayed on the y axis.

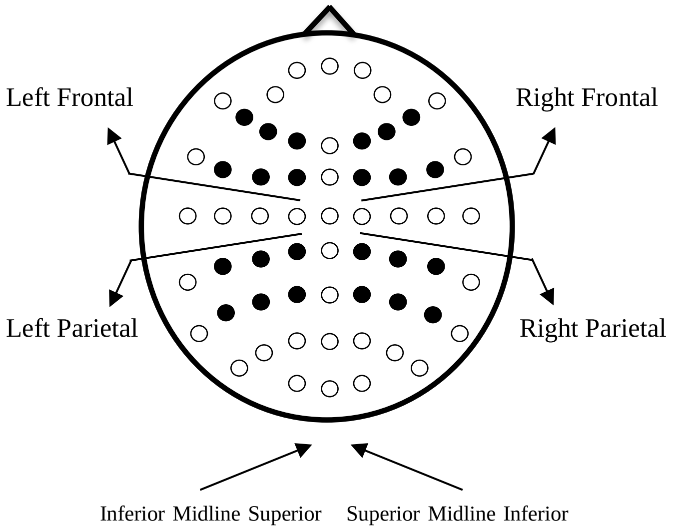

Figure 6.5: Map of the 62 recording electrodes. Electrodes used in the main analysis appear in black.

6.3.2.1. Left Parietal old/new effect

Figure 6.6 shows the Grand average ERPs for High, Low, Guess and Correct Rejection responses at electrode P3. High precision responses elicit more positive going neural activity than Low precision responses; both High and Low are more positive than Guess responses, and all response categories are more positive going than Correct Rejections. The distributions of Left Parietal old/new effects is illustrated in Figure 6.7: all response categories exhibit parietal old/new activity, with a clear left compared to right hemisphere asymmetry. The old/new activity appears maximal over the Left Parietal scalp location for High and Guess responses; and additional bilateral frontal activity is also observed for High and Low precision responses.

Initial ANOVAs examining the ERP effects found over parietal electrodes compared each response category to correct rejections, revealing significant main effects of

Category for High precision [F(1,21) = 11.18, p = .001], Low precision [F(1,21) = 13.73, p = .001] and Guess [F(1,21) = 6.54, p < .05] responses. Results also revealed that ERPs were larger over the left hemisphere compared to right hemisphere, with significant Category by Hemisphere interactions for High precision [F(1,21) = 16.31, p = .001], Low precision [F(1,21) = 24.64, p < .001], and Guess [F(1,21) = 4.75, p < .05] responses. In addition, significant Category by Hemisphere by Site interactions were also observed for High precision [F(1.48,31.02) = 8.9, p < .01], Low precision [F(1.71,35.95) = 15.04, p < .001] and Guess [F(1.34,28.17) = 4.37, p < .05] responses, indicating that activity over the left hemisphere was maximal over the medial sites – consistent with the presence of a Left Parietal old/new effect.

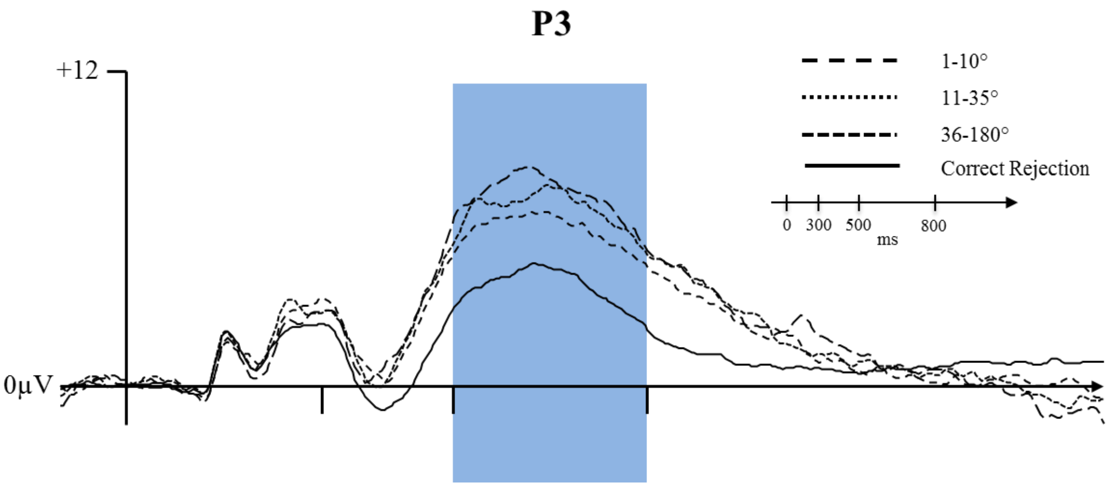

Figure 6.6: Grand Average ERPs for High Precision Responses, Low Precision Responses, Guess Responses and Correct Rejections at electrode P3 during the 500-800ms time window.

The previous analysis demonstrated that significant Left Parietal old/new effects were present. A topographical analysis was also carried out to assess whether the Left Parietal old/new effects (revealed in the previous analysis) could have been generated from different neural populations. An initial ANOVA with factors of Category [High/Low/Guess], Location [Frontal/Fronto-Central/Central-Parietal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior] was carried out on subtraction data (i.e., recollected/guess response categories minus Correct Rejections) to assess whether there were any distributional differences between Categories. If significant interactions were found, the data were rescaled and the ANOVA was carried out again – i.e., to assess whether the initial interactions were generated by separate neural generators or simply reflected differences in effect size. The initial ANOVA revealed a significant Category by Location by Site interaction [F(3.12,65.43) = 3.27, p < .05], reflecting the additional activity exhibited by High and Low precision responses over the frontal electrodes at superior sites compared to Guess responses. Critically, when the data was rescaled, no significant interactions were observed, suggesting that the original interaction reflected a change in mean amplitude strength from a common set of neural generators.

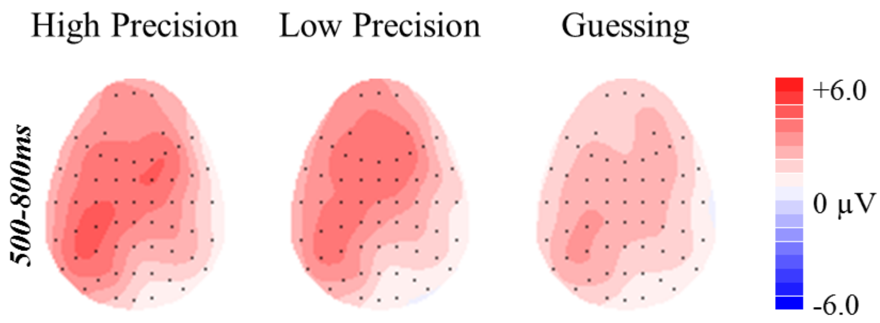

Figure 6.7: Topographic maps illustrating the Left Parietal old/new effects for High Precision Responses, Low Precision Responses and Guess Responses within the 500-800ms time window. The scale bar represents the voltage range (µV).

Consistent with the scalp maps shown in Figure 6.7, examination of the data revealed that the Left Parietal old/new effects were maximal over the Left Parietal scalp region: more specifically, electrode CP3 for High (mean = 3.85µV, s.d. = 4.26) and Low (mean = 3.26µV, s.d. = 3.53) and Guess (mean = 2.25µV, s.d. = 3.21) response categories. The pattern of Left Parietal effects observed in Figure 6.8 clearly indicates the presence of a graded Left Parietal old/new effect with the size of the effect scaling with precision: i.e., largest for High responses, with a reduced effect for Low responses, and smallest for Guesses responses. A stringent series of planned comparisons was carried out to examine the magnitude of the Left Parietal old/new effect (measured by averaging across all 6 Left Parietal electrodes) across response categories (mean data illustrated in Figure 6.8). Bonferonni corrected one-tailed t-tests ($\alpha = .01$) revealed that the Left Parietal old/new effect was significantly larger for High precision compared to Guess responses [$t(1,22) = 2.55$, $p = .01$], but did not differ compared to Low precision responses. Finally, no significant differences were observed between Low and Guess responses.

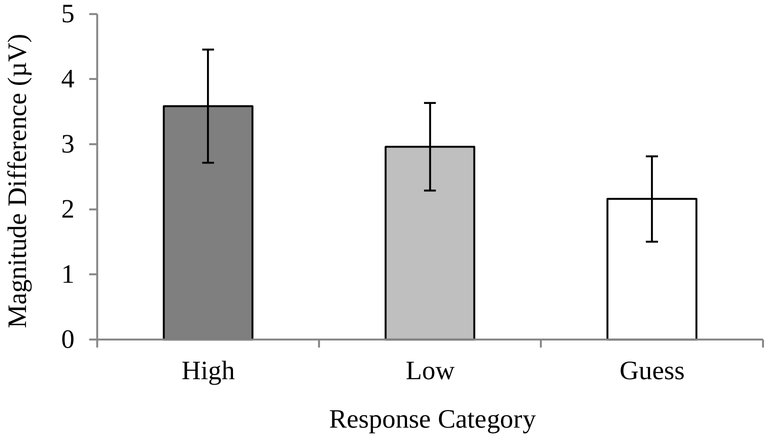

Figure 6.8: The mean magnitude (and standard error bars) of the Left Parietal old/new effect for High Precision, Low Precision and Guess Responses within the 500-800ms time window.

6.3.2.2. Mid-Frontal old/new effect

From the grand average shown in Figure 6.9, it is clear that old/new differences were also observed over the frontal region within the 300-500ms time window. In addition, the distribution of old/new effects shown in Figure 6.10 demonstrates a frontally distributed effect clearly evident for High and Low precision responses, with a less clearly defined old/new effect for Guess responses. Additional analysis was therefore carried out to assess whether Mid-Frontal old/new effects associated with familiarity were present. Data from 6 frontal electrode pairs were employed (FC5/F5, FC3/F3, FC1/F1, FC6/F6, FC4/F4, FC2/F2: see Figure 6.5). Analysis was again carried out on each response category separately, using an ANOVA with factors of Category [High, Low or Guess/Correct Rejection], Hemisphere [Left/Right] and Site [Inferior/Middle/Superior].

The analysis revealed significant main effects of Category for High [F(1,21) = 16.42, p = .001], Low [F(1,21) = 28.69, p < .001] and Guess [F(1,21) = 10.26, p < .01] responses, reflecting more positive going activity for all three response categories compared to Correct Rejections. Significant Category by Site interactions were also observed for High [F(1.09,22.87) = 19.75, p < .001], Low [F(1.14,24.03) = 19.38, p < .001] and Guess [F(1.08,22.43) = 9.21, p < .01] responses, reflecting a superior distribution. Critically, no interactions with Hemisphere were observed for High and Low precision responses – consistent with the presence of a Mid-Frontal old/new effect. Significant Category by Hemisphere [F(1,21) = 5.11, p < .05] and Category by Hemisphere by Site [F(1.23,25.73) = 6.28, p = .01] interactions were, however, also found for Guess responses, reflecting superior maxima over the right compared to left hemisphere.

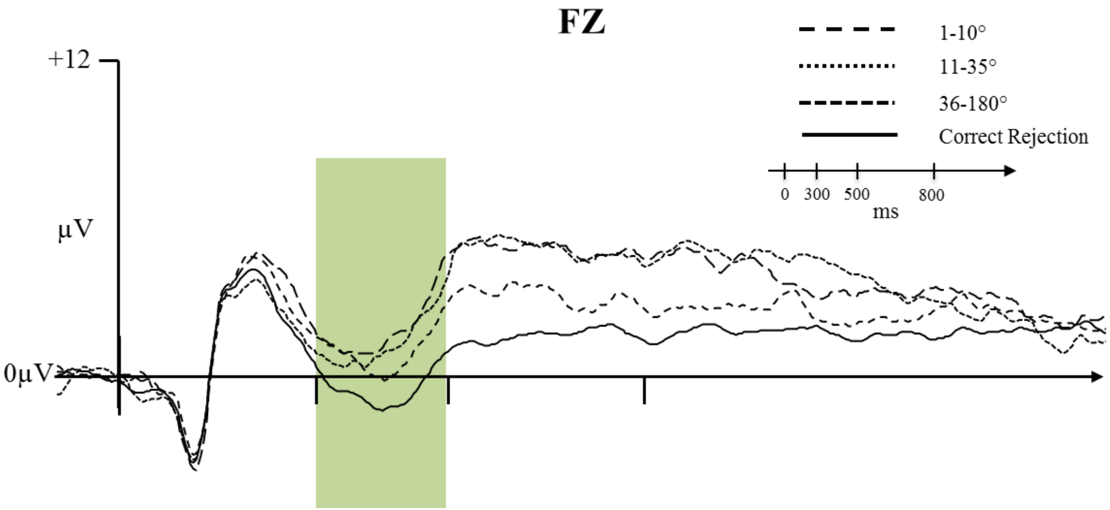

Figure 6.9: Grand Average ERPs for High Precision Responses, Low Precision Responses, Guess Responses and Correct Rejections at electrode FZ during the 300-500ms time window.

Having previously demonstrated significant frontal old/new activity exhibited by High, Low and Guess responses, topographic analysis was carried out to assess whether the observed frontal activity could have been generated by different neural populations. As with the previous topographic analysis, an initial ANOVA was carried out on the subtraction data with factors of Category [High/Low/Guess], Location [Frontal/Fronto-Central/Central Parietal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Analysis revealed no significant interactions, reflecting similar topographies for all three response categories within the 300-500ms time window.

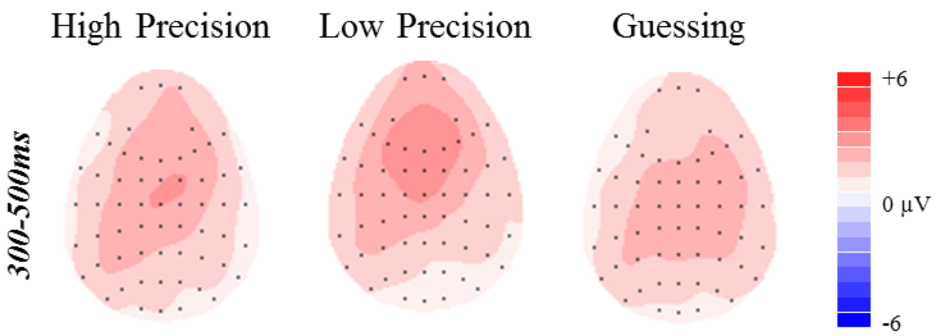

Figure 6.10: Topographic maps illustrating the distribution of old/new effects for High Precision Responses, Low Precision Responses and Guess Responses within the 300-500ms time window.

Further exploration of the data revealed that the frontal effect was maximal at FC2 for High (mean = 2.20µV, s.d. = 2.23) and Guess responses (mean = 1.91 µV, s.d. = 2.57), and maximal at electrode FCZ for Low precision responses (mean = 2.54 µV, s.d. = 2.20). To assess potential magnitude differences of the Mid-Frontal old/new effect (associated with the contribution of familiarity), paired t-tests were carried out on an averaged cluster Mid-Frontal electrodes (F1/FC1, FZ/FCZ, F2/FC2) across all three response categories (bonferroni corrected α = .01). The results did not reveal any statistical differences in the size of the Mid-Frontal old/new effect between response categories.

6.3.2.4. Fine grained analysis of Left Parietal old/new effect

Fine-grained analysis controlling for bin size was planned to test whether a graded pattern of Left Parietal old/new effects could be a result from a data averaging artefact (i.e., see Section 5.1). To be clear, as guessing is random, the responses will follow a uniform distribution around the circle. By creating ERP bins of equal size, each bin will carry the same level of guessing but will vary in the contribution of recollection. The subsidiary analysis, however, was not carried out given the lack of a statistically significant graded pattern of Left Parietal old/new effects.

6.4. Discussion

The current experiment aimed to discriminate between the Graded and All-or-None accounts of the Left Parietal old/new effect. To this end, a novel source memory paradigm (Harlow & Donaldson, 2013) was employed that provided a continuous measure of recollection as a function of positional source accuracy. A significant graded pattern of Left Parietal old/new activity would confirm that the underlying neural signal of recollection is itself variable much like the behavioural expression of recollection. Alternatively, if an all-or-none pattern was observed, the underlying neural mechanism of recollection would be shown to operate differently from recollection measured at a behavioural level. Analysis of the behavioural data supported the some-or-none account of recollection proposed by Harlow and Donaldson (2013). By contrast, the ERP results were less clear, exhibiting a pattern of Left Parietal old/new effects that appeared to scale with precision, although the pattern was not supported statistically. Below the behavioural and ERP data are discussed in turn.

6.4.1. Behavioural overview

Discrimination accuracy confirmed that participants were able to successfully perform the old/new recognition task. In addition, the observed error distributions for the source task replicate the results of Harlow and Donaldson (2013) supporting the finding that recollection exhibits a threshold and sometimes fails completely. In the current experiment, the rate of recollection was higher than previously reported ($\lambda =$ 70% reported by Harlow & Donaldson, compared to 84% in the present data) indicating that participants were recollecting well above chance, and well below ceiling. The higher rate of recollection in the present experiment more than likely reflects the changes made to the original paradigm. The inclusion of an old/new decision, for instance, will have resulted in a number of trials carrying a weaker source signal being incorrectly identified as ‘new’ – resulting in fewer sub-thresholded trials being included in the distribution of errors. By contrast, the original Harlow and Donaldson (2013) study will have included more sub-threshold responses since participants had to make a source decision on every trial.

The improved source performance observed in the current experiment was also evident from the increased precision compared to Harlow and Donaldson (s = 8.48 compared to 9.68). Again, the improved precision is more than likely a result of the additional old/new decision task (whereby participant’s source judgements are made when they have already accurately responded ‘old’). Regardless of the difference in performance between the current study and that of Harlow and Donaldson, the general pattern of source accuracy observed here supports the existence of a behavioural threshold suggesting that when recollection is successful, the information returned is of variable quality, in line with a ‘some-or-none’ process (Parks & Yonelinas, 2009). The pattern of results, however, is difficult to reconcile with single process theories that predicts there should always be some (however weak) information retrieved from memory, because this kind of continuous model cannot account for the observed distribution of error responses.

6.4.2. Overview of the Mid-Frontal old/new effect

In the current experiment, the contribution of recollection and familiarity were examined by measuring their closely associated neural correlates – i.e., the Left Parietal and Mid-Frontal old/new effects respectively. Here, we discuss each correlate in turn, beginning with the Mid-Frontal old/new effect. Although the experiment was a test of recollection, it was possible that the behavioural expression of recollection may actually reflect the contribution of familiarity – widely believed to be a continuous process (Murdock, 1974; Gillund & Shiffrin, 1984; Mandler, 1980; Yonelinas, 1994, 2001a, 2001b). Although the source task was designed by Harlow and Donaldson (2013) to limit the contribution of familiarity, they did not provide any direct test of this assumption, relying simply on the requirement to make source discrimination to isolate recollection. In the current experiment however, the contribution of familiarity was likely given the presence of an old/new item recognition task. Analysis of the data, however, revealed that although Mid-Frontal old/new effects were present, the magnitude of the effect did not significantly differ between response categories. Although caution should always be taken when interpreting a null result, the pattern of ERP data taken together with an experimental paradigm that discourages familiarity for source information supports the assumption made by Harlow and Donaldson (2013) that source accuracy mainly reflected recollection.

6.4.2. Overview of the Left Parietal old/new effect

The primary aim of the current experiment was to test between the Graded and All-or-None accounts of the Left Parietal old/new effect. As expected, analysis of the ERP data revealed significant Left Parietal old/new effects for all three response categories within the 500-800ms time window, reflecting the contribution of recollection. The pattern of data revealed a graded pattern, with the magnitude of the Left Parietal old/new effect being larger for High precision responses, reducing in size for Low precision responses and smallest for Guessed responses. Statistical analysis of the data partially confirmed that a graded pattern was present. To be clear, the Left Parietal old/new effect was statistically larger for High precision responses compared to Guessed responses, but not between High and Low, or Low and Guessed, responses.

The pattern of Left Parietal old/new effects is difficult to interpret. In one instance, the current pattern of Left Parietal old/new effects may reflect the nature of the underlying neural signal supporting recollection. Perhaps the recollection signal is only significantly different from guessing when trials are recollected with fairly high precision – resulting in a significantly large Left Parietal old/new effect. Alternatively, recollection associated with lower precision trials may be more variable than high precision trials resulting in a signal that is both indistinguishable from activity elicited by either high and guess responses. How this pattern of data fits with the existing models of recollection is however, unclear. For example, it is possible that the neural signal supporting recollection operates in an all-or-none fashion. By this account, no differences were observed between High and Low responses because both exceed a recollection threshold. The absence of any significant differences in the size of the Left

Parietal old/new effect between Low and Guessed responses, however, is difficult to reconcile with an all-or-none account – i.e., the magnitude of the Left Parietal old/new effect was not statistically different for Low responses that reflect above-thresholded responses, and Guessed responses that reflect sub-thresholded responses.

Alternatively, it is possible that the Left Parietal old/new effect is in fact graded, but the experimental paradigm was not sensitive enough to detect the differences between High, Low, and Guessed response categories. The inclusion of an old/new task, for example, meant that potential changes in recollection due to source accuracy were confounded with recollection for 'old' items. Although the old/new task facilitates comparisons with previous ERP source experiments, it more than likely introduces additional non-criterial recollection of information not related to the source task. Further, the nature of the adapted source recollection task also meant that participants did not provide an equal number of source judgements (as a result of the initial old/new recognition task), resulting in large variability of response frequencies. More specifically, the difference among individual thresholds among participants, for example, may have resulted in a significant proportion of recollected trials being incorporated into the guess bin – particularly for those participants with low thresholds (i.e., those thresholds above 90°). These recollected trials may have resulted in a larger left parietal old/new effect than would be expected if the bin only reflected non-criterial recollection associated with the old/new task. In short, the ERP results reveal that the underlying neural signal associated with recollection was present and was larger for High compared to Guessed responses but the predicted graded pattern did not reach statistical significance.

6.4.3. Summary

The aim of the current experiment was to test between the Graded and All-or-None accounts of the Left Parietal old/new effect during a novel source task. The behavioural data was entirely consistent with the finding that the behavioural expression of recollection is both variable and thresholded. The ERP data, by contrast, failed to differentiate between a Graded and All-or-None account of the underlying neural mechanism supporting recollection. Although the graded Left Parietal old/new effect observed in the current study did not reach significance, the pattern of data suggests that the underlying neural mechanism may be sensitive to positional response accuracy. Given the possible insensitivity of the current task to detect a graded pattern in the ERP data, it was decided to remove the old/new task and provide a more direct measurement of retrieval success. The results of this experiment are reported in the next chapter.

Chapter 7

Detecting a Threshold in the Neural Signal Supporting Recollection

The aim of Chapter 6 was to test between the Graded and All-or-None accounts of the Left Parietal old/new effect. To this end, a novel source task was employed that measured recollection in terms of positional source accuracy. Although a graded pattern was observed, it was not statistically significant, making it difficult to interpret of the data within a Graded or All-or-None framework. The current study aims to replicate the previous experiment with one key change: the removal of the old/new distractor task. By doing so, we can also extend the focus of the study by addressing whether the Left Parietal effect, much like the behavioural expression of recollection, is variable and thresholded. A positive result would clarify the nature of the neural mechanism underlying episodic memory, providing novel evidence in support of threshold models of recollection.

7.1. Introduction

Attempts to characterise the nature of the underlying neural signal supporting recollection has generally framed the debate between a Continuous or All-or-None thresholded process. To date, the consensus is that the Left Parietal old/new effect reflects a Continuous process, providing evidence that the Left Parietal old/new effect is sensitive to the amount of information retrieved (Wilding, 2000; Vilberg & Rugg, 2008). Due to the interpretational problem outlined in Chapter 5, however, it has been relatively difficult to firmly rule out an All-or-None process. In light of recent behavioural evidence (see Harlow & Donaldson, 2013), demonstrating that recollection is variable when successful, but entirely absent when recollection fails, it is possible that the underlying mechanism supporting recollection may operate in a similar Some-or-None fashion. According to a Some-or-None perspective, the Left Parietal effect would scale with precision when recollection is variable (e.g., similar to the Continuous process) but would be absent when recollection failed (e.g., indicative of a threshold). By testing between these three alternative accounts of the Left Parietal effect, progress can be made in appropriately characterising how the neural mechanisms underlying recollection operate. Below, we briefly review the behavioural distinction between the Continuous and Some-or-None processes before introducing the aims of the current experiment.

Behaviourally, an important nuance of the Harlow and Donaldson (2013) results lies in the distinction between two broad classes of threshold model: All-or-None versus Some-or-None. In the former case recollection is considered to be binary, with memory cues either leading to no output, or triggering a discrete (fixed) output from memory. By contrast, some-or-none models allow the output to vary (e.g., in the amount of information recovered, or the precision of the information remembered) when retrieval is successful. Whilst some early models of recollection characterized the threshold as reflecting an All-or-None process (e.g., Yonelinas, 1994), more recent models tend to characterise recollection as Some-or-None (e.g., Parks & Yonelinas, 2009). The results from Harlow and Donaldson (2013) clearly supported a Some-or-None account; i.e., correct recollection responses varied in precision and when memory was tested after a longer study-test delay both the rate and precision of recollection decreased. As Harlow and Donaldson highlighted, behavioural models that treat recollection as thresholded but not variable will therefore underestimate the contribution of recollection to performance. Recollection should instead be behaviourally modelled as thresholded, but when successful, as yielding information of varying quality. In short, recollection should be characterised as a ‘Some-or-None’, rather than an ‘All-or-None’, retrieval process (Parks & Yonelinas, 2009).

Although data from the novel source task developed by Harlow and Donaldson (2013) demonstrates that behavioural expression of recollection is thresholded and variable, by definition the data say nothing about the underlying neural mechanism that supports retrieval. To be clear, even if recollection is thresholded behaviourally, from a theoretical perspective it is nonetheless reasonable to propose that the behavioural outcome stems from a neural process which is itself continuous (for interesting discussion of a possible mismatch between a thresholded behaviour and a graded neural signal in the realm of attention see Vul, Hanus & Kanwisher, 2009). The presence of a threshold behaviourally need not necessarily imply a neural threshold. The purpose of the current experiment is therefore to ask whether the neural signal underlying recollection responses is, in fact, also thresholded

At a neural level of analysis, what separates the Continuous and Some-or-None accounts is the presence or absence of recollection (and by extension the Left Parietal effect) for guessed responses. The previous data from Chapter 6 could not distinguish between these accounts because some recollection was expected for guessed responses regardless of source accuracy (i.e., reflecting the retrieval of non-criterial information).

To be clear, the previous experiment was unsuitable for testing between the Continuous and Some-or-None accounts as Left Parietal old/new effects were expected to be observed for guessed responses. By contrast, in the current experiment the old/new decision is removed, making it unlikely that non-criterial recollection will contribute to source judgements – i.e., all words presented at test will have been presented previously with source information.

Therefore, in the current experiment, we are able to explicitly test the different predictions made by threshold (i.e., either All-or-None or Some-or-None) and Continuous accounts in relation to guess responses made in the absence of recollection. To elaborate, if recollection reflects a Continuous neural signal, then the Left Parietal effect should diminish in size as a function of precision, but still be present even when participants are guessing – because guesses are based on weak recollection (see Figure 7.1a). By contrast, if recollection is All-or-None, then similar to the prediction described in Chapter 6, the Left Parietal effect will be equivalent for both High and Low precision responses (i.e., above threshold responses) and absent for guess trials (see Figure 7.1b). Finally, a Some-or-None account would predict that the Left Parietal effect should be largest for high precision trials, becoming smaller for less precise trials, and absent when guessing – because guesses are made in the absence of recollection (see Figure 7.1c).

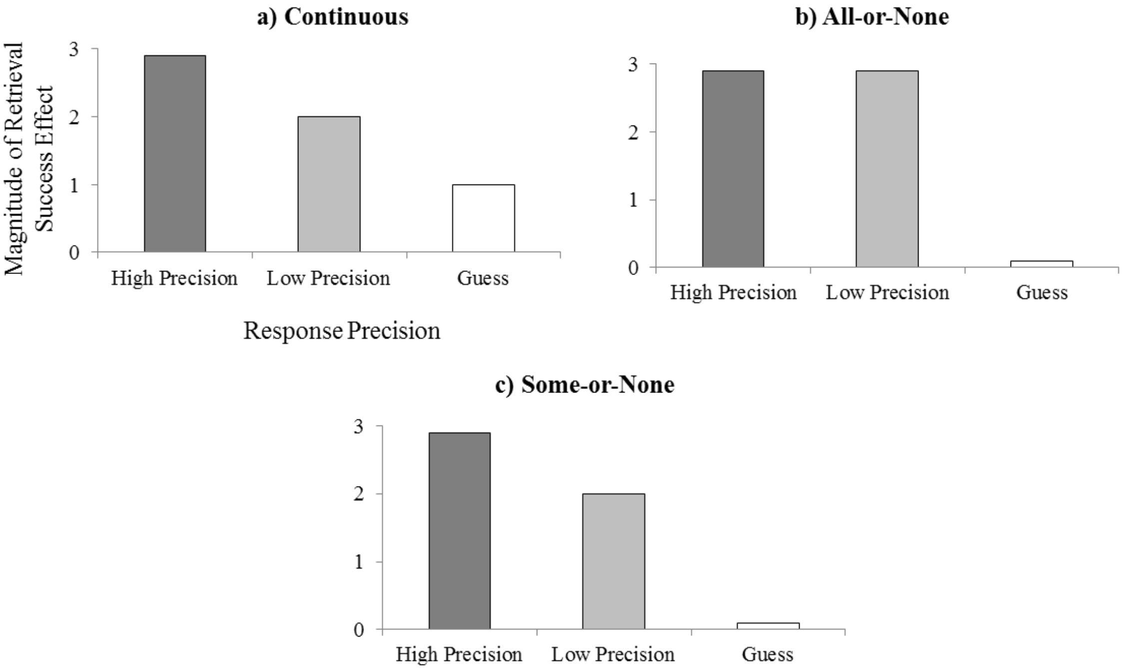

Figure 7.1: An illustration of the possible patterns of Left Parietal old/new effects. A Continuous account predicts a pattern of Left Parietal effects that scale with precision. It is important to note that Left Parietal effects are still expected for Guess responses. Alternatively, the All-or-None account predicts that trials that exceed a threshold will result in equal amounts of recollection but no Left Parietal effects are expected for Guess responses. The Some-or-None account predicts that the Left Parietal effect will scale with precision when recollection is successful (i.e., above-threshold response), but when recollection fails, no Left Parietal effects are expected (i.e., sub-thresholded response).

7.2. Method

7.2.1. Participants

Thirty University of Stirling students took part in the study gave informed consent (approved by the University of Stirling Psychology Ethics Committee). Six participants were excluded due to insufficient trial numbers in at least one critical condition. The remaining 24 participants (20 female) had a mean age 20.7 (range 18-30 years).

7.2.2. Stimuli

The stimuli are identical to those described in the General Method (Section 5.3.1.). To reiterate, 240 words were selected from the MRC psycholinguistic database (www.psych.rl.ac.uk – Coltheart, 1981). Words shared similar length (5-7 letters) and were selected with low imagability (mean = 414, s.d. = 55), concreteness (mean = 351, s.d. = 63) and Kucera Francis word frequency (mean = 33, s.d. = 31). An additional 9 words were used for the practice block.

7.2.3. Procedure

For a general description of the experimental procedure see the General Method (Section 5.3.1). In the current experiment, participants were required to complete a short practice (using 9 word/location pairs) before taking part in the experimental blocks. The main experiment involved 15 study/test blocks, each consisting of 16 word/location pairs. Each test block immediately followed the preceding study block.

Participants began every study trial (see Figure 7.2a) by pressing a response button, and were then presented with a fixation cross (+) for 2000ms. The cross was followed by a blank screen for 1000ms after which a black cross located on a grey circle outline was shown for 2000ms. After a further 1000ms blank screen a word was presented for 2000ms. Participant’s attention to the location was then tested by asking them to verify the (now hidden) location using the mouse. Responses within 20 pixels (~ 6°) from the target advanced participants to the next trial. If the participant’s response was over 20 pixels way, the target location was presented again for 250ms and the verification task was repeated.

During every test trial (see Figure 7.2b), participants were presented with a fixation cross for 1000ms followed by 500ms blank screen. A word from the previous study block was then shown for 2000ms, after which a blank screen was shown for 1000ms. Participants were then presented with a grey circle outline and were asked to recall the paired location by moving the mouse cursor to the remembered location and clicking the left mouse button. A red marker then appeared on the circle to indicate the chosen location. No response time limit was set and participants were free to change their decision. Participants finalized their response with a response box button press, which initiated the next trial. After the experiment was completed the precision of each test response was calculated, converting the screen co-ordinates selected by the participant into degrees: the remembered location was compared to the target location to provide the degree of error for that chosen location.

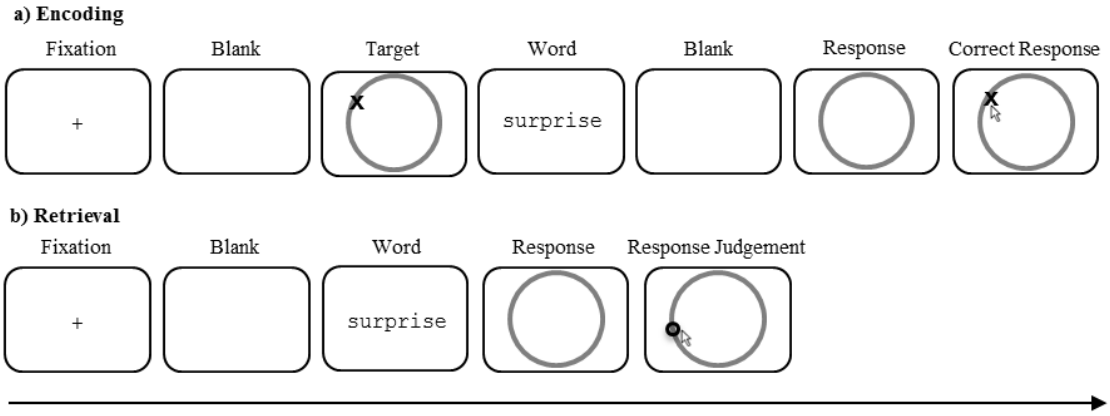

Figure 7.2: An illustration of the source memory task. **a)** At encoding, participants were required to memorize single words paired with locations, indicating the location after each trial to ensure they were paying attention. **b)** At retrieval, participants were shown a single word presented in the previous encoding block and were required to recall the position using the mouse.

7.2.4. ERP recording

The general EEG recording procedure is identical to that described in the General Method (see Section 5.4.2). In the current experiment, ERPs were analysed by examining mean amplitudes (relative to the pre-stimulus baseline) during *a priori* defined time-windows, designed to capture the neural correlates of familiarity (300-500ms) and recollection (500-800ms). To allow retrieval success effects to be calculated, all average ERPs were compared to the Baseline ERP, made from trials attracting responses over 90º from the target location. The baseline was chosen because error responses in the opposite half of the circle from the target are not based on recollection, providing an ERP baseline that is analogous to Correct Rejections used during standard old/new analysis. All ERP data analysis was carried out using repeated measures ANOVA (specific factors and levels are described where appropriate in the results). Topographic analyses were carried out on subtraction waveforms (i.e. Recollected response categories minus Guess) and were re-scaled using the min/max method (McCarthy & Wood, 1985).

7.3. Results

7.3.1. Behaviour

Analysis of the encoding data revealed that participants were highly accurate at verifying the target location: analysis of participant’s initial responses confirmed that 92% were within 10º of the target. By contrast, analysis of responses at test revealed a far lower level of accuracy: only 29% of responses were within 10º of the target. The overall pattern of test responses is shown in Figure 7.3. The pattern of error responses is very similar to that observed in Chapter 6, clearly suggesting a threshold at retrieval – indicated by the raised level of responses at locations far from the target, which reflects a plateau of random guessing. As observed previously by Harlow and Donaldson (2013) and in Chapter 6, the pattern of responses at test more closely follows a Cauchy distribution, with a greater frequency of very accurate and inaccurate responses than a Gaussian distribution can accommodate.

As in Chapter 6, analysis of the behavioural data followed the procedure proposed by Harlow and Donaldson (2013). To briefly reiterate, in order to test between a threshold or continuous pattern each participant's data (n = 24) was fitted to a threshold model, with two free parameters: λ denoted the proportion of trials where recollection succeeded (larger values indicating more recollection); *s* denoted the spread of responses (larger values indicating greater mean error, i.e., less precision). The results of the likelihood ratio test revealed that a threshold model (i.e., λ can vary below 1, allowing recollection to fail on some responses and resulting in random guessing) fit the data significantly better than a Continuous model (i.e., fixing λ at 1 so that all responses are based on a variable amount of recollection) [mean $\lambda = .73$, $\chi^2(24) = 830.79$, $p<.001$]. In short, the distribution of error responses was more accurately modelled with a threshold.

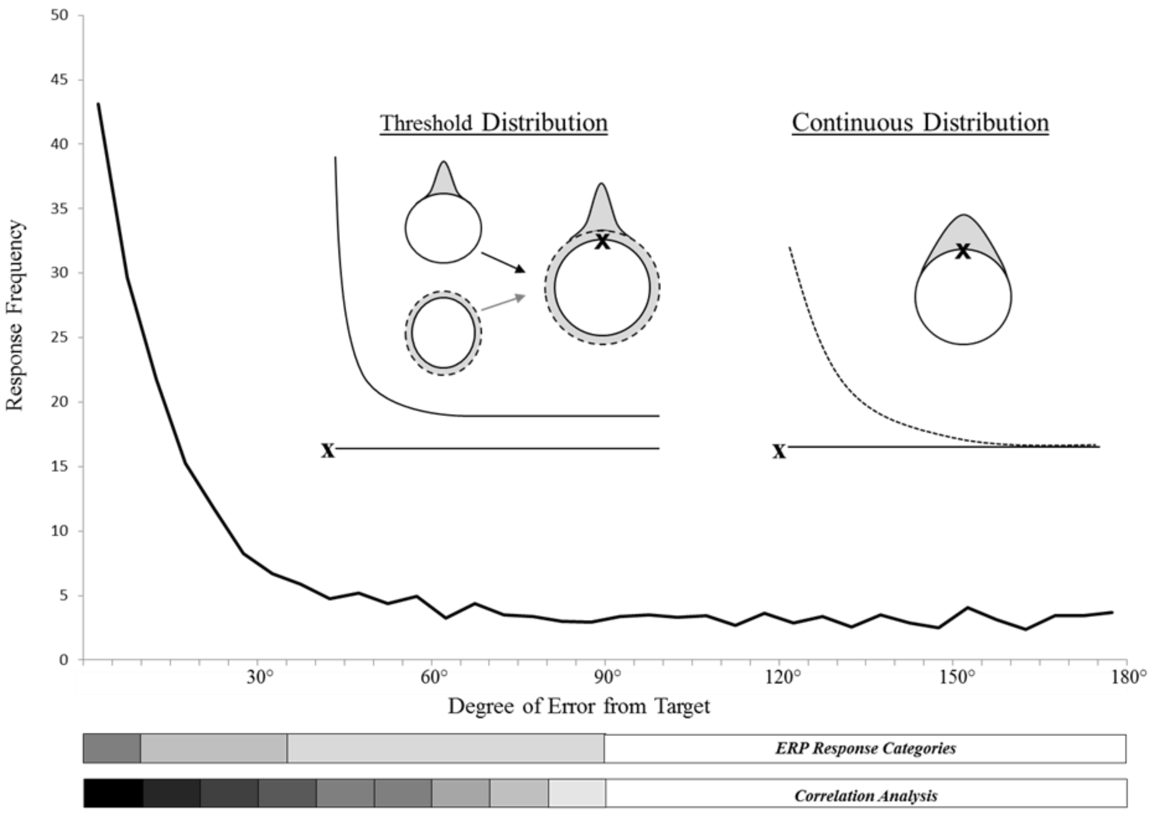

Figure 7.3: Observed error distribution. The pattern of error responses clearly demonstrates responses clustered around the target but also exhibited sub-threshold guessing (recollection failure). Inset is the distribution of errors predicted by both a Threshold and Continuous accounts. Below the error distribution is an illustration of the ERP Response Category bins, aimed at capturing High precision trials (<10°), Low precision responses (11>35°), Guess responses (36>90°) and Baseline responses (>91°). Below the ERP Response Category bins are the bins used in the Correlation Analysis: i.e., every 10° up to 90° and a baseline over 91°.

In line with Chapter 6, individual variability was also examined to assess the consistency of the response threshold across participants. Individual response profiles are shown in Figure 7.4. As can be observed from the figure, the pattern of responses observed for a majority of participants is indicative of a threshold and closely matches the averaged data. In a small proportion of participants, the pattern is less clearly evident, with some exhibiting little guessing, whilst others demonstrate far greater guessing with a flatter profile of responses around the circle. Nonetheless, analysis of individual data revealed that 23 out of the 24 participants show the threshold when analysed by themselves. Despite the consistent presence of a threshold, examination of the data revealed that the value of λ and s differed across participants (values ranged from .53 to .90 and 5.2 to 19, respectively) reflecting considerable variation in the rate and precision of recollection. Consistent with Chapter 7, a linear regression was conducted on each individual participant's data to determine the exact point participants began to guess - this was achieved by determining when the slope of the distribution curve became non-significant from 0. The range of thresholds across participants was dramatic (i.e. 4-64°), again reflecting the considerable variation in response accuracy among participants. Analysis of the overall distribution across all participants revealed that the mean threshold was at 59° and supports our assumption that guessing had asymptoted well before our baseline of 90°.

7.3.2. Event Related Potentials

ERPs were formed for each participant, averaging EEG data recorded at test into four separate response categories. The response categories were designed to capture ERP activity elicited by different rates of positional response accuracy (i.e., precision), whilst also providing sufficient trial numbers to form ERPs across participants: 'High Precision' ERPs were designed to capture only the most precise responses, defined as under 10º from the target location; 'Low Precision' ERPs captured less precise responses, ranging from 11º to 35º from target; 'Guessing' ERPs captured trials associated with guessing, ranging from 36º to 90º. Critically, the Guesses ERPs reflect responses in the same half of the circle as the target, but from a part of the distribution largely accounted for by the plateau of random guessing. Finally, ‘Baseline’ ERPs were formed from all trials falling over 90º from the target location (i.e., the other half of the circle, analogous to wrong answers in a binary source task). The mapping of ERP response categories to the behavioural data is illustrated in Figure 7.2.

The experimental prediction that the Left Parietal effect would be sensitive to precision was tested by averaging across Parietal and Centro-Parietal strings of electrodes (CP5/P5, CP3/P3, CP1/P1, CP6/P1, CP4/P4, CP2/P2: see Chapter 6, Section 6.3.2) and comparing activity elicited for correctly recollected, guessed and baseline responses. Initial ANOVAs were performed on each response category to test for within category retrieval success effects, with factors of Category [High, Low or Guess/Baseline], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior] during the 500-800ms time window. The outcomes of these analyses are described below, followed by subsidiary analyses as appropriate.

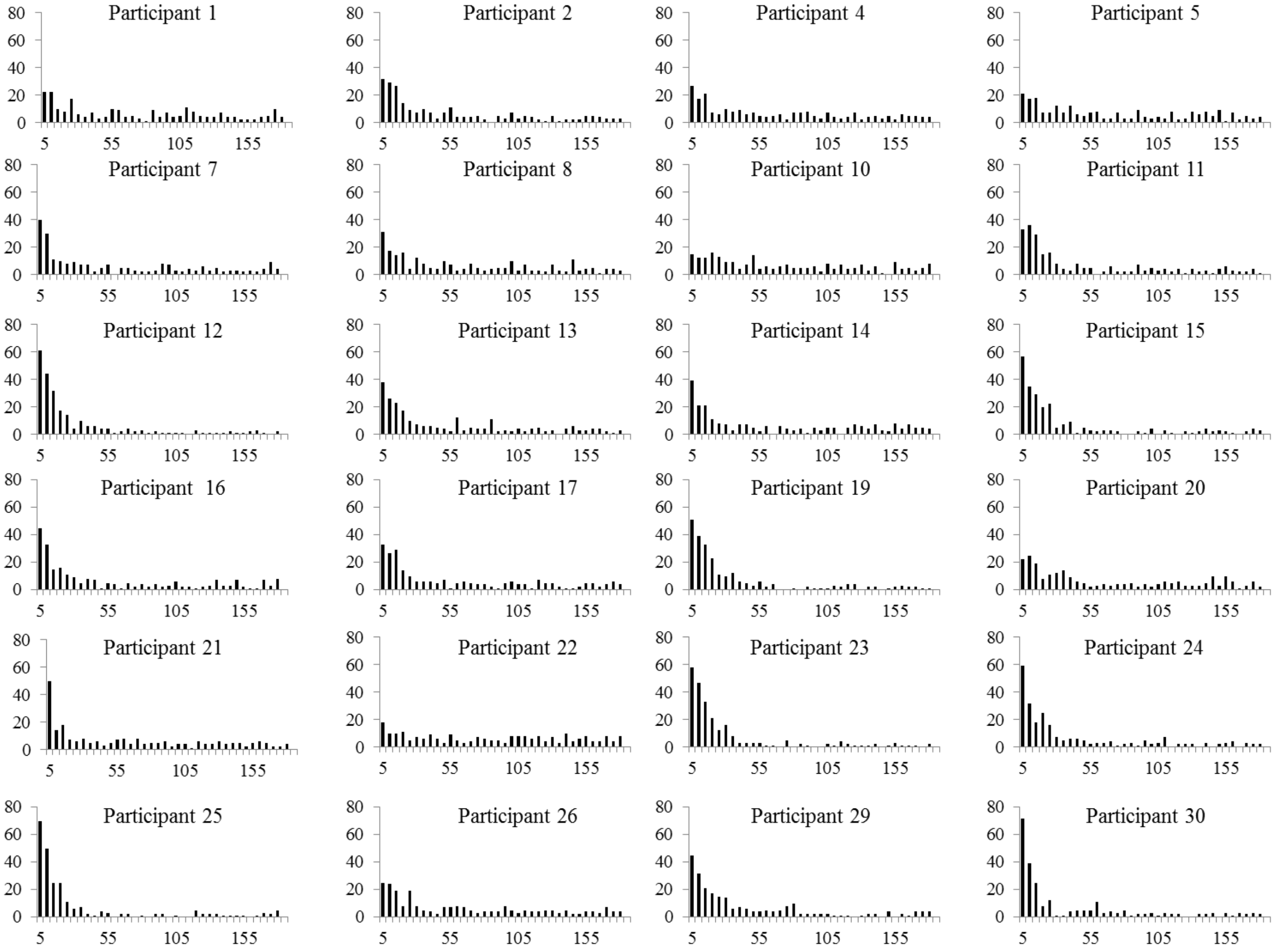

Figure 7.4: Individual response frequencies for all 24 participants. Error distance is displayed on the x axis and degrees of error are displayed on the y axis

7.3.2.1. Left Parietal retrieval success effects

Figure 7.5 shows the Grand average ERPs for High, Low, Guess and Baseline responses at electrode P3. High precision responses elicit more positive going neural activity than Low precision responses; both High and Low are more positive than Guessing and Baseline responses. The distribution of Left Parietal effects is illustrated in Figure 7.6; both High and Low precision responses exhibit clear maxima over the left parietal scalp region, whereas Guess responses elicit no clear retrieval success effect. This observation was confirmed by a series of initial ANOVAs comparing each response category to baseline. These analyses revealed significant main effects of Category for both High [F(1,23)=19.84, p<.001] and Low precision responses [F(1,23)=7, p=.01], while no main effects or interactions were observed for Guessing. In addition, significant Category by Hemisphere interactions were observed, again for both High [F(1,23)=4.65, p<.05] and Low responses [F(1,23)=5.36, p<.05], confirming that the ERPs exhibit a left greater than right hemispheric asymmetry, consistent with the presence of left parietal retrieval success effects.

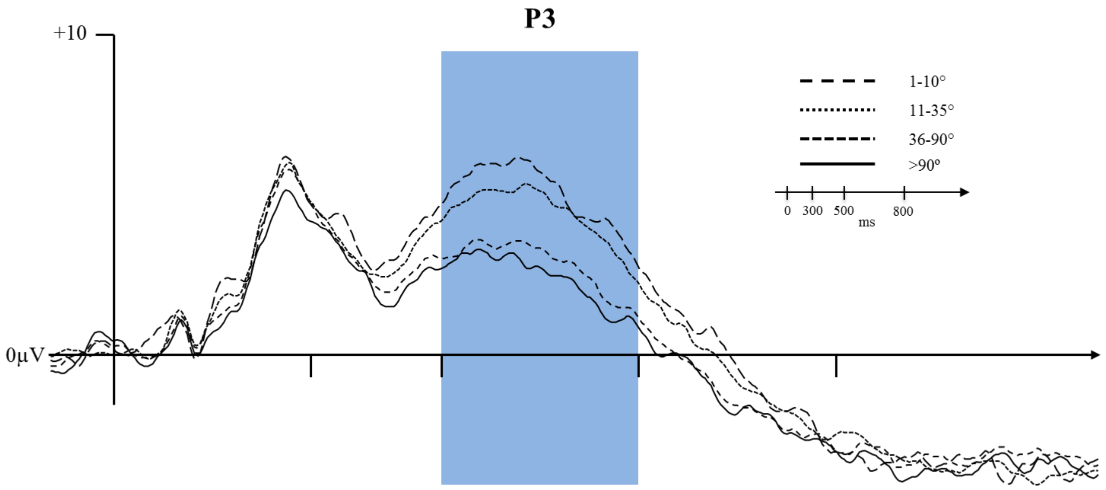

Figure 7.5: Grand average ERPs for High precision, Low precision, Guessing and Baseline responses at electrode P3. The 500-800ms time window is highlighted in blue.

Having demonstrated that retrieval success effects were present, a topographic analysis was conducted to assess whether the retrieval success effects observed for High and Low precision responses could have been generated by different neural populations. Guessing response ERPs were excluded from this analysis because no significant retrieval success effects were found in the initial analysis. An ANOVA was performed using rescaled subtraction data (High Precision minus Baseline, and Low Precision minus Baseline) with factors of Category [High/Moderate], Location [Frontal/Fronto-Central/Central-Parietal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Middle/Superior], providing a global assessment of the topography of effects across the scalp. Results did not reveal any significant main effects or interactions, confirming that the retrieval success effects associated with High and Low response categories originated from the same neural population.

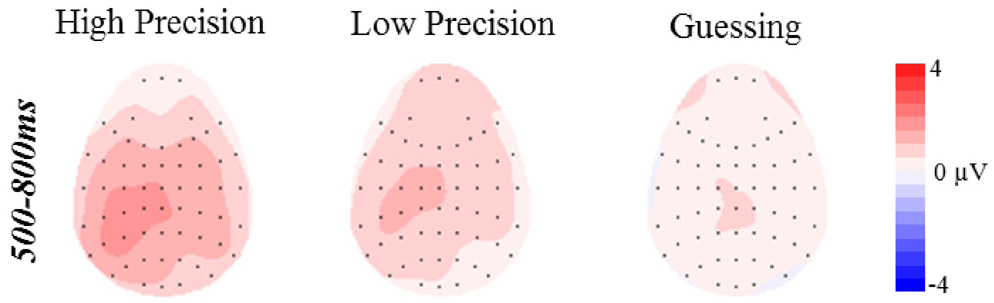

Figure 7.6: Topographic maps illustrating the Left Parietal old/new effects for High Precision Responses, Low Precision Responses and Guess Responses within the 500-800ms time window. The scale bar represents the voltage range (µV).

Consistent with the scalp maps shown in Figure 7.6, examination of the data revealed that the retrieval success effects were maximal over left parietal scalp: electrode CP3 for both High (mean = 2.29µV, s.d. = 2.46) and Low (mean = 1.50 µV, s.d. = 1.98) response categories. A stringent series of planned comparisons was also carried out to examine the magnitude of retrieval success activity (measured by averaging across all 6 left parietal electrodes) across response categories (mean data illustrated in Figure 7.7). Bonferonni corrected one-tailed t-tests [$\alpha = .02$] confirmed that High ($t(23) = 4.73$, $p < .001$) and Low ($t(23) = 3.30$, $p < .01$) precision responses, but not Guessing ($F = 1.34$), exhibited significant retrieval success effects over left parietal scalp. Critically, results also revealed that retrieval success activity was significantly larger for High ($t(23) = 4.22$, $p < .001$) and Low ($t(23) = 2.12$, $p = .02$) precision responses compared to Guessing, and perhaps most importantly, the retrieval success effect was also significantly larger for High than Low precision responses [$t(23) = 2.08$, $p = .02$].

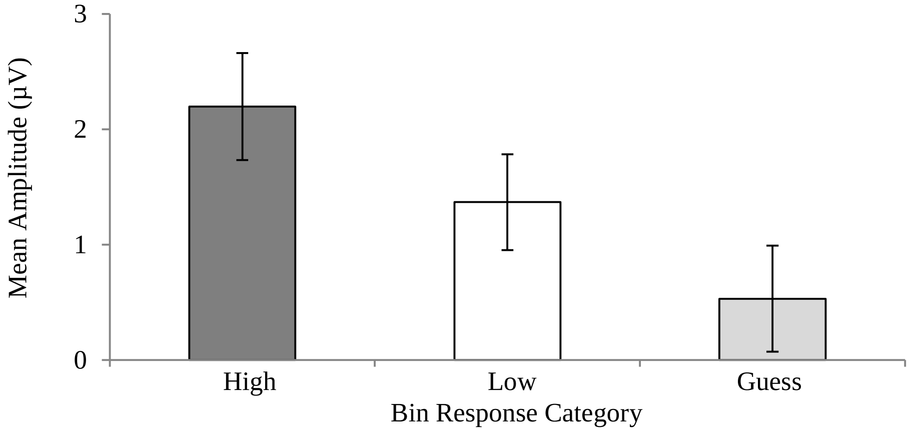

Figure 7.7: The mean magnitude (and standard error) of Left Parietal effects for High, Low and Guess responses during the 500-800ms time window.

7.3.2.2. The Mid-Frontal effect

It is clear from Figure 7.8 that both High and Low precision ERPs exhibit small retrieval differences prior to the onset of the Left Parietal Effect. We therefore carried out an additional set of analysis using data from a 300-500ms time window, allowing us to assess whether Mid-Frontal retrieval success effects associated with familiarity were present. Data from 6 frontal electrode pairs were employed (FC5/F5, FC3/F3, FC1/F1, FC6/F6, FC4/F4, FC2/F2: see Chapter 6, Section 6.3.2.). These data were submitted to ANOVA with factors of Category [High, Low or Guess/Baseline], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. No main effects or interactions were observed for High, Low or Guessing responses, suggesting that the Mid-Frontal effect associated with familiarity was not present, regardless of the accuracy of responding.

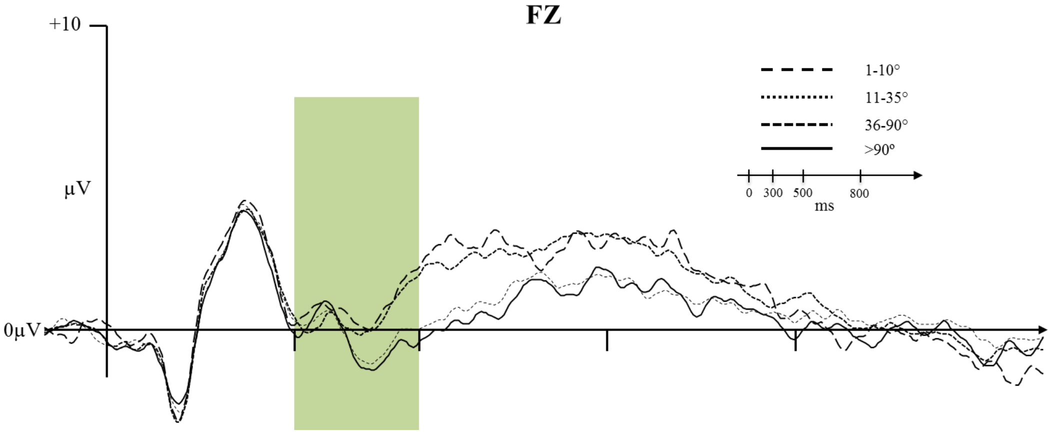

Figure 7.8: Grand average waveforms exhibited by the High precision, Low precision, Guessing and Baseline responses at representative electrode FZ. The 300-500ms time window is highlighted in green.

7.3.2.3. Fine grained analysis

The use of different bin sizes to define precision is open to the interpretational problem described in the introduction. To demonstrate that the gradation in the present data set is valid and not a function of an all-or-non signal being mixed with different amounts of guessing, we conducted a subsidiary analysis focused on the correlation between the Left Parietal effect and degree of error from target. If the Left Parietal effect does track precision, we should expect to observe the magnitude of the effect decrease as participants become less precise. The correlational analysis was focused on the left parietal effect, therefore, only electrodes across the left parietal region were included

[CP5, CP3, CP1, P5, P3, P1]. We first created bins of 10˚ and averaged every trial within participants that fell within these bins, before averaging across participants. As we were interested in gradation of the neural signature of successful retrieval, we subtracted from each bin the averaged activity from guessing responses (i.e., 90° to 180°). The interpretational problem with concern to successful guessing is accounted for by using bins of equal size – across bins the probability of guessing is equal, due to the random distribution of guess responses around the circle. Finally, using smaller bin sizes ultimately lead to disproportionate number of trials being averaged per bin, with more trials contributing to the average for highly precise bins (i.e., 1-10°) compared to highly imprecise bins (i.e., 81-90°). We therefore used weighted least squares regression, which assigns weights that are inversely proportional to the error variance of each bin – i.e. more precise bins are given greater weight in the regression than more imprecise bins which exhibit greater variance. Analysis revealed a significant negative correlation between the magnitude of the Left Parietal effect and the degree of error from the target location between 1˚ and 90˚ [r=.60, p<.001], accounting for 57% of the variance (see Figure 7.9).

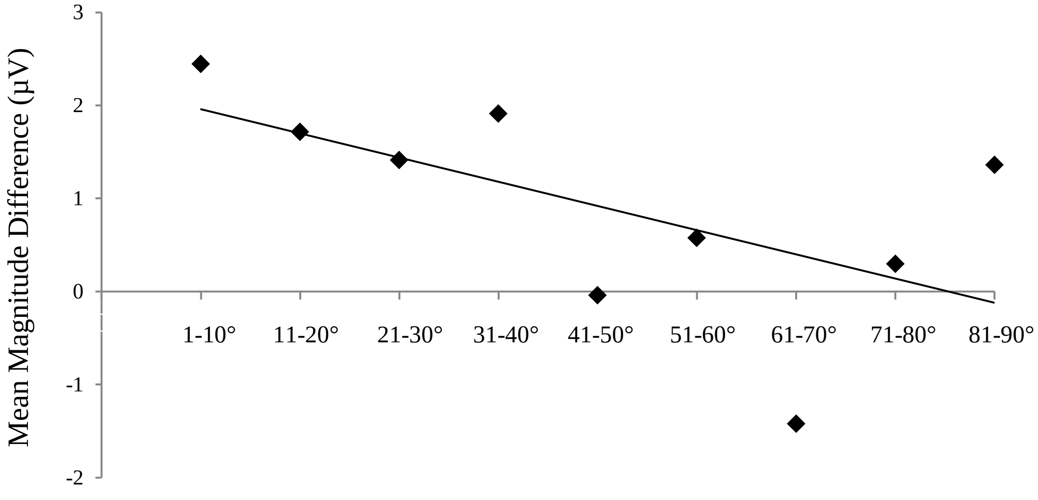

Figure 7.9: Weighted correlational analysis of fine grained bins. Each data point represents the mean magnitude of the Left Parietal effect (i.e., activity within each 10° bin – baseline) within the 500-800ms time window.

7.4. Discussion

The current experiment aimed to characterize the neural mechanism that underlies the recollection of contextual information about previously encoded events. We were motivated by recent behavioural findings from a novel test of source accuracy (Harlow & Donaldson, 2013) that reveals recollection to be both thresholded and variable. Here we investigated whether the underlying neural mechanism supporting recollection also exhibits a threshold. To this end, using the same novel source task, we assessed the sensitivity of a known neural correlate of recollection, the Left Parietal ERP effect, to precision. Results revealed that when recollection failed behaviourally, the Left Parietal effect was absent, however, when recollection succeeded, the magnitude of the Left Parietal effect scaled with the precision of test responses. To be clear, like the behavioural output, the underlying neural mechanism associated with recollection was found to be thresholded and variable. Below we discuss the implications of these findings for theories of episodic memory, and for functional accounts of the neural signal supporting recollection.

7.4.1 Behavioural overview

The present behavioural findings replicate the results of Harlow and Donaldson (2013) and are consistent with behavioural pattern observed in Chapter 6, demonstrating that recollection exhibits a threshold and sometimes fails completely. Here, the rate of recollection was lower compared to rate of recollection observed in Chapter 6 (λ = 73% compared to 80%), but nonetheless confirms that participants were recollecting at well above chance levels and well below ceiling. In addition, the precision of recollection was also poorer compared to Chapter 6 (s = 11.40 compared to 8.48). The change in rate and precision of recollection most likely reflects the removal of the distractor task in the current experiment (i.e., responses are recorded from every trial as opposed to source responses made after a participant had responded ‘old’). The current source accuracy data and that observed in Chapter 6, clearly demonstrates that a behavioural threshold exists, suggesting that recollection may fail on a sub-set of trials but is graded when recollection is successful – consistent with the ‘Some-or-None’ account (Harlow & Donaldson, 2013; Parks & Yonelinas, 2009). To reiterate from Chapter 6, it is difficult to reconcile the pattern of behavioural responses with Continuous models that predict that there should always be some information retrieved from memory.

Although the observed threshold (both from a behavioural and neural level of analysis) is interpreted is as a characteristic of recollection at retrieval, it is also worth considering an alternative explanation – namely, that the observed threshold was actually introduced at encoding. According to some continuous models, for instance, a threshold may be evident at retrieval because participants did not attend to certain items during study, resulting in the absence of information for unattended stimuli at retrieval (DeCarlo, 2003). In theory, an encoding threshold model could account for the data presented in the current experiment (although participants did attend to 92% of the study trials). The encoding account is unlikely, however, given that it would predict that the proportion of guessing trials should be equivalent across both short and long study-test delays. When Harlow and Donaldson (2013) directly tested this prediction, they found that the proportion of guessed trials increased with test delay, indicating that the observed threshold occurred at retrieval, rather than encoding.

7.4.2. Overview of the Mid-Frontal Effect

Consistent with Chapter 6, the Mid-Frontal effect was also analysed to rule out the possibility that familiarity may have contributed to source judgements. To reiterate briefly, Harlow and Donaldson (2013) designed the source task to limit the contribution of familiarity, but did not provide a direct test of this assumption. The graded precision observed for successfully retrieved locations could therefore potentially be driven by a continuous process such as familiarity, rather than by recollection *per se*. In the current experiment, our measurement of neural signals allowed us to assess whether or not familiarity contributed to retrieval. Alongside the Left Parietal correlate of recollection, ERP studies of memory retrieval typically reveal an earlier onsetting effect between 300 and 500ms post-stimulus, maximal over mid-frontal electrodes, that is associated with familiarity (see Rugg & Curran, 2007, but for an alternative view see Paller et al., 2007). Crucially, regardless of precision, no significant frontal ERP effects were found (mean difference from baseline of .48µV across Mid-Frontal electrodes). The ERP findings therefore provide additional support for the claim that the source memory task used here limits successful retrieval exclusively to recollection.

7.4.3. The Left Parietal Retrieval Success Effect

Crucially, the ERP data reveal that the Left Parietal effect, a neural mechanism associated with recollection, was also thresholded and graded. We examined the neural mechanism underlying recollection by comparing the magnitude of retrieval success effects as a function of the precision of source memory responses. Several features of the data are important. First, analysis confirmed that the time course and distribution of the retrieval success effects matched those of the Left Parietal old/new effect – consistent with the behavioural evidence that performance relied on recollection. The observation of significant Left Parietal effects also serves to validate our use of a distracter free memory task, which forces the use of an alternative baseline (source error responses over 90° from the target location) rather than the typical old/new baseline (correctly rejected new items). Second, the pattern of retrieval success effects was clearly thresholded: the Left Parietal effect was absent when recollection failed (guess responses with error between 36° and 90°), but the magnitude of the effect scaled with precision when recollection was successful. Responses that were retrieved with high precision (1° to 10°) were found to elicit a significantly larger left parietal effect than responses made with low precision (11° to 35°). The lack of a significant left parietal effect when recollection failed suggests that these responses were made in the absence of retrieved information, rather than on the basis of weak or partial recollection (as predicted by continuous models).

Although the findings reported here suggest that the neural mechanism supporting recollection is thresholded, the interpretation of neural data must be made with caution. As stated previously in Chapter 6, it is possible to observe a graded some-or-none pattern across conditions, when in fact the underlying signal is all-or-none, simply because of the averaging process. To be clear, if the proportions of trials without recollection (e.g., guesses or responses based on familiarity) varies across conditions, then an all-or-none signal will appear graded when average ERPs are formed. This interpretational problem has been highlighted repeatedly in studies examining the neural correlates of episodic memory (e.g., Wilding & Rugg, 1996; Wilding, 2000; Vilberg et al., 2006), preventing definitive conclusions from being reached. Here, however, we were able to carry out a secondary set of analysis that effectively ruled out averaging as a confound. We formed ERPs that varied in precision, but were matched in range (i.e., every 10°). As guessing is randomly distributed around the circle, the contribution of guessing to these averaged waveforms should be equivalent. Importantly, the results of the subsidiary analysis revealed that when guessing was equated, the magnitude of the Left Parietal effect was still observed to increase with the precision of responses. We can, therefore, be confident that the Left Parietal effect reflects a graded some-or-none signal rather than an all-or-none signal (that is simply present on different numbers of trials across conditions).

7.4.4. Implications of a recollection threshold

The present findings help to clarify the functional significance of the Left Parietal effect. Previous results have been taken as evidence that the Left Parietal effect is sensitive to the amount of information retrieved (Wilding & Rugg, 1996; Wilding, 2000, Vilberg et al., 2006), typically based on the analysis of subjective reports about recollection (i.e., confidence ratings or remember/know paradigms). Here, by employing a less noisy and more objective method for assessing retrieval success by examining source accuracy directly, we demonstrate that the Left Parietal effect is sensitive to the precision of recollected information. According to this account, variation in the size of the Left Parietal effect actually reflects the quality of information retrieved. This distinction is important given that the threshold account of recollection comprises two independent dimensions of precision (i.e., the quality of information recollected) and rate (i.e., the quantity of information recollected), although it is currently unclear how these two dimensions interact. Regardless, one key question that arises from current findings is whether the Left Parietal effect indexes changes in retrieval quantity independent of quality – that is, would equivalent changes in the magnitude of the Left Parietal effect be found if recollection rate was manipulated within participants? Clearly, based on the current findings, ERPs provide a potentially useful tool for investigating the impact that changes in the rate and precision of recollection have under different experimental conditions.

More broadly, the present findings lead us to question the utility of existing functional accounts of the Left Parietal effect. A number of broader theoretical accounts have been proposed to account for ERP and fMRI evidence of parietal retrieval success effects.

For example, the attention-to-memory model (Cabeza, 2008) views parietal activity as a reflection of the orientation of attention to recovered episodic information. Alternatively, the episodic buffer model (Vilberg & Rugg, 2008, 2009) relates Left Parietal effects to the on-line maintenance of episodic information within working memory. Whilst useful as interpretative frameworks, these accounts do not in themselves help to characterize the neural mechanism supporting recollection. The pattern of ERP effects reported here can be accounted for by either theory – with neither providing (a substantial explanation) for why a threshold is present in the data. Our alternative view is that the presence of the threshold is what is informative – and this should constrain accounts of what recollection is, and how it operates[1].

7.4.5. Summary

The present experiment demonstrated that, much like the behavioural expression of recollection, the underlying neural mechanism supporting recollection is also thresholded – i.e., the Left Parietal effect scales with precision when recollection is successful but is absent when recollection fails. The data suggest that recollection is unreliable, failing to support successful retrieval on a number of trials. Given that the ability to retrieve associations has long been thought to depend on recollection, we next ask whether, under certain circumstances, alternative retrieval processes such as familiarity may also support associative retrieval. The following chapters aim to clarify particular circumstances that result in the contribution of familiarity towards successful associative recognition.

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[1] For further discussion of a neural threshold and the broader implications in terms of memory failure (particularly in aging) see the General Discussion.

Chapter 8

Unitization of Novel Associations through Mental Imagery

In the last chapter the neural signal supporting recollection was found to reflect a Some-or-None process – i.e., recollection could fail, but when it was successful the magnitude of the neural signal varied with precision. Given the fact that recollection sometimes fails to provide any information from memory, the question arises as to how (and on what basis) participants respond in this circumstance. To be clear, even when recollection fails on some occasions, participants are still able to make correct associative judgements. Whilst simple guessing could account for some proportion of these correct associative responses, it remains possible that other memory retrieval processes may also contribute. In this vein, the traditional assumption of dual process theory that only recollection contributes to associative retrieval has recently been challenged by a growing body of evidence demonstrating that, under certain circumstances, associative retrieval may be supported by familiarity. In contrast to recollection, however, relatively little is known about the circumstances that result in familiarity based associative recognition. The aim of the current chapter is to investigate a particular encoding strategy, known as ‘unitization,’ which is considered to be a potential mechanism for encouraging familiarity during retrieval of associative information.

8.1. Introduction

While there is agreement among dual process models that both recollection and familiarity support retrieval of single items (Clark & Burchett, 1994; Gronlund, Edwards, & Ohrt, 1997; Jacoby, 1991; Yonelinas, 1997; see Parks & Yonelinas, 2007 for a review), exactly how the two processes interact to support associative recognition is less clear. Traditional dual process models propose that during associative memory tests, participants rely on recollection to discriminate between old and recombined (studied items in new combinations) pairs (Hockley & Cristi, 1996; Yonelinas, 1997). To be clear, as each item will be familiar within an old and recombined pair, recollection of the association between pairs must be relied upon to make a successful associative judgment. Recent evidence, however, has shown that when items are unitized – i.e. encoded as a single stimulus configuration – successful associative judgments may be additionally supported by familiarity.

As discussed in Chapter 1, unitization is typically operationalised as a mechanism for creating a single novel ‘representation’ distinct from its components. During associative recognition tasks the unitized stimulus can be used to judge prior occurrence by engendering a sense of familiarity for the whole, rather than the retrieval of the association between items. Unitization gives rise to the possibility of successful associative recognition based on the contribution of familiarity in both the presence of recollection (i.e., equivalent to item recognition in relation to healthy populations) and potentially the absence of recollection (Quamme et al., 2007; although see Mayes, Montaldi, & Migo, 2007 for an alternative explanation). The aim of the current chapter is to investigate further the appropriate circumstances under which familiarity contributes to successful associative recognition.

As previously discussed in Chapter 1, the Dual Process Signal Detection model (DPSD) proposes that familiarity may contribute to associative recognition when stimuli have been sufficiently unitized. There is strong behavioural evidence to support the DPSD account, however, these studies often rely upon Receiver Operating Characteristics (ROC, a plot of the relationship between hit rates and false alarm rates as a function of confidence) analysis to estimate the contribution of familiarity and recollection (Diana et al., 2008, 2011; Quamme et al., 2007; Diana et al., 2010; Yonelinas et al., 1999; Haskins et al., 2008). To reiterate, although ROCs are a useful tool for behaviourally separating familiarity and recollection, they are also highly model specific, so that the same data fitted to a different model will lead to vastly different conclusions (see Wixted, 2007). Thus, to further assess whether familiarity can contribute to successful associative recognition, evidence from alternative methods of measuring familiarity and recollection is required that do not rely on subjective confidence ratings.

As reviewed in Chapter 4, in two separate associative recognition studies carried out by Rhodes and Donaldson (2007, 2008) conditions that encouraged unitization were found to selectively modulate of the Mid-Frontal old/new effect. Critically, in both studies the Left-Parietal old/new effect did not differ either as a function of stimulus relationship or encoding instruction. Together, both studies suggest that conditions designed to manipulate unitization result in a selective modulation of the underlying neural correlate of familiarity during associative recognition.

One potential problem with the Rhodes and Donaldson studies, however, is the use of pre-established word pairs. Although any experiment manipulating memory for word pairs could not be considered a pure test of episodic memory, employing related pairs may have resulted in added contributions of pre-established semantic knowledge. For instance, some of the early dual process models adequately account for familiarity during retrieval of pre-established representations either through the activation of lexical nodes (Atkinson & Juola, 1973), or simply through item activation (Mandler, 1980). These traditional models, however, explicitly state that familiarity cannot support the retrieval of *novel* associations. By contrast, the DPSD account (Yonelinas, 1997) predicts that familiarity can support the learning of novel associations, so long as they have previously been unitized.

It is therefore unclear, based on the findings of Rhodes and Donaldson (2007, 2008), whether or not familiarity can contribute to successful retrieval of arbitrary associations. A more adequate test of unitization would be to use completely unrelated word pairs, attempting to manipulate familiarity in the absence of established conceptual knowledge. The question of whether familiarity can support the retrieval of novel associations has important implications not only for testing the predictions of certain dual process models, but more importantly validating the studies already carried out on patients with severe recollection deficits that have demonstrated preserved retrieval of novel information.

So far, only Bader et al., (2010) have attempted to manipulate unitization of unrealated word pairs, although their data (as reviewed in Chapter 4 and Chapter 9) did not reveal the typical ERP effects representative of either the Mid-Frontal or Left-Parietal old/new effect, making it difficult to interpret their data in terms of familiarity and recollection. To date, the results of previous ERP studies currently demonstrate an increase in familiarity after unitization for existing associations (i.e., Rhodes & Donaldson, 2007, 2008), but have failed to show a clear increase in familiarity for novel associations. It is unclear, however, whether Bader and colleagues failure to show an increase in familiarity was a result of the use of novel associations or the use of an alternative encoding task. The aim of the current study is to address the apparent inconsistency within the ERP literature – namely, why in some circumstances but not others is the neural correlate of familiarity is modulated by unitization.

The current study aims to investigate the contribution of familiarity for newly learnt associations in an attempt to address the inconsistency (described above) within the ERP literature. By clarifying the role of familiarity – as indexed by the Mid-Frontal old/new effect – during the retrieval of arbitrary associations, further progress can be made in understanding the sufficient circumstances that allow for successful associative retrieval. The contribution of familiarity to the retrieval of novel associations is of particular importance especially given the vulnerability of recollection to failure, cognitive decline and disease. To this end, we investigate whether or not unitization can encourage familiarity for novel associations using an established method that has been proven to modulate the Mid-Frontal old/new effect – namely, the mental imagery paradigm employed by Rhodes and Donaldson (2008).

Expanding on the findings of Rhodes and Donaldson (2008), the current experiment aims to address whether unitization can enhance familiarity – indexed by the Mid-Frontal old/new effect – for completely arbitrary associations. Here we replicate the comparison of Interactive and Item imagery encoding instructions used by Rhodes & Donaldson (2008), employing the same associative recognition task (requiring discrimination between intact, recombined and new word pairs at test). As with previous ERP studies (see Rhodes and Donaldson, 2007; Bader et al., 2010) recombined word pairs are presented at test to prevent participants correctly recognising intact word pairs from identification of a single word from a pair. To facilitate comparison with other ERP studies, however, only behavioural and ERP data related to traditional old/new effects elicited by correctly identified intact and new word pairs are examined. In addition, given that unitization is a process identified with episodic memory, word pairs were only presented once during encoding to prevent repetition effects associated with implicit priming. Finally, a Remember/Know/Guess (Gardiner, Ramponi, & Richardson-Klavehn, 1998) procedure was used to provide an additional behavioural measure of familiarity. On the basis of previous findings it was predicted that interactive imagery, but not item imagery would encourage participants to form a novel unitized representation resulting in increased discrimination accuracy and response times, a selective increase in Know responses and an enhanced Mid-Frontal old/new effect – indexing the contribution of familiarity. As memory for study details is assumed to be constant regardless of encoding instructions, recollection was predicted to be equivalent – i.e., no observable differences in magnitude of the Left-Parietal old/new effect was expected.

8.2. Method

8.2.1. Participants

Forty five participants from the University of Stirling took part in the study. Data from four participants was rejected due to an insufficient number of ERP trials in at least one experimental condition and a further seven were excluded due to poor behavioural performance. The remaining thirty four participants (20 female) had a mean age of 21 (range: 18-26).

8.2.2. Stimuli

The stimuli are identical to those described in Chapter 5 (see Section 5.3.1). To reiterate, 640 associatively and semantically unrelated word pairs were randomly assigned to two lists of 320 word pairs each. Both stimulus lists were divided into 10 study-test blocks of 32 word pairs, half used for each task (Interactive versus Item imagery), with order of encoding task counterbalanced[1]. Across participants each list of words was presented equally often with either Item or Interactive imagery instructions, and the presentation order of blocks as well word pairs presented within blocks was randomised. A single study block contained 24 word pairs: 8 Intact (to-be-presented in the same pairing at test) and 16 Recombined pairs (to-be-presented in a different pairing at test). The extra recombined pairs were included so that partners of the recombined items could be disregarded at test to prevent potential cueing effects. At study, for example, the to-be-recombined pairs ‘Dog-Table’ and ‘Sea-Cube’ would be presented as ‘Dog-Cube’ at test whilst ‘Table’ and ‘Sea’ would not. A single test block contained

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[1] To assess the potential confound of order effects, discrimination accuracy was compared between participants who viewed the Sentence Frame or Compound Definition task first. The results of independent t-tests confirmed that discrimination accuracy did not differ between groups for either the Sentence Frame and Compound Definition tasks, suggesting that order effects did not influence overall discrimination accuracy.

24 word pairs; 8 Intact (repeated from study), 8 Recombined (repeated from study, but in rearranged pairings) and 8 New pairs (not previously presented during study). Stimuli were presented equally often within each test status across participants, and the presentation of stimuli within blocks at study and test was randomized.

8.2.3. Procedure

The general experimental procedure is the same as described in Chapter 5 (see Section 5.3.2). In the current experiment, participants were initially required to complete a practice session comprising 12 pairs at study and 12 pairs at test (using additional stimuli not employed in the experiment proper) before commencing Interactive and Item imagery tasks. Both verbal and written instructions were given to participants. After the practice, the experimenter verbally verified that the participant had understood both the encoding and test instructions. Participants had the opportunity to repeat the practice if they were unsure about the task.

The experimental procedure is illustrated in Figure 8.1. Each study trial began with a fixation cross (+) presented for 1000ms to ensure the participants focused on the centre of the screen and to indicate the presentation of a word pair was imminent. The cross was followed by a blank screen for 500ms after which the word pair was presented for 1500ms. Participants were instructed to either generate a single mental image of both words interacting together (Interactive imagery) or to generate two mental images (Item imagery). These instructions were intended to encourage or discourage unitization of word pairs. Each trial ended with a 2000ms blank screen before the next trial began. In total, participants had approximately 3500ms to perform the imagery task for each word pair. Each study block was immediately followed by a test block. Each test trial began with a central fixation cross presented for 1000ms, followed by a blank screen for 500ms. Word pairs were presented for 2000ms, followed by a 500ms blank screen. Participants were required to make an Intact/Recombined/New response while the word pair was presented. Responses were made using the far left, middle and far right buttons on a 5 button response box using the index, middle and ring finger of the right hand. The mapping of 'Intact' and 'New' to left and right buttons was counterbalanced. Once an Intact response was made participants were required to make a further Remember/Know/Guess response (mapped to the second, third and fourth button respectively). After a Remember/Know/Guess, 'Recombined,' or 'New' response, the trial was ended.

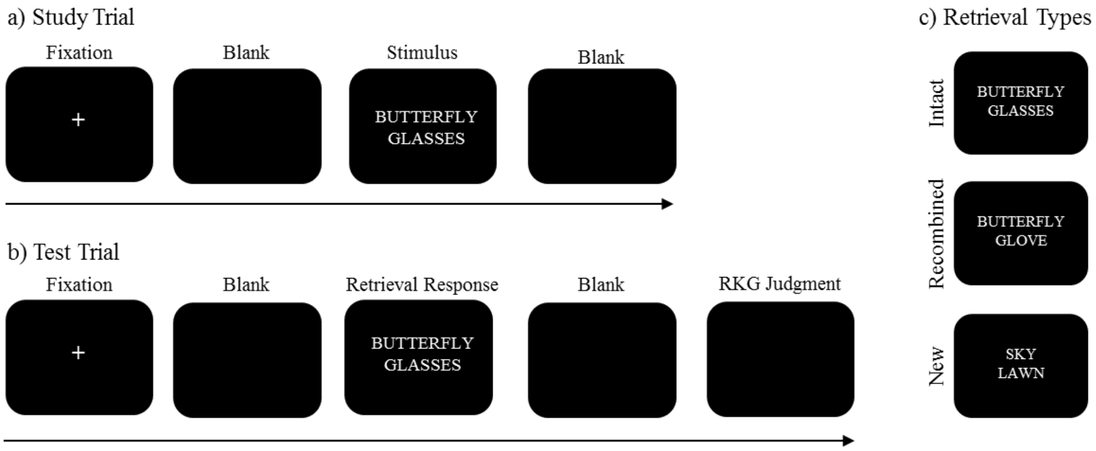

Figure 8.1: Panel a represents a single study trial. Panel b represents a single test trial - only identified Intact pairs received a further R/K/G response. Panel c represents the various retrieval types.

The general ERP recording procedure was identical to that described in Chapter 5 (Section 5.4.2). To reiterate, ERPs were analysed by examining mean amplitudes (relative to the pre-stimulus baseline) during *a priori* defined time-windows, designed to capture the neural correlates of familiarity (300-500ms) and recollection (500-

800ms). Initial analysis was performed on the data from the two encoding tasks separately, characterising the pattern of old/new effects [i.e., a subtraction of activity elicited by Intact Hits (here after simply referred to as Hits) and Correct Rejections]: see Figure 7.2. Similar to Rhodes and Donaldson (2008), analysis employed a repeated measures ANOVA confined to frontal [F5, F3, F1, F2, F4, F6] and parietal [P5, P3, P1, P2, P4, P6] strings (see Figure 8.2, left) with factors of Retrieval [Hits/Correct Rejections], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Only significant effects involving the factor of Retrieval are reported. Once old/new effects had been established within conditions, using subtraction waveforms a subsequent ANOVA with factors of Task [Item/Interactive], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior] was carried out to assess potential topographical differences across tasks. If topographical differences were observed between tasks, a follow up ANOVA on rescaled data (as per McCarthy and Wood, 1985: see Section 5.4.3) was conducted to assess whether the observed topographical differences were driven by the contribution of different neural generators or simply variation in the strength of a shared set of generators.

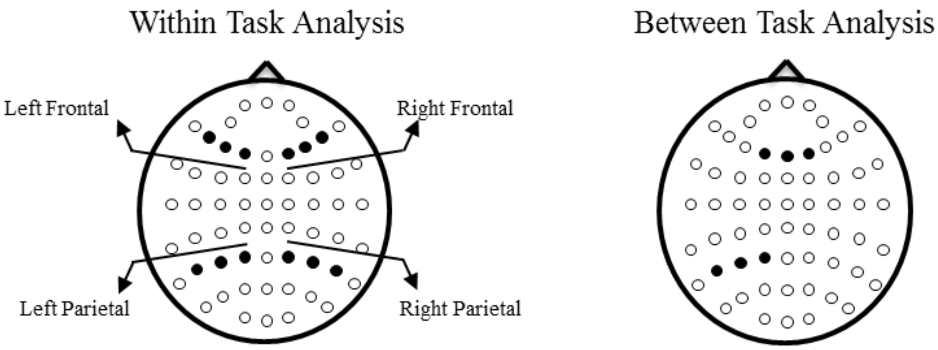

Figure 8.2: Schematic illustration of electrodes used in the ERP analysis within tasks (left side) and between tasks (right side).

Finally, having statistically identified the presence of old/new effects within tasks, additional focused analysis of the difference waveforms was conducted to compare the magnitude of effects between tasks. Between task analyses (see Figure 8.2, right) were performed using focused t-tests, confined to *a priori* selection of electrodes from the bilateral frontal (F1, FZ, F2) and left parietal (P1, P3, P5) regions of the scalp. The use of targeted analyses is advantageous because they protect against the increased risk of making type 1 errors as a result of interpreting large ERP datasets.

In all analysis the Greenhouse-Geisser correction for non-sphericity was applied where appropriate and adjusted degrees of freedom are reported where necessary. A significance level of .05 was used for all statistical analyses. The mean number of trials contributing to the grand average were; Item imagery: Intact (44), New (57), Interactive imagery: Intact (54), New (59).

8.3. Results

8.3.1. Behavioural data

The mean Hit rate for the Item imagery task was 58% (s.d. = 19%) with a False Alarm rate of 1% (s.d. = 1%). The mean Hit rate for the Interactive imagery task was 80% (s.d. = 12%) with a False Alarm rate of 1% (s.d. = 1%)[2]. It is important to note that False Alarms (1 - Correct Rejection) were divided among Intact and Recombined responses, hence the discrimination measure for Intact pairs illustrated in Figure 7.3 (right panel) [Pr: Hit-FA] reflects only those False Alarms to Intact pairs and not the proportion of False Alarms responded to as Recombined. Discrimination accuracy for the Interactive and Item imagery task are illustrated in Figure 7.3 (left panel). Analysis confirmed that old/new discrimination was significantly higher for Interactive [mean Pr = .79 (s.d. = .13)] compared to Item [mean Pr = .57 (s.d. = .18)] imagery [t(1,34) = 8.69, p < .001].

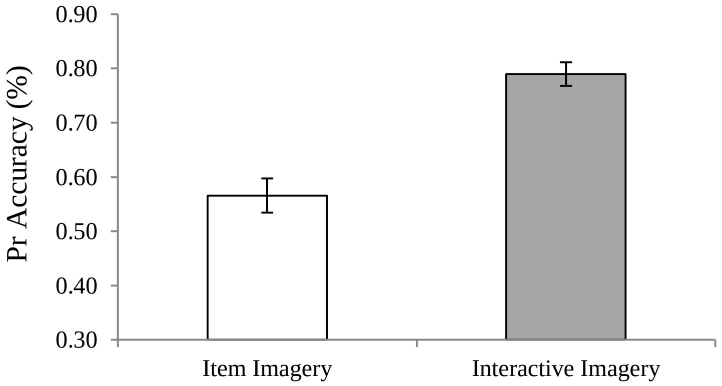

Figure 8.3: Means (standard error) of old/new discrimination accuracy (Pr).

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[2] The low False Alarm rates for Intact pairs is a result of the three-way decision employed in the current task. It was found that when participants were unsure of their response, they generally made a Recombined response (i.e., Item imagery False Alarm = 18%, Interactive imagery False Alarm = 16%).

Reaction time data for correct responses to each type of word pair are illustrated in Figure 8.4, demonstrating a clear reduction in reaction time for correctly identified Intact responses (Hits) with little difference in response times for New pairs (Correct Rejections) following the Interactive compared to Item imagery task. An ANOVA with factors of Retrieval [Intact/New] and Task [Single Item imagery/Interactive imagery] revealed a main effect of Retrieval [F(1,33) = 6.28, p < .05], a main effect of Task [F(1,33) = 12.67, p = .001] and a significant interaction [F(1,33) = 30.34; p < .001]; reflecting the selective reduction in response times for Intact pairs only when encoded with Interactive imagery compared to Item imagery.

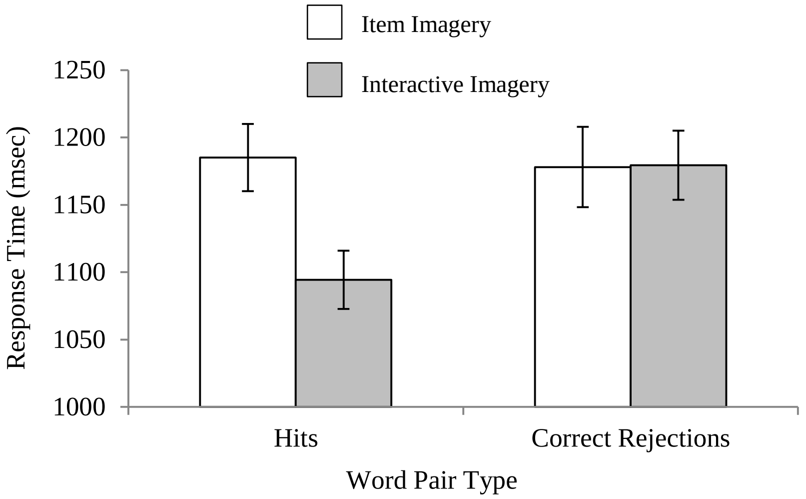

Figure 8.4: Mean reaction times (and standard error) for correctly identified Intact (Hits) and New (Correct Rejections) word pairs for both Item imagery and Interactive imagery tasks.

Behavioural estimates of recollection and familiarity were obtained by asking participants to make a ‘Remember’, ‘Know’ or ‘Guess’ response if they had responded Intact at test. As ‘Remember’ and ‘Know’ responses are mutually exclusive, ‘Know’ responses alone underestimate familiarity (because they do not capture the familiarity that is experienced on ‘Remember’ trials). To obtain a more accurate measure of familiarity, an Independent Remember/Know (IRK) rescaling procedure was used (‘Know’ responses are divided by the proportion of pairs not assigned ‘Remember’ [Know/1-Remember]; see Yonelinas & Jacoby, 1995). As can be seen in Figure 8.5, a larger proportion of ‘Remember’ responses were made for Intact pairs encoded with Interactive imagery than Single Item imagery, whereas more ‘Guess’ responses were made for the Item imagery task. Critically, the proportion of IRK responses appear not to differ. A repeated measures ANOVA with factors of Response [Remember/IRK/Guess] and Task [Item/Interactive] revealed a main effect of Response [F(2,66) = 135.00, p < .001], a main effect of Task [F(1,33) = 10.60, p < .01] and a significant interaction [F(2,66) = 12.61, p <.001]; reflecting significantly more ‘Remember’ responses than either IRK or ‘Guess’ responses, and more ‘Remember’ responses for Intact word pairs following Interactive compared to Item imagery. The results also confirmed that significantly more ‘Guess’ responses were made following Item imagery compared to Interactive imagery. Critically, no difference in IRK responses between tasks was observed.

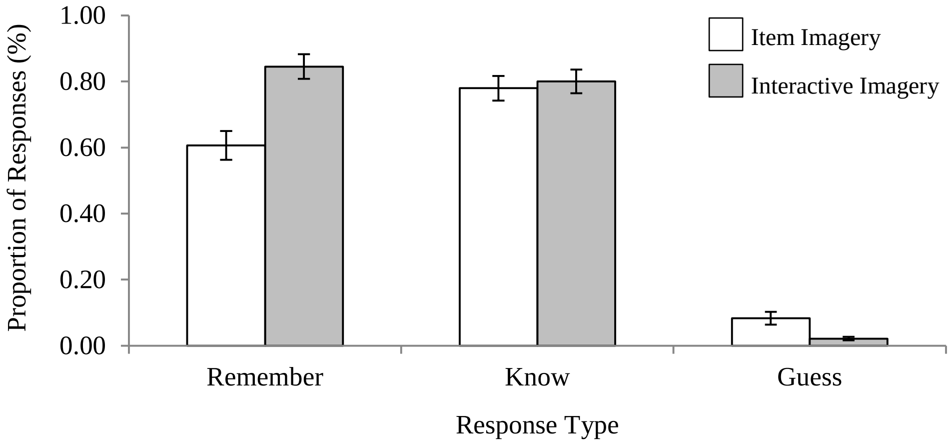

Figure 8.5: Illustrates the mean proportion (and standard error) of Remember/Know/Guess responses made to correctly identified Intact word pairs within the Item and Interactive imagery tasks. Know responses are corrected [K/1-R] in accordance with the IRK procedure.

8.3.2. Event Related Potentials

From Figure 8.6, it can be observed that neural activity elicited by Hits and Correct Rejections diverged around 300ms post-stimulus onset over both frontal and parietal channels. Overall, neural activity appears to be more positive going for Hits compared to Correct Rejections. The topography of old/new effects is illustrated in Figure 7.6, averaged over the 300-500ms and 500-800ms time windows. During the early 300-500ms time window a clear Mid-Frontal old/new effect is visible for word pairs that have been encoded with Interactive imagery, with a slightly smaller effect seen following Item imagery. During the later 500-800ms time window both tasks exhibit Left Parietal old/new effects. For the Item Imagery task the old/new effect exhibits a clear left lateralized distribution over the parietal electrodes, whereas the Interactive Imagery task exhibits right frontal maxima (reflecting the continued impact of the early frontal old/new effect for this task, as can be seen in Figure 8.6) with additional activity extending across the left hemisphere over parietal electrodes.

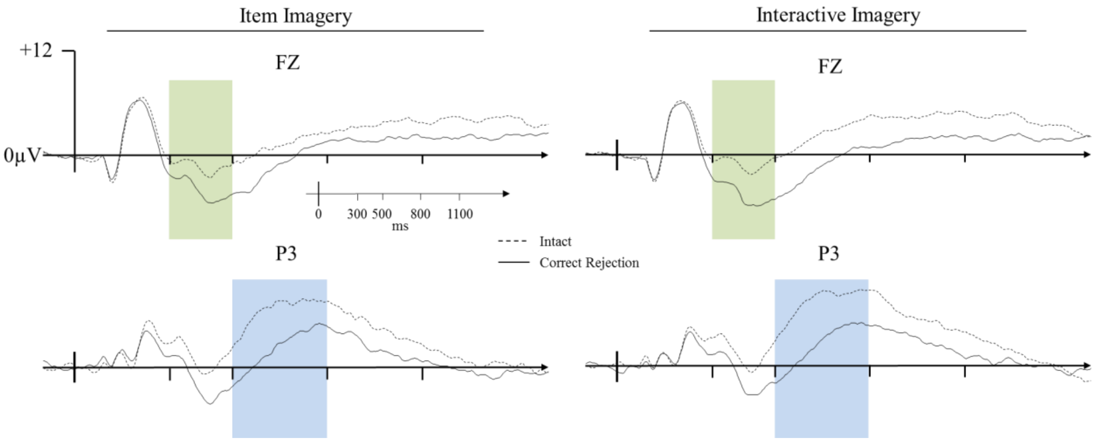

Figure 8.6: Grand average ERPs for Single Item (left) and Interactive (right) imagery tasks for correctly identified Intact (illustrated with a dashed line) and New word pairs (illustrated with a solid black line). Waveforms are presented at representative electrodes, illustrating the Mid-Frontal old/new effect (FZ) and left parietal old/new effect (P3). The 300-500ms time window is marked with a green border and the 500-800ms time window in blue.

8.3.2.1. The Mid-Frontal old/new effect

The initial ANOVA revealed significant main effects of Retrieval for both Item [F(1,33) = 59.27, p < .001] and Interactive imagery tasks [F(1,33) = 45.52, p < .001], reflecting greater positivity for Hits compared to Correct Rejections. Analysis of old/new differences within the Item imagery task also revealed a significant Retrieval and Site interaction [F(1,33) = 17.06, p < .001], reflecting greater old/new differences at superior sites. Crucially, no Location interaction was present for the Item imagery task providing little evidence of a specific frontal distribution.

Analysis of the Interactive imagery task, by contrast, produced a number of significant interactions including a two way interaction between Retrieval and Location [F(1,33) = 6.50, p = .01], Retrieval and Hemisphere [F(1,33) = 9.04, p = .01] and Retrieval and Site [F(1.09,36.1) = 12.95, p < .001]. Further three-way interactions were also present between Retrieval, Hemisphere and Site [F(1.33,43.87) = 7.82, p < .001], and Retrieval, Location and Site [F(1.24,40.83) = 4.59, p < .05]. As can be seen in Figure 8.6, the Interactive imagery task exhibits an early old/new effect that is largest over the frontal location than the parietal location, and larger over superior compared to inferior sites. Over frontal electrodes, the old/new difference is largest over the right hemisphere than the left.

Although the old/new differences within the Interactive imagery task demonstrate a frontal focus, the old/new differences within the Item task appears to have a broader distribution across frontal and parietal locations. To assess whether there was a significant topographical difference between tasks within the 300-500ms time window, an ANOVA was carried out on the difference waveforms [Hits - CR] with factors of Task [Item/Interactive], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. The analysis revealed a significant interaction between Task and Hemisphere [F(1,33) = 4.69, p < .05], reflecting the increased magnitude of old/new activity across the right hemisphere within the Interactive imagery compared to the Item imagery task. In addition, old/new activity also appeared to differ across location, although the Task and Location interaction was marginally non-significant [F(1,33) = 3.39, p = .07], the trend implies that old/new activity differed between tasks over frontal, rather than parietal electrode locations (consistent with Figure 8.7). To assess whether the topographical difference between tasks reflected the contribution of separate neural generators, the topographical analysis was conducted again with rescaled data. The results of the rescaled analysis, however, did not reveal any significant main effects or interactions, implying that the original interaction with hemisphere (and marginally non-significant interaction with location) reflected a quantitative change in amplitude rather than the contribution of different neural generators.

Finally, targeted comparison of the mid-frontal electrodes was carried out, licenced by the specific experimental hypothesis regarding the enhancement of the Mid-Frontal old/new effect following Interactive compared to Item imagery. To directly examine the Mid-Frontal old/new effect between Item and Interactive imagery tasks, a focused one-tailed t-test was carried out on the difference waveforms averaged across a cluster of frontal electrodes (F1,FZ,F2: see Figure 8.2) within the 300-500ms time window. Results revealed that the Mid-Frontal old/new effect was significantly greater in amplitude when encoding encouraged Interactive rather than Item imagery [t(33) =

1.69, p = .05]. The overall pattern of data therefore indicates that regardless of encoding task, successful recognition of Intact pairs elicited the same Mid-Frontal old/new activity during the 300-500ms time window, but critically the activity was enhanced following Interactive compared to Item imagery (see Figure 8.7).

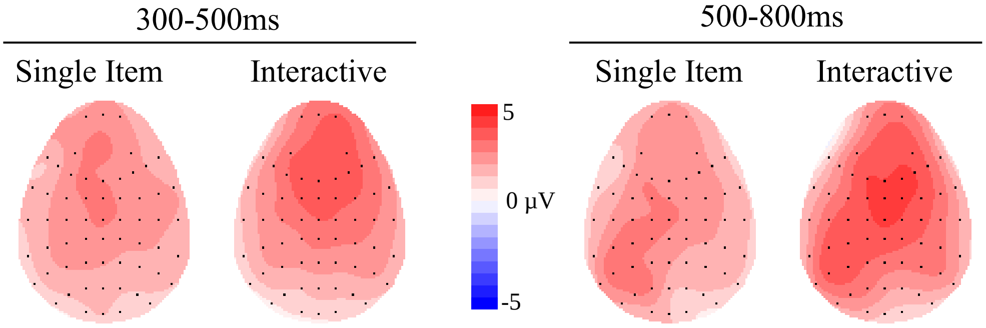

Figure 8.7: Topographic maps illustrating the distribution of old/new effects within the 300-500ms and 500-800ms time windows for Item and Interactive imagery tasks. The scale bar reflects the voltage range (µV).

8.3.2.2. The Left Parietal old/new effect

Analysis of the 500-800ms time window revealed main effects of Retrieval for both Item imagery [F(1,33) = 32.91, p < .001] and Interactive imagery [F(1,33) = 45.85, p < .001] tasks, signifying that activity to Intact pairs was more positive going than Correct Rejections. Analysis of the Item imagery task also revealed significant three-way interactions between Retrieval, Location and Hemisphere [F(1,33) = 10.63, p < .001] and Retrieval, Hemisphere and Site [F(1.18, 38.96) = 12.60, p < .001], along with a significant four-way interaction between Retrieval, Location, Hemisphere and Site [F(1.48,48.85) = 13.84, p < .001]. As can be seen in Figure 8.7, these interactions reflect the presence of a Left Parietal old/new effect – maximal over parietal electrodes with a left sided asymmetry maximal at inferior sites. Similar results were obtained for the Interactive imagery task with significant interactions including Retrieval and Site

[F(1.13,37.17) = 28.68, p < .001], Retrieval, Location and Hemisphere [F(1,33) = 11.96, p < .001], along with a significant four way interaction between Retrieval, Location, Hemisphere and Site [F(1.51,49.74) = 10.14, p < .001]. As illustrated in Figure 8.7 the old/new effect is present at frontal and parietal locations, with a right-sided asymmetry over frontal sites, and a left-sided asymmetry over inferior parietal sites.

To assess any topographical differences between tasks within the 500-800ms time window, an ANOVA was conducted on difference waveforms (Hit – Correct Rejection) with factors of Task [Item/Interactive], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Results revealed a significant main effect of Task [F(1,33) = 4.36, p = .05] and a significant Task and Hemisphere interaction [F(1,33) = 4.21, p = .05]. The pattern of results is consistent with the impression given in Figure 8.7 whereby old/new activity is more broadly distributed within the Interactive imagery task with maximal activity over the right frontal electrodes compared to the left parietal maxima observed for the Item imagery task. Finally, to investigate whether the observed old/new differences between tasks were generated by the same neural configuration, data were again submitted to topographical analysis on rescaled data using an ANOVA with factors of Task [Item/Interactive], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Results revealed a significant Task and Hemisphere interaction [F(1,33) = 4.62, p < .05], with greater old/new activity over the right hemisphere following the Interactive compared to Item imagery task. To assess whether the initial interaction reflected hemispherical differences at parietal electrodes, separate ANOVAs were carried out on each location. The results revealed a Task by Hemisphere interaction was only significant over the frontal location [F(1,33) = 6.41, p < .05]. To be clear, the hemispherical differences in old/new activity appear to be driven by the additional right frontal old/new maxima which is present in the Interactive imagery task but is absent in the Item imagery task.

Having demonstrated the presence of Left Parietal old/new effects within both the Interactive and Item imagery tasks, a planned comparison was carried out on the difference waveforms averaged across a cluster of electrodes (P5,P3,P1), chosen to capture the Left Parietal old/new effect. Results revealed that the magnitude of the Left Parietal old/new effect did not significantly differ between tasks (t = 1.58) suggesting that recollection contributed equally to both tasks (as illustrated in Figure 8.8).

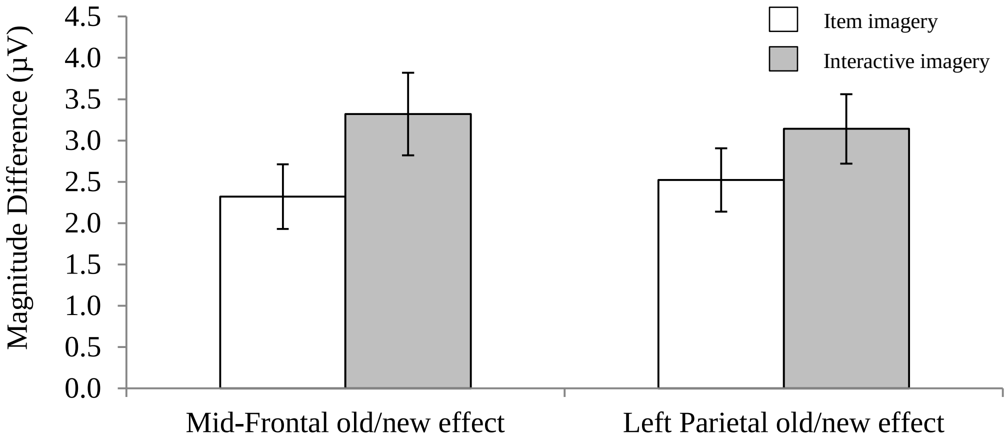

Figure 8.8: A comparison of the mean (and standard error) magnitude differences (Hits - Correct Rejection) of the Mid-Frontal (300-500ms) and Left Parietal (500-800ms) old/new effects between the Item and Interactive imagery tasks.

8.3.2.3. Time window comparison

The previous analysis confirmed that significant old/new differences were present within both tasks during the 300-500ms and 500-800ms time windows. To ensure that topographical differences were present across time windows, an additional ANOVA was performed with factors of Time (300-500ms/500-800ms), Location (Frontal/Parietal), Hemisphere (Left/Right) and Site (Inferior/Medial/Superior) for both Item and Interactive imagery tasks. The ANOVA revealed a significant Time, Location, Hemisphere and Site interaction for both the Item [F(1.39,45.93,) = 24.22, p < .001] and Interactive [F(1.36,44.79) = 24.28, p < .001] imagery tasks, reflecting the change in distribution over time. Critically, when the data was submitted to topographic analysis using re-scaled data the four way interaction for both tasks survived [Item: F(1.47,48.55) = 20.24, p < .001; Interactive: F(1.37,45.23) = 24.14, p < .001], supporting a qualitative change in scalp topography across time windows.

8.3.2.4 Subsidiary analysis: Remember/Know/Guess Responses

Initially, subsidiary analyses were planned to explore ERPs divided by ‘Remember’ and ‘Know’ responses. Relatively few trials were assigned a ‘Know’ response, however, resulting in not enough trials being available to form an adequate Grand Average.

8.3.2.5. Subsidiary analysis: 300-800ms.

As can be seen in Figure 8.7, the frontal maxima is observed following Interactive imagery is not restricted to the 300-500ms and is also present within the 500-800ms time window. The sustained nature of the effect is also evident from the ERP waveforms recorded from electrode FZ, illustrated in Figure 8.6. To investigate whether the sustained frontal old/new activity was significantly larger following Interactive imagery compared to Item imagery, a targeted analysis of the Mid-Frontal old/new effect was carried out on the same cluster of electrodes analysed in the previous Mid-

Frontal comparison (i.e., F1, FZ, F2). As can be observed in Figure 8.9, Mid-Frontal old/new activity larger during the 300-800ms time window following Interactive compared to Item imagery (mean magnitude difference = 1.26µV). The results of a pair-wise t-test confirmed that the magnitude of the Mid-Frontal old/new activity between 300-800ms was significantly larger following Interactive imagery compared to Item imagery [t(1,33) = 2.05, p = .05]: see Figure 8.9.

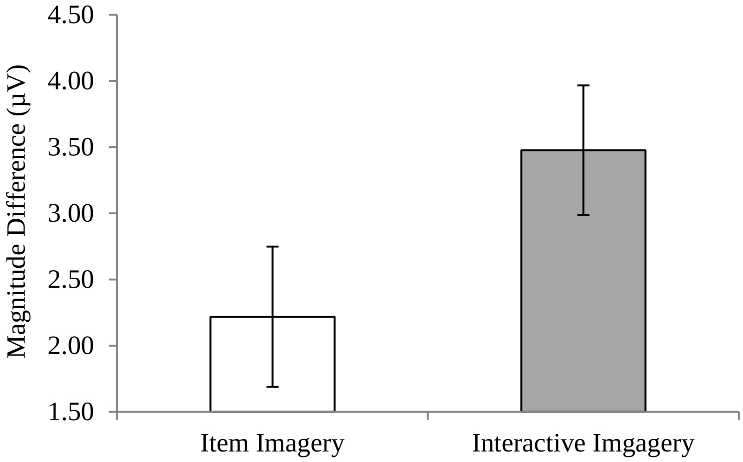

Figure 8.9: A comparison of the mean (and standard error) magnitude of the Mid-Frontal old/new effect between the Item and Interactive imagery tasks within the 300-800ms time window.

8.4 Discussion

The current experiment aimed to investigate whether familiarity – as indexed by the Mid-Frontal old/new effect – could contribute to the associative retrieval of semantically and associatively unrelated word pairs. To be clear, the use of pre-experimentally novel word pairs allowed us to test one of the main predictions of unitization – namely, that the processing of distinct stimuli as a single unit influences later memory retrieval. Secondly, by demonstrating an enhanced Mid-Frontal old/new effect for arbitrary associations, the results could address the apparent inconsistency regarding the Mid-Frontal old/new effect – namely, that previous evidence reveals that Mid-Frontal old/new activity is enhanced for conceptually related but not unrelated word pairs. The current study was motivated by findings from Rhodes and Donaldson (2008), who demonstrated that semantically related word pairs encoded with Interactive imagery compared to Item imagery produced significantly larger Mid-Frontal old/new effects. In the current experiment, unitization was again manipulated with mental imagery, but unrelated pairs were used to provide a more direct assessment of unitization without the contamination of pre-experimental knowledge.

The results of the ERP data are clear: the contribution of familiarity – as indexed by the Mid-Frontal old/new effect – towards successful recognition of unrelated word pairs was greater for Intact pairs encoded with instructions that encouraged unitization compared to instructions that discouraged unitization. The influence of encouraging unitization was selective, in so much as no significant difference was observed in the magnitude of the Left Parietal old/new effect – indicative of recollection. To be clear, this experiment provides the first demonstration, to date, that task instructions encouraging unitization modulate the Mid-Frontal old/new effect for rapidly learnt, arbitrary associations. Below, the results are examined in more detail focusing on the behavioural data, the Left-Parietal old/new effect and Mid-Frontal old/new effect respectively.

8.4.1. Behavioural overview

Analysis of the behavioural data confirmed that encoding word pairs with Interactive imagery compared to Item imagery significantly improved memory. The results showed that the probability of successfully discriminating Intact from New word pairs was higher for word pairs previously encoded with Interactive imagery instructions. Furthermore, reaction time data also indicated that participants were much quicker at responding to Intact pairs following Interactive compared to Item imagery. The behavioural results are therefore consistent with previous studies demonstrating a benefit of unitization to overall recognition (Giovanello, Keane & Verfaellie, 2006; Jäger et al., 2006a; Opitz & Cornell, 2006; Quamme et al., 2007; Rhodes & Donaldson, 2008). Although not all experiments aimed at manipulating unitization show a behavioural benefit (Ford, Verfaellie & Giovanello, 2010; Speer & Curran, 2007), a significant improvement for unitized pairs may be indicative of a familiarity 'boost' to successful associative recognition. Although the discrimination data for Intact pairs largely supported the prediction that Interactive imagery would improve recognition performance, the results of the RKG data challenge the assumption that the improved memory performance was attributable to an increase in familiarity.

The inclusion of the RKG was used to provide further behavioural assessment of the contributions of recollection and familiarity. The results, however, were unexpected. It was found that the proportion of 'Remember' responses was significantly larger for Intact word pairs encoded with Interactive imagery instructions, whereas no difference in the proportion of 'Know' responses was observed. To be clear, the results from the RKG data are inconsistent with previous unitization experiments employing the RKG procedure (Giovanello et al., 2006) and ROC analysis (Yonelinas et al., 1999; Diana et al., 2008; Haskins et al., 2008, Quamme et al., 2007). Two possible explanations arise from this result – either Interactive imagery in the current experiment lead to increased recollection for unitized pairs or alternatively participants misunderstood the RKG instructions. The former explanation is difficult to reconcile with previous behavioural ratings showing a selective increase in the contribution of familiarity for unitized pairs. Additionally, no evidence from behavioural, neurophysiological or neuroimaging studies has demonstrated any relationship between unitization and recollection. A more likely explanation is that the RKG instructions used in the current experiment (i.e., Gardiner et al., 1998) mislead participants to report their assessment of confidence rather than subjective feelings of familiarity and recollection (see Donaldson, 1996; Hirshman & Master, 1997; Inoue & Bellezza, 1998). Further, it has been demonstrated that depending on whether or not remember/know instructions separate or confound confidence can have a considerable impact on how judgements are made during retrieval (Geraci, McCabe & Guillory, 2009).

To assess whether the current RKG judgements may have reflected confidence, a follow up study (n = 12) was conducted that replicated the current experimental paradigm employing RKG instructions that did not conflate confidence (i.e., Rajaram, 1993). Results from this short study revealed that although discrimination accuracy and response times benefited from interactive encoding instructions (replicating the current behavioural results), Remember, Know and Guess responses did not significantly differ across tasks. Why then, does the behavioural estimate of familiarity not differ in either the current experiment or the follow up study? Critics of the remember/know procedure argue that the task may not necessarily index separate memory categories, such as recollection and familiarity, but instead reflect the difficulty of the experimental task, expectations regarding performance, or other aspects of the experience that participants deem relevant (Bodner, 2003). Although the RKG procedure was employed in an attempt to provide additional behavioural evidence for the contribution of familiarity and allow for follow up analysis of ERPs locked to Remember and Know responses, the results of the RKG procedure highlight the limitations of relying on behavioural subjective reports to separate recollection and familiarity. By contrast, ERPs arguably provide a more objective measure of retrieval processing not influenced by subjective reports, which is why we now move on to the results of the ERP indexes of retrieval processes (described further below).

8.4.2. Overview of the Left Parietal old/new effect

The current study investigates unitization using ERP data to index memory, and therefore relies on the interpretation of ERP old/new effects as neural correlates of recollection and familiarity. Here, we discuss each ERP effect in turn, beginning with the neural correlate of recollection – i.e. the Left Parietal old/new effect. In line with the experimental predictions, the Left Parietal old/new effect was present in both the Interactive and Item imagery tasks suggesting that recollection contributed to retrieval. Although the magnitude of the Left Parietal effect was numerically larger for word pairs encoded with Interactive imagery compared to Item imagery, the difference did not reach significance (i.e. Interactive: 3.04 µV; Single Item: 2.38 µV). To be clear, the data suggests that recollection, as indexed by the Left Parietal old/new effect, contributed equally in both tasks. In short, the finding that recollection did not differ between encoding instructions designed to manipulate unitization is in agreement with the majority of studies demonstrating that unitization selectively influences familiarity.

8.4.3. Overview of the Mid-Frontal old/new effect

The ERP data from the current experiment showed that Interactive imagery instructions aimed at encouraging unitization resulted in an enhanced Mid-Frontal old/new effect compared to the Item imagery instructions. Three aspects of the data are important. First, a clearly distributed frontal distribution of old/new activity was present for the Interactive imagery task (i.e. a significant Retrieval by Location interaction was observed). By contrast, the Item task revealed a broadly distributed old/new difference with no clearly defined topography (i.e. no interaction of Location). Secondly, a targeted comparison of the magnitude of the Mid-Frontal old/new effect between tasks in the early 300-500ms time window further supported the experimental prediction that activity over the frontal electrodes was selectively enhanced with word pairs encoded with Interactive instructions compared to Single Item instructions (i.e., Interactive imagery: 3.27 µV; Item imagery: 2.32 µV). Lastly, from the scalp topographies it was clear that the frontal old/new difference observed for the Interactive imagery task was not restricted to the early time window. When an extended 300-800ms time window was analysed, targeted analysis of the Mid-Frontal old/new effect was again found to be selectively enhanced following Interactive (3.48 µV) compared to Item imagery (2.22 µV) encoding. The results of the extended time window therefore imply that the difference in old/new activity across the frontal electrodes follows a much broader time course than is typically assumed for familiarity (see the general discussion for a more detailed interpretation of extended distribution of the Mid-Frontal old/new effect). In general, however, the data was consistent with previous unitization studies demonstrating a modulation of the Mid-Frontal old/new effect for related word pairs (Rhodes & Donaldson, 2007, 2008).

The present findings not only support but also build upon the findings of Rhodes and Donaldson (2007, 2008), by demonstrating that familiarity can also be encouraged for the retrieval of novel associations – confirming a fundamental prediction of unitization. The current ERP data also confirms that mental imagery manipulation is an effective manipulation of unitization. To be clear, it was shown that encoding instructions encouraging interactive mental imagery enhanced the contribution of familiarity (for an alternative interpretation of the Mid-Frontal old/new effect, including a conceptual priming account, please see Chapter 11 and the General Discussion) compared to Item imagery designed to discourage unitization. Further, the use of unrelated pairs is important because they permit a greater control over the degree of pre-experimental integration of word pairs between encoding tasks allowing for a more direct assessment of the influence of unitization – uncontaminated by pre-established conceptual knowledge. In addition, by measuring familiarity for rapidly learnt arbitrary associations we can draw valid comparisons with other ERP associative recognition experiments that found no modulation of the Mid-Frontal old/new effect (as discussed in more detail in the following section).

8.4.4. Comparison to other studies

Another aim of the current experiment was to address the apparent inconsistency regarding ERP studies of unitization – namely, that unitization appears to modulate the Mid-Frontal old/new effect for related but not unrelated word pairs. The current experiment was able to demonstrate that the use of mental imagery instructions at encoding selectively modulated the Mid-Frontal effect during retrieval of novel associations. These findings are difficult to reconcile with the argument that unitization of conceptually related and unrelated word pairs result in distinct topographic effects (i.e. see Bader et al., 2010). In these experiments unitization of unrelated word pairs resulted in broad parietal old/new differences that were interpreted as modulations of the N400 effect – sensitive to conceptual fluency. Bader et al., (2010) argue that since completely novel pairings were used, unitization served to integrate pairs into a semantically integrated whole that then allowed for the assessment of absolute familiarity (rather than relative familiarity) as a diagnostic signal of prior occurrence. According to their account, pre-experimentally existing representations already carry an absolute signal and so relative familiarity (as indexed by a more frontally distributed effect) becomes more diagnostic of whether a word pair was previously studied. Interpretation of their findings, however, is difficult because they did not observe the traditional ERP effects associated with recollection and familiarity.

The results from the current study are difficult to reconcile with the findings of Bader et al., (2010) as the use of unrelated word pairs in the current experiment produced the expected old/new effects associated with recollection and familiarity, whilst theirs did not. Arguably then, the creation of novel unitized stimulus configurations cannot adequately explain the different ERP effects observed between studies using mental imagery instructions (Rhodes & Donaldson, 2008) versus lexical encoding instructions (Bader et al., 2010). Given that a selective modulation of the Mid-Frontal old/new effect was observed in the current experiment using unrelated word pairs, it is important to address the question of whether different encoding strategies that manipulate the level of unitization (i.e. the mental imagery method and the lexical method) influence how unitized representations are retrieved at test.

8.4.5. Summary

The current experiment aimed to assess whether unitization could encourage familiarity – as indexed by the Mid-Frontal old/new effect – for completely unrelated word pairs. The results confirmed that unitization selectively enhanced the Mid-Frontal old/new effect when Interactive imagery was encouraged for unrelated pairs. The contribution of familiarity for the successful associative recognition of unrelated pairs supports the assumption of specific dual process models (specifically, the DPSD model). The results of the current experiment also have important practical implications, particularly for those individuals with selective recollection deficits. These implications, however, will be described in the more detail in the general discussion.

Given that the Mid-Frontal old/new effect was observed for unrelated pairs in the current experiment, it still remains unclear why the effect was not observed by Bader et al., (2010), considering that both experiments also attempted to manipulate unitization. The differences in ERP effects across studies are of considerable concern given that both mental imagery instructions and lexical encoding have both been demonstrated to influence familiarity during associative recognition at a behavioural level. Resolving this inconsistency is therefore important if we are to begin making progress in understanding, at a neural level, how familiarity contributes to associative recognition. In the next chapter, we further attempt to resolve the discrepancy between the Mental Imagery and Lexcial unitization tasks by replicating the Lexical method under similar experimental conditions employed in the current chapter.

Chapter 9

Investigating Unitization with Compound Definitions and Sentence Frames

In Chapter 8 the data suggested that encoding instructions designed to encourage unitization selectively enhanced the contribution of familiarity – as indexed by the Mid-Frontal old/new effect. To date, however, an enhancement of the early Mid-Frontal old/new effect has only been demonstrated using mental imagery encoding instructions and it is currently unclear whether alternative manipulations of unitization also modulate early Mid-Frontal old/new activity. A positive result would suggest that there are multiple routes to achieving unitization that selectively influence the same underlying neural mechanism. Demonstrating that the Mid-Frontal old/new effect can be modulated by alternative unitization instructions would allow future research to validly compare between unitization techniques – using the engagement of the Mid-Frontal old/new effect as evidence for how well unitization has been achieved. The aim of the current chapter is to further assess the circumstances that allow familiarity to contribute to successful associative retrieval.

9.1. Introduction

A critical feature of unitization is the encoding of two previously separate stimuli into a single integrated item. Whether unitization is manipulated by encouraging participants to encode stimuli with mental imagery (see Rhodes & Donaldson., 2008) or with mediating sentences (see Quamme et al., 2007) should largely be immaterial. In practice however, ERP studies manipulating unitization with mental imagery and mediating sentences have observed an inconsistent pattern of old/new effects. Manipulating unitization with mental imagery at encoding, for example, has been found to selectively modulate the magnitude of the Mid-Frontal old/new effect (i.e., the neural correlate of familiarity), while the Left-Parietal old/new effect (i.e., the neural correlate of recollection) does not differ between tasks (see Rhodes & Donaldson, 2008; Pilgrim, Murray & Donaldson, 2012; Chapter 8 of the current thesis). By contrast, ERP studies manipulating unitization with mediating sentences (i.e. compound definitions and sentence frames), have found atypical ERP old/new effects not related to recollection or familiarity. In the following section, we describe why these contrasting ERP old/new effects might be observed, in order to clarify the motivation for the current experiment. The overall aim of the chapter is to investigate if the mediating sentence manipulation of unitization modulates the underlying neural signal of familiarity, thereby further elaborating upon the circumstances that give rise to familiarity during successful associative retrieval and addressing the inconsistency among ERP studies of unitization.

To reiterate from Chapter 2, the mediating sentence manipulation of unitization encourages unitization using compound definitions that serve to define a new concept (e.g., VEGETABLE BIBLE: A reference book used by gardeners). By contrast, sentence frames are presented to discourage unitization by maintaining the meaning of each word in a pair (e.g., VEGETABLE BIBLE: The ___ could be found directly opposite the ___). The mediating sentence method has been used to confirm a number of important predictions regarding unitization. Quamme et al., (2007), for instance, demonstrated that amnesiac patients, with selective recollective deficits, exhibited preserved associative retrieval for novel word pairs encoded with compound definitions compared to sentence frames. More recently, Haskins et al., (2008) employed the mediating sentence manipulation during an fMRI study, predicting that unitized stimuli may be stored within the perirhinal cortex (PRc), believed to be preferentially correlated with item familiarity. Results revealed that PRc activity was selectively increased during encoding for previously unrelated word pairs learnt using compound definitions, and was highly correlated with familiarity estimates at retrieval (derived from confidence ratings). Collectively, both studies imply that compound definitions and sentence frames are sufficient for manipulating the level of unitization and selectively modulate familiarity during associative retrieval.

The Quamme et al., (2007) and Haskins et al., (2008) studies, however, derived their estimates of familiarity and recollection from ROC analysis which is highly model specific (see Chapter 2). As discussed in Chapter 8, the variation in confidence that leads to curvilinear ROCs (indicative of familiarity) could equally be explained by a recollection signal that is modelled as both variable and thresholded (as observed in Chapter 7). To validate the important findings of preserved associative retrieval among patients with recollective deficits, as well as enhanced familiarity during associative retrieval among healthy participants, it is important to derive estimates of recollection and familiarity using more objective measures not dependent on confidence.

As previously discussed in Chapter 1, the only ERP study attempting to manipulate unitization with mediating sentences was conducted by Bader et al., (2010). Contrary to other ERP studies of unitization (namely, Diana et al., 2011; Jäger, Mecklinger & Kipp, 2006; Pilgrim, Murray & Donaldson, 2012; Rhodes & Donaldson, 2007, 2008) an incidental between participant design was used to prevent contamination of encoding instructions. Participants were, therefore, required to learn unrelated word pairs accompanied with either compound definitions or sentence frames and were later given a surprise associative recognition test. The ERP effects observed during recognition, however, were not typical of the Mid-Frontal and Left-Parietal old/new effects associated with familiarity and recollection respectively. Instead, a selective broad parietal old/new effect was observed for compound definitions within a 350-500ms time window; an effect that was topographically distinct from a later broadly distributed effect across the scalp for sentence frames between 500-700ms post stimulus onset (see Figure 9.1).

Bader et al., (2010) interpreted their early broad parietal old/new effects as reflecting the engagement of absolute familiarity (i.e., the absolute strength of a memory representation) that is more diagnostic of prior occurrence when using pre-experimentally novel word pairs. According to Bader et al., (2010) the use of related word pairs (as per Rhodes and Donaldson, 2008), facilitates the engagement of relative familiarity that is associated with a more frontally distributed old/new effect and is topographically distinct from absolute familiarity – which they argue is maximal over parietal electrodes (citing evidence from studies of recognition for faces by McKenzie & Donaldson, 2007). To be clear, Bader et al. (2010) argue that the distinct ERP old/new effects observed between unitization studies (i.e. between mental imagery and mediating sentence methods) are a direct result of the pre-established relationship between word pairs.

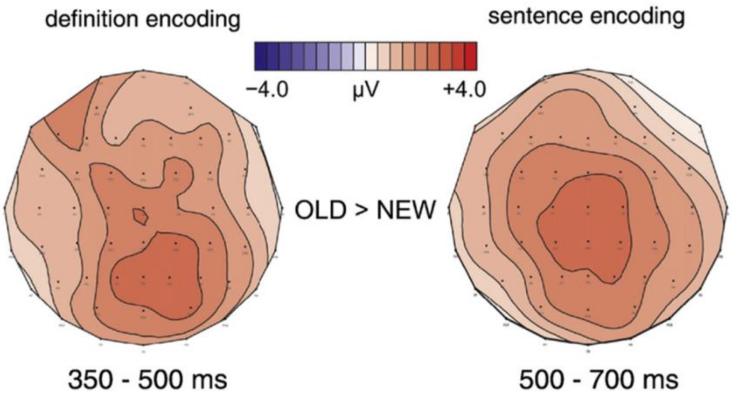

Figure 9.1: Adapted from Bader et al., 2010. The figure shows topographical old/new effects elicited during retrieval of an associative recognition task. On the left is the topographical distribution of a broad parietal old/new effect elicited by word pairs encoded with compound definitions between 350-500ms post stimulus on-set. Displayed on the right side is a broad central old/new effect elicited by word pairs encoded with sentence frames between 500-700ms post stimulus on-set.

Specific caveats about the Bader et al., (2010) study, however, make interpretation of their data within a unitization framework difficult. First, the lack of any clearly defined Mid-Frontal old/new effect is difficult to reconcile with a familiarity interpretation, especially considering the limited evidence supporting a distinction between absolute and relative familiarity. In addition, evidence of early Mid-Frontal old/new effects elicited for unrelated word pairs in Chapter 8 clearly rules out relationship type between words as a possible explanation for the discrepancy of ERP effects across unitization studies. To be clear, the selective enhancement of the early Mid-Frontal old/new effect for unrelated word pairs encoded with interactive imagery suggests that the effect is sensitive to encoding instructions that directly manipulate the level of unitization regardless of relationship type.

Second, Bader et al., (2010) were unable to demonstrate a direct behavioural difference between the sentence frame and compound definition tasks in terms of the proportion of correct responses or response times. The lack of any behavioural difference is difficult to reconcile with evidence from ERP studies of unitization demonstrating a clear behavioural advantage to recognition performance that is often associated with unitized stimuli (Rhodes & Donaldson, 2007, 2008; Pilgrim et al., 2012; Opitz & Cornell, 2006; Jager et al., 2006). Finally, the absence of a specific parietal old/new effect between 500-700ms for either task suggests that Bader et al., (2010) were also unable to detect the contribution of recollection – a process that is consistently been found to be engaged during associative recognition (for a review see Yonelinas, 2002). Given that the Bader et al., (2010) study was designed to manipulate unitization within an associative recognition task, it is currently unclear why they failed to find the ERP correlates of either familiarity or recollection.

One potential explanation for the inconsistency between ERP unitization studies is the alternative experimental procedures employed by Bader et al., (2010) and Rhodes and Donaldson (2008). Although both studies implemented an associative recognition paradigm, Rhodes and Donaldson (2008) employed an intentional within-participant design compared to the incidental between-participant paradigm adopted by Bader et al., (2008). Both designs have their advantages and disadvantages; however, it is currently unclear whether the distinct experimental design differences or experimental manipulations of unitization account for the inconsistency between ERP results. It would, therefore, be of interest to assess the mediating sentence manipulation of unitization under similar conditions to studies employing mental imagery. By keeping the experimental design consistent with ERP studies of unitization that have demonstrated the typical Mid-Frontal and Left Parietal old/new effects, we can assess whether word pairs encoded with mediating sentences results in similar modulations of

ERP effects observed with mental imagery. A positive result would validate the mediating sentence method as a sufficient manipulation of unitization and lend further evidence in support of the dual process account of the contribution of familiarity during associative recognition of arbitrary associations.

In the current study, we further explore the sufficient circumstances that give rise to familiarity during associative retrieval. To date, it is currently unclear whether methods of manipulating unitization other than mental imagery modulate the neural correlate familiarity. Here, we use the mediating sentence manipulation of unitization within the same experimental procedure employed in Chapter 8 and by Rhodes and Donaldson, (2008). To be clear, we used a within participant design whereby the presentation order of the Compound Definition and Sentence Frame tasks was counterbalanced across participants. In addition, participants were also aware that they were taking part in a memory experiment, consistent with the same study-test blocked design implemented by Rhodes and Donaldson, (2008). At test participants discriminated between intact, recombined and new word pairs. As with previous ERP studies (i.e., Rhodes & Donaldson, 2007; Bader et al., 2010; Weigand et al., 2011 and Chapter 8) recombined pairs are presented at test to prevent participants identifying intact word pairs based on item recognition and only behavioural and ERP data related to traditional old/new effects elicited by correctly identified intact and new word pairs are examined.

In line with previous ERP studies demonstrating traditional ERP old/new effects associated with familiarity and recollection, we predicted that unrelated word pairs encoded with compound definitions would result in enhanced familiarity, as indexed by an early Mid-Frontal old/new effect, and improved behavioural performance compared to sentence frames. As recollection is believed to be equivalent across encoding tasks, no observable difference in the magnitude of the Left Parietal old/new effect was expected.

9.2. Method

9.2.1. Participants

Thirty two participants from the University of Stirling took part in the study. Data from two participants were rejected due to an insufficient number of ERP trials in at least one experimental condition and a further five were excluded due to poor behavioural performance. The remaining 25 participants (12 female) had a mean age of 20 (range: 18-23).

9.2.2. Stimuli

The stimulus properties are identical to those described in Chapter 4. A total of 440 word pairs were pseudo-randomly constructed from 880 single words. Although words were initially randomised to form unrelated word pairs, some pairs had to be rearranged in order to construct meaningful sentence frames and compound definitions. Word pairs were then divided into two lists of 220 pairs each (i.e., list 1 and list 2). Both lists were presented with either sentence frames or compound definitions, counterbalanced across participants. As described in Chapter 4, lists were matched for word length, word frequency, familiarity, concreteness, associative strength and semantic relatedness.

The lists were divided into 10 study/test blocks comprised of 36 word pairs per block. To be clear, 5 study-test blocks comprised list 1 word pairs and 5 study-test blocks comprised list 2 word pairs. The order of encoding condition (i.e., Sentence Frame blocks or Compound Definition blocks) was counterbalanced so that half of the participants would take part in the Sentence Frame task first[1]. A single study block consisted of 12 'Intact' word pairs and 24 'Recombined' word pairs. The additional Recombined pairs were presented so that the partner of each Recombined pair at retrieval could be disregarded thereby preventing possible cueing effects. The order of words within a Recombined pair was always held constant so that if a word appeared first during the study block, it would be presented first during the test block. To be clear, if the word pairs 'VEGETABLE BIBLE' and 'CLOUD LAWN' were presented at study, then 'VEGETABLE LAWN' would be presented at test. A single test block consisted of 12 'Intact' (presented in the same order from study) word pairs, 12 'Recombined' pairs and 12 'New' (unstudied) word pairs. Stimuli were presented equally often as an 'Intact,' 'Recombined' and 'New' pairs across participants. Presentation of word pairs within blocks and order of blocks was randomised across participants.

A sentence frame and compound definition was constructed for each of the 440 word pairs. A compound definition served to combine two words into a new concept. For every definition the second word in the pair was treated as the head noun modified by the first word in the pair. Definitions ranged from 5 to 10 words in length. The

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[1] To test for potential order effects, discrimination accuracy was compared between those participants who viewed the Sentence Frame or Compound Definition task first. The results of independent t-tests revealed that discrimination accuracy did not significantly differ between groups for either the Sentence Frame or the Compound Definition tasks, confirming that order effects were not present.

definitions contained only synonyms or associates to study words, to both avoid repetition and to facilitate comparison with the sentence frame task. For example, the word pair ‘VEGETABLE BIBLE’ may be defined as a ‘Reference Book used by Gardners.’ The sentence frames contained blank spaces so that the first word in a pair fitted the first blank and the second word in the pair fitted the second blank - i.e., ‘VEGETABLE BIBLE’ was given ‘The ___ cast a shadow over the ___. All sentence frames and compound definitions were presented centrally below the word pairs.

9.2.3. Procedure

Each study trial (see Figure 9.2a) began with a fixation cross (+) for 200ms to ensure the participants focused on the centre of the screen and to indicate the presentation a word pair was imminent. The cross was followed by a blank screen for a further 200ms, after which the word pair and corresponding sentence frame or compound definition was presented for 5000ms. Participants were instructed to insert each word into the blank spaces or to read the definition. After the 5000ms had elapsed, participants were required to make a judgement about the prior sentence frame or compound definition. For sentence frames, participants were instructed to rate how well the words fitted into the blank spaces to make a plausible sentence using a range of response buttons: i.e., 1 (not very well) to 5 (very well). For compound definitions, participants were instructed to rate how well the definitions combined the two words into a sensible compound from 1 (not very well) to 5 (very well)[2]. Once a judgement was made the trial was ended.

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[2] The relatedness judgements were included in the current experiment to replicate the encoding procedure employed by Bader et al., (2010). Although subsidiary ERP analysis was planned examining neural activity to different relatedness judgements, a programming error meant that a significant proportion of judgments were not recorded and therefore the data could not be analysed.

A test block followed on from its corresponding study block (see Figure 9.2b). Test trials began with a central fixation cross presented for 500ms, followed by a blank screen for a further 300ms. Word pairs were presented for 700ms, followed by a 2000ms blank screen. To be clear, participants were given a total of 2700ms to make an Intact/Recombined/New judgement, starting from the initial onset of the word pair presentation and continuing until the maximum time had elapsed on the blank screen. Responses were made using buttons 1, 3 and 5 on a 5 button response box and participants were instructed to use their index, middle and ring finger of the right hand. The mapping of 'Intact' and 'New' to buttons 1 and 5 was counterbalanced across participants. Once a judgement has been made, or the maximum response time had elapsed, the trial was ended.

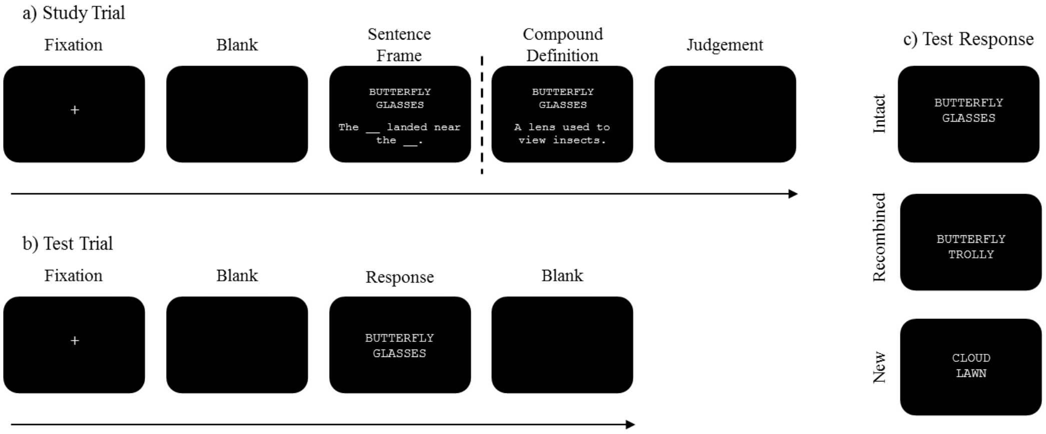

Figure 9.2: Panel a) represents a single study trial. Panel b) represents a single test trial and panel c) represents the Intact, Recombined and New test response.

The general ERP recording procedure was identical to that described in Chapter 5. ERPs were analysed by examining mean amplitudes (relative to the pre-stimulus baseline) during *a priori* defined time-windows, designed to capture the neural correlates of familiarity (300-500ms) and recollection (500-800ms). Data were initially analysed for the Sentence Frame and Compound Definition tasks separately, characterising the pattern of old/new effects within tasks (electrode selection was identical to Chapter 8). This analysis employed repeated measures ANOVA with factors of Retrieval [Hits (Intact)/Correct Rejection], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Only significant effects involving the factor of Retrieval are reported.

Once old/new effects had been established, potential differences in scalp topographies were assessed between tasks by conducting an ANOVA on subtraction data [Hits - Correct Rejections] with factors of Task [Compound Definition/Sentence Frame], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. If topographical differences were observed between tasks, a follow up ANOVA on rescaled data (as per McCarthy and Wood, 1985) was conducted.

Finally, if old/new effects had been observed within the 300-500ms and 500-800ms time windows, planned comparison of the Mid-Frontal and Left Parietal old/new effects were carried out between tasks. Between task analysis was performed using focused t-tests confined to an *a priori* selection of electrodes from the Mid-Frontal (F1, FZ, F2) and Left Parietal (P1, P3, P5) regions of the scalp (identical to the analysis conducted in Chapter 8). The mean numbers of trials contributing to the Grand Average ERPs were: Sentence Frame task: Intact (35), New (41); Compound Definition task: Intact (40), New (40).

9.3. Results

9.3.1 Behavioural data

The mean hit rate for the Sentence Frame task was 67% with a False Alarm rate of 3%. The mean hit rate for the Compound Definition task was 75% with a False Alarm rate of 3%. As in Chapter 8, False Alarms (1 - Correct Rejections) were calculated separately for Intact and Recombined responses. To be clear, the discrimination accuracy illustrated in Figure 9.4 is calculated from false alarms to Intact pairs. From Figure 9.4, it can be seen that discrimination accuracy was greater following Compound Definitions [mean Pr = 73% (s.d. = 15%)] compared to Sentence Frames [mean Pr = 64% (s.d. = 16%)]. This observation was confirmed with a pairwise t-test, revealing that mean old/new discrimination accuracy was statistically greater following the Compound Definition compared to the Sentence Frame task [$t(24) = 4.11$, $p < .001$].

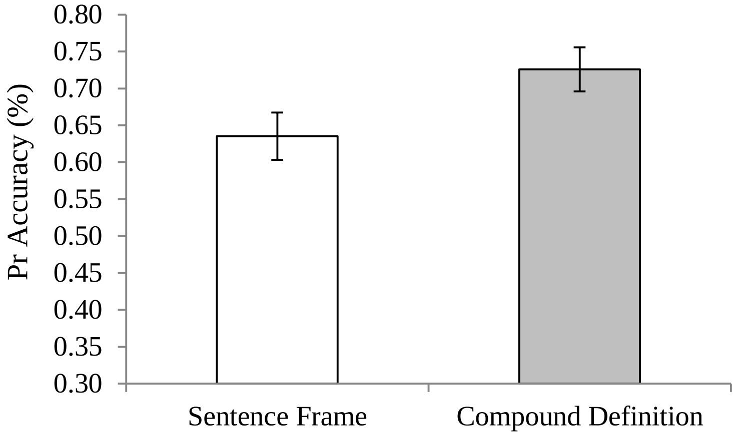

Figure 9.3: Means (and standard error) for discrimination accuracy (Pr) between the Sentence Frame and Compound Definition tasks.

From Figure 9.4, it can be observed that reaction times to correctly identified Intact pairs are quicker following Compound Definitions compared to Sentence Frames. By contrast, reaction times do not appear to differ for correctly identified New pairs. An ANOVA was carried out with factors of Retrieval [Intact/New] and Task [Sentence Frame/Compound Definition] that revealed a main effect of Task [F(1,24) = 7.23, p = .01] and a significant interaction [F(1,24) = 12.80; p < .01]; reflecting the selective reduction in response times for Intact pairs when encoded with Compound Definitions as opposed to Sentence Frames.

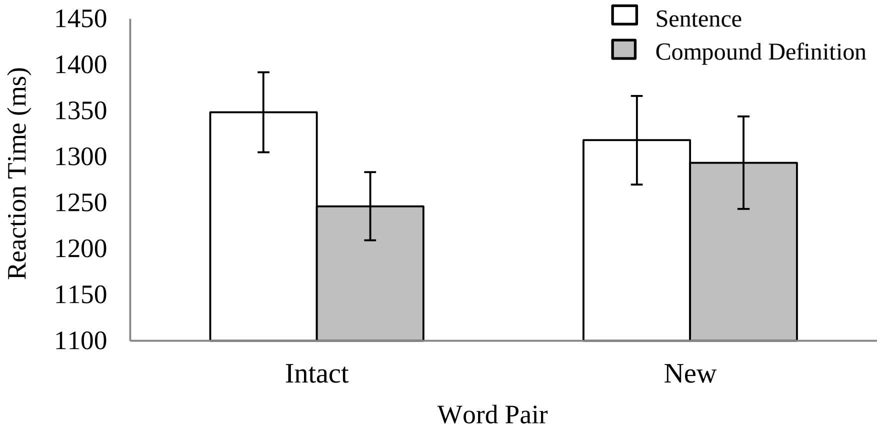

Figure 9.4: Mean reaction times (and standard error) for correctly identified Intact and New word pairs for both Sentence Frame and Compound Definition tasks.

9.3.2. Event Related Potentials

Figure 9.5 illustrates the Grand Average activity for both correctly identified Intact (Hits) and New (Correct Rejections) responses at representative electrodes. For both tasks, activity observed for Hits diverges from Correct Rejections around 360 milliseconds post stimulus on-set, with activity being more positive going for Hits. The distributions of old/new effects are illustrated in Figure 9.6. Within the 300-500ms time window no clear maxima is evident in either task, although old/new activity is broadly distributed over the left hemisphere in the Sentence Frame task and frontally distributed in the Compound Definition task. Within the 500-800ms time window, both tasks show old/new activity that is clearly maximal over parietal electrodes, with a left sided asymmetry. An additional frontal maxima with a bilateral distribution is also evident for the Compound Definition task, but this effect is absent in the Sentence Frame task.

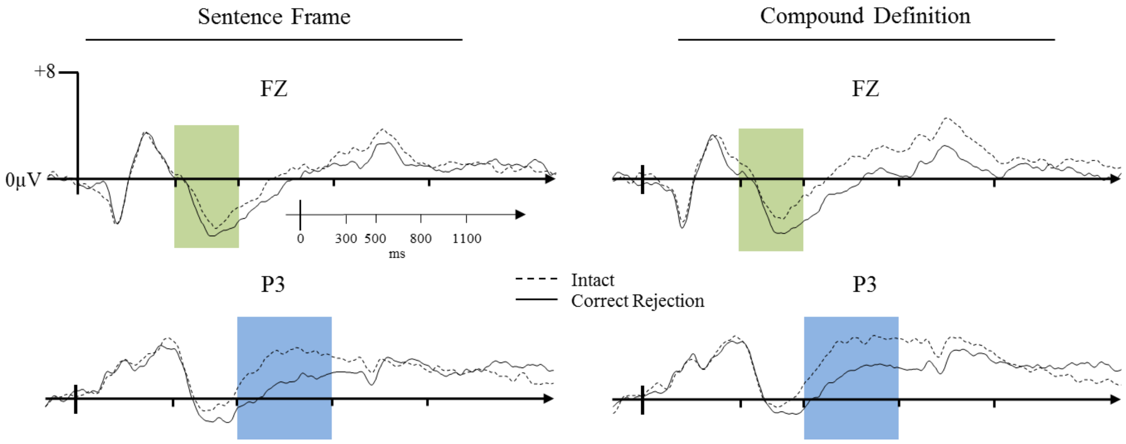

Figure 9.5: Grand average ERPs for Sentence Frame (left) and Compound Definition (right) tasks for correctly identified Intact (illustrated with a dashed line) and New word pairs (illustrated with a solid black line). Waveforms are presented at representive electrodes reflecting the Mid-Frontal old/new effect (FZ) and Left Parietal old/new effect (P3).

9.3.2.1. The Mid-Frontal old/new effect

The initial ANOVA conducted for the Sentence Frame task did not reveal a significant main effect of Retrieval. The results, did however, reveal a significant Retrieval by Hemisphere [F(1,24) = 6.23, p < .05] and Retrieval by Hemisphere by Site [F(1.12,26.29) = 6.09, p < .05] interaction, reflecting a broad distribution of old/new activity with a left sided asymmetry maximal at the medial sites. Crucially, no interaction with Location was found that would specifically define a Mid-Frontal effect.

By contrast, the Compound Definition task revealed a marginal main effect of Retrieval [F(1,24) = 4.07, p = .055] suggesting that activity was more positive going for Hits compared to Correct Rejections over both locations. No interactions were found for the Compound Definition task.

In light of the experimental prediction about an enhanced Mid-Frontal old/new effect, further analyses were conducted at frontal and parietal locations separately for both tasks. Analysis for the Sentence Frame task confirmed that activity was broadly distributed over the left hemisphere, with significant Retrieval by Hemisphere by Site interactions present at both frontal [F(1.21,29.06) = 3.96, p = .05] and parietal [F(1.18,28.77) = 4.32, p < .05] locations. By contrast, further analysis of the Compound Definition task revealed that the main effect of Retrieval was driven by old/new differences at the frontal [F(1,24) = 4.46, p = .05] but not parietal [F = 1.64] location. However, for the Compound Definition task, no interactions with hemisphere and site were observed.

The previous analysis suggests that the distribution of old/new effects within the Sentence Frame task have a left sided asymmetry, broadly distributed across locations, whereas the main effect of Retrieval observed in the Compound Definition task was only reliable over frontal electrodes. To assess whether there were any significant topographical differences between tasks, an ANOVA was carried out on the subtraction data [Hits - Correct Rejections] with factors of Task [Sentence Frame/Compound Definition], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Although no main effect of Task was observed, the results did reveal a significant interaction between Task and Hemisphere [F(1,24) = 6.10, p < .05] and a significant three way interaction between Task, Hemisphere and Site [F(1.39,33.32) = 5.54, p < .05]. The results confirm that old/new activity in the Sentence Frame task exhibited a left greater than right hemisphere asymmetry, whereas the Compound Definition exhibited a right greater than left asymmetry. To confirm whether the topographical differences between tasks were driven by separate neural configurations, the analysis was resubmitted to the ANOVA with rescaled data. The results revealed that the original interactions between Task by Hemisphere [F(1,24) = 6.16, p < .05] and Task, Hemisphere by Site [F(1.22, 29.17) = 5.6, p < .05] survived reanalysis, reflecting a qualitative difference in topography between tasks.

Finally, planned comparison of the magnitude of the Mid-Frontal old/new effect (qualified by the presence of old/new differences in both tasks) was carried out across a cluster of Mid-Frontal electrodes (F1/FZ/F2). Although the magnitude of the Mid-Frontal old/new effect was numerically larger for the Compound Definition task (mean = .96 µV) compared to Sentence Frame task (mean = .57 µV), the difference was not statistically significant.

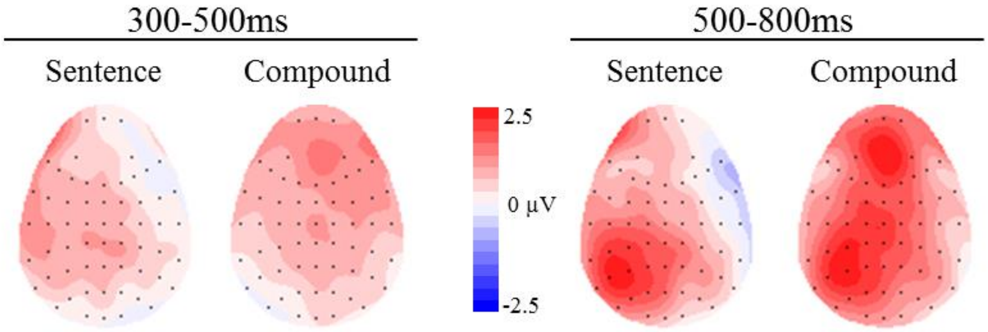

Figure 9.6: Topographic maps illustrating the distribution of old/new effects within the 300-500ms and 500-800ms time windows for both the Sentence Frame and Compound Definition tasks. The scale bar represents the voltage range (µV).

9.3.2.2. The Left Parietal old/new effect

Analysis of the 500-800ms time window revealed main effects of Retrieval for both the Sentence Frame [F(1,24) = 4.44, p < .05] and Compound Definition [F(1,24) = 13.21, p < .001] tasks; confirming that activity was more positive for Intact responses compared to Correct Rejections. The Sentence Frame task also produced a number of significant interactions, including Retrieval by Location [F(1,24) = 4.63, p < .05], Retrieval by Hemisphere [F(1,24) = 18.68, p < .001], Retrieval by Hemisphere by Site [F(1.27,30.52) = 11.93, p < .001] and critically, a four way interaction between Retrieval, Location, Hemisphere by Site [F(1.51,36.19) = 3.62, p = .05]. Taken together the interactions are consistent with the presence of a Left Parietal old/new effect that is maximal at the inferior site over the left hemisphere (see Figure 9.6). The Compound Definition task also produced a number of significant interactions including Retrieval by Site [F(1.12,26.77) = 6.76, p = .01], Retrieval by Location by Site [F(1.24, 29.67) = 4.13, p < .05] and Retrieval by Location by Hemisphere [F(1,24) = 8.16, p < .001], reflecting a superior maxima over the left parietal electrodes compared to a superior maxima with a bilateral distribution over frontal electrodes.

Analysis of within task old/new effects revealed significant Left Parietal effects for both tasks. As with the 300-500ms time window, subsidiary analysis was carried out to assess any potential differences in scalp topography. An initial ANOVA was carried out on the subtraction data [Hits - Correct Rejections] with factors of Task [Sentence Frame/Compound Definition], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. No main effects or interactions were observed confirming that the scalp topographies did not qualitatively differ between tasks.

Finally, planned comparison of the magnitude of the Left-Parietal old/new effect between tasks was carried out by averaging across a cluster of Left Parietal electrodes (P5/P3/P1). The comparison did not, however, reveal any statistically significant difference in the magnitude of the Left-Parietal old/new effect between the Sentence Frame (mean = 2.02 µV) and Compound Definition (mean = 2.00 µV) tasks, suggesting that recollection contributed equally to successful recognition in both tasks.

9.3.2.3. Time window comparison

The above analyses revealed reliable differences in old/new activity between Hits and Correct Rejections in both the 300-500ms and 500-800ms time windows. To demonstrate that the distribution of these effects changed over time for both tasks, additional analyses were conducted on difference waveforms (Intact - Correct Rejection) and submitted to an ANOVA with factors of Time [300-500ms/500-800ms], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. The ANOVA identified a significant Time by Location by Hemisphere by Site interaction for both the Sentence Frame [$F(1.44,34.63) = 7.77$, $p <$

.01] and Compound Definition [F(1.35,32.44) = 7.82, $p < .01$] tasks, reflecting a change from a broad distribution of activity between 300-500ms to a more focused Left Parietal maximum within the 500-800ms time window. Critically, when topographical analyses were conducted on rescaled data, significant Time by Location by Hemisphere by Site interactions for both Sentence Frame [F(1.33,31.87) = 4.56, $p < .05$] and Compound Definition [F(1.31,31.49) = 4.51, $p < .05$] tasks. These results confirm that the observed change in old/new effects reflected topographical rather than mean amplitude differences.

9.3.2.4. Analysis of fine grained time windows

From Figure 9.5, it can be seen that the onset of old/new differences at electrode Fz occurs slightly after 300ms and therefore the typical 300-500ms time window may have been insufficient to capture the Mid-Frontal old/new effect. The difference in old/new activity at Fz also has a much broader time course and appears greater following Compound Definitions in comparison to Sentence Frames. This observation is bolstered by visual inspection of the scalp topographies in Figure 9.6, indicating that the frontal old/new activity is greater in the later 500-800ms time window following Compound Definition encoding compared to the 300-500ms time window. To further investigate the time course of this observed Mid-Frontal old/new activity, analysis was performed on several 100ms time windows covering the period from 0 to 800msec post-stimulus onset for both the Sentence Frame and Compound Definition tasks. As this follow up analysis was primarily focused on the time course of the Mid-Frontal effect, analyses were restricted to the fronto-central electrodes (F1/FZ/F2) where the effect has been shown to be maximal (see Curran, 2000).

An initial Time [0-100ms/100-200ms/300-400ms/400-500ms/500-600ms/600-700ms/700-800ms] by Retrieval [Intact/Correct Rejection] by Site [Left/Centre/Right] ANOVA was conducted for both the Sentence Frame and Compound Definition tasks. The analysis of the Sentence Frame task failed to detect both an overall difference between Intact and Correct Rejection responses as well as any change across time, suggesting that no specific Mid-Frontal activity was present. By contrast, analysis of the Compound Definition task revealed a significant main effect of Retrieval [F(1,24) = 7.53 p = .01] and a significant Time by Retrieval interaction [F(3.95,94.87) = 4.93, p = .001]; suggesting that overall Intact pairs elicited more positive activity than Correct Rejections and that this old/new effect varied over time (see Figure 9.7). Follow up analysis (corrected α = .01) of the Compound Definition task revealed significant old/new differences occurred between 400-500ms [F(1,24) = 7.04, p = .01] post stimulus onset, and were significant throughout the 500-600ms (F(1,24) = 8.74, p < .001], 600-700ms [F(1,24) = 10.30, p < .001] and 700-800ms [F(1,24) = 9.73, p = .01] time windows.

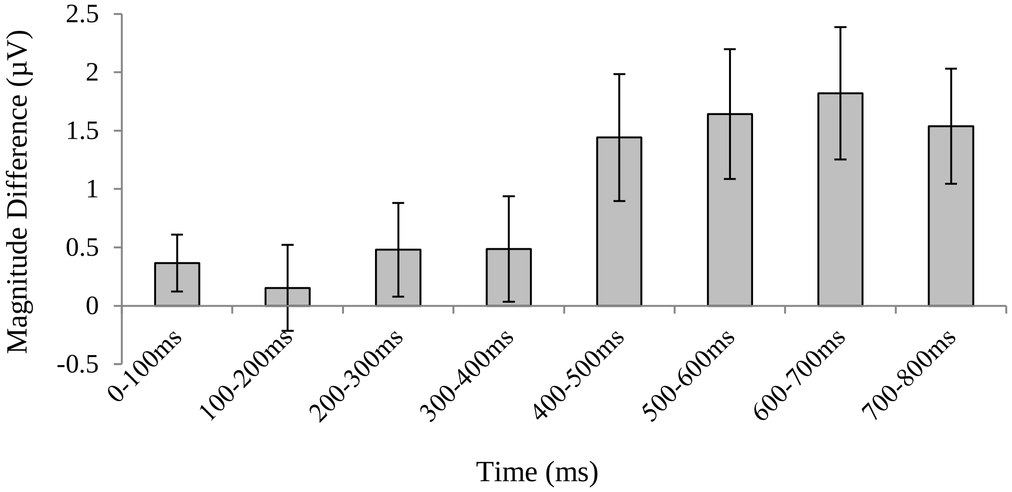

Figure 9.7: Mean (and standard error) of Mid-Frontal old/new effects over 8 consecutive time windows for the Compound Definition task. Mid-Frontal activity is not represented for the Sentence Frame task given the absence of any observable main effects or interactions.

9.4. Discussion

The present study aimed to further examine circumstances that allow familiarity to contribute to successful associative recognition. The experiment was motivated by Bader et al., (2010) who observed atypical ERP effects whilst attempting to manipulate unitization using Sentence Frames and Compound Definitions. In Chapter 8 we effectively ruled out relationship type between words as a possible explanation for their alternative ERP effects. The current study therefore employed the Sentence Frame and Compound Definition manipulation employed by Bader et al., (2010) with an incidental within-participant design similar to Rhodes and Donaldson (2008) wherein the standard old/new effects of familiarity and recollection have been observed. Consistent with the findings of Chapter 8, we predicted that unrelated word pairs encoded with Compound

Definitions compared to Sentence Frames would improve associative recognition and enhance familiarity as indexed by an increase in the early Mid-Frontal old/new effect.

At a behavioural level of analysis, the data is broadly consistent with the findings from Chapter 8 – i.e., Compound Definitions aimed at encouraging unitization resulted in improved memory performance compared to Sentence Frames. The ERP results, however, were less clear. As predicted a significant Left Parietal old/new effect was present for both tasks and did not differ in magnitude. By contrast, the presence of Mid-Frontal old/new activity in the 300-500ms time window was less clearly defined compared to the later Left Parietal old/new effect. Although old/new activity was significant at frontal electrodes in the Compound Definition task, no distinct frontal activity was observed for the Sentence Frame task – which exhibited a left sided asymmetry uniformly distributed across frontal and parietal locations. Planned comparison of the magnitude of the Mid-Frontal old/new effect, however, did not reach significance. In addition, a selective Mid-Frontal old/new effect was present for the Compound Definition task along with a significant Left Parietal old/new effect in the later 500-800ms time window. In essence, the results of this study indicate that although the neural correlate of familiarity is present for the Compound Definition task, the effect is relatively weak and not adequately captured within the traditional 300-500ms time window. Below, the results are examined in more detail, focusing on the behavioural data and ERP data in turn.

9.4.1. Behavioural overview

The behavioural results are broadly consistent with the prediction that unitization should improve overall memory performance (Rhodes and Donaldson, 2007, 2008; Diana et al., 2008; Giovanello et al., 2006; Jager et al., 2006). Discrimination accuracy was found to be significantly greater for word pairs encoded with Compound Definitions compared to Sentence Frames. In addition, response times were also significantly reduced for correctly identified ‘Intact’ pairs encoded with Compound Definitions as opposed to Sentence Frames, while response times to ‘New’ pairs did not differ. Overall, the behavioural data are consistent with the results presented in Chapter 8, demonstrating that encoding instructions specifically designed to manipulate unitization modulate associative recognition performance at a behavioural level.

Although unitization provides a possible explanation of the current data, it is important to note that other explanations also exist. For example, an overall difference in memory performance between tasks that differ only in encoding instructions could also be adequately explained by a levels-of-processing account (Craik & Lockhart, 1972). According to the levels-of-processing theory, items that are encoded with greater meaning (i.e., deep encoding) result in improved memory performance compared to items that are encoded from a surface level (i.e. shallow encoding). The current behavioural data could reflect, for example, different levels of encoding, whereby Compound Definitions result in deeper encoding than Sentence Frames. Within the context of the wider unitization literature, however, the levels-of-processing account is unlikely. For example, deep encoding manipulations have consistently demonstrated a larger increase in recollection, whereas shallow encoding results in an increased reliance on familiarity (Gardiner, 1988; Gardiner, Ramponi & Richardson-Klavehn, 1996; Yonelinas et al., 1998; Rugg et al., 1998: see Yonelinas, 2002,'; for a review); a result inconsistent with the selective impact upon familiarity demonstrated by manipulations of unitization.

9.4.2. Overview of the Left Parietal old/new effect

In line with the previous chapter, the current experiment used ERPs to index memory retrieval, and therefore relies on the interpretation of ERP old/new effects as neural correlates of recollection and familiarity. Consistent with Chapter 8, each ERP effect is discussed in turn, beginning with the neural correlate of recollection – i.e., the Left Parietal old/new effect. As predicted, the Left Parietal old/new effect was present in both the Compound Definition and Sentence Frame tasks, suggesting that recollection contributed to episodic retrieval in both tasks (i.e. consistent with the dual process account of associative recognition). Importantly, the magnitude of the Left Parietal old/new effect did not differ between the Sentence Frame and Compound Definition tasks, implying that the overall behavioural benefit following Compound Definition encoding is unlikely to be attributed to an increase in recollection. Within the context of the ERP literature, the equivalent Left Parietal old/new effects observed in the current experiment that employed mediating sentences is broadly consistent with alternative manipulations of unitization, such as mental imagery (see Rhodes & Donaldson, 2008; Pilgrim et al., 2012; Chapter 8).

9.4.3. Overview of the Mid-Frontal old/new effect

Of primary interest in the current experiment was the Mid-Frontal old/new effect associated with familiarity. Although a planned comparison of the magnitude of Mid-Frontal old/new effects in the 300-500ms time window between tasks did not reach significance, there are two aspects of the data that imply familiarity contributed to retrieval within the Compound Definition task but not the Sentence Frame task. First, a significant frontal old/new effect was only observed in the early 300-500ms time window for the Compound Definition task. Interpreting the effect as Mid-Frontal, however, is difficult considering that no interaction with site was observed – although the lack of any hemispherical difference suggests that the effect was evenly distributed across frontal electrodes. The frontal old/new effect observed for the Compound Definition task was also topographically distinct from the left sided old/new distribution observed within the Sentence Frame task – an effect that is difficult to interpret given the uniform distribution across frontal and parietal locations. In short, a frontal, albeit weak, old/new effect was observed for the Compound Definition task which was topographically distinct from the old/new effect observed in the Sentence Frame task.

Secondly, the fine grained analysis of the 100ms time windows revealed that the time course of the familiarity signal was detected slightly later than is traditionally assumed – i.e., only becoming significant from 400ms. In addition, the observed Mid-Frontal old/new activity was only present between 400-800ms following Compound Definitions, an effect that was not found for the Sentence Frame task. The later occurring Mid-Frontal effect, however, is difficult to interpret with a familiarity account given that the effect occurred within the time window normally associated with recollection. The pattern of data, however, is consistent with later occurring Mid-Frontal old/new activity observed by Rhodes and Donaldson (2008), who interpreted the effect as reflecting the sustained impact of familiarity observed in the earlier 300-500ms time window. Although the data in the current experiment is less likely to reflect the sustained impact of an early occurring Mid-Frontal effect (given the relatively weak signal), analysis of the fine-grained windows does imply that familiarity was simply detected slightly later than is traditionally assumed. Overall, the data from the current experiment suggests that familiarity contributed to successful retrieval when encoding instructions encouraged unitization with Compound Definitions, but the neural correlate of familiarity was not sufficiently strong enough to be detected when encoding word pairs with Sentence Frames.

In the current study, the original comparison of the magnitude of the Mid-Frontal old/new effect did not reach significance. Post-hoc analysis of 100ms time windows revealed a possible explanation as to why no magnitude differences were found – namely, the slightly later time course of the Mid-Frontal old/new effect observed in the Compound Definition task. It is currently unclear why there is a discrepancy in the time courses of the Mid-Frontal old/new effect observed between Compound Definitions and Interactive mental imagery (i.e. the Mid-Frontal old/new effect observed in Chapter 8). One possible explanation may be the distinct design differences inherent to both manipulations. For instance, familiarity has been found to be sensitive to the perceptual match between study and test blocks. According to some global matching accounts (see Clark & Gronlund, 1996, for a review), familiarity reflects processing that detects overall similarity between test cues and studied information – an account of familiarity supported by the finding that the Mid-Frontal old/new effect is sensitive to perceptual similarity between study and test phases (Nyhus & Curran, 2009).

In the current experiment, word pairs and mediating sentences are provided at study, whereas only word pairs are presented at test (see Figure 9.2). Arguably, unitization achieved through mediating sentences should not be affected by this perceptual difference, since what is important is the retrieval of a unitized stimulus rather than the way that the stimuli are presented. If familiarity is affected by perceptual mismatch, however, then it is possible that the perceptual difference between study and test phases could slightly delay the onset of the Mid-Frontal old/new effect – given that the familiarity signal may be too weak to be detected any earlier. The global matching account may explain why the Mid-Frontal old/new effect was clearly observed within the 300-500ms time window during mental imagery (i.e., when study and test phases were perceptually identical: see Chapter 8) but was less clear in the current experiment that employed mediating sentences.

It is also possible that the mediating sentence manipulation and mental imagery manipulation achieve varying levels of unitization. Yonelinas et al., (2010) have argued that unitization is not a dichotomous variable, but rather a continuous process allowing for stimuli to become unitized to a greater or lesser degree. By this argument, the differing time windows between unitization methods may be dependent on how well (i.e., to what degree) separate stimuli have become unitized. According to this account, a more successfully unitized representation will result in a greater contribution of familiarity during retrieval compared to word pairs encoded with alternative instructions, which may allow the underlying neural mechanism to differentiate old from new items more quickly. Making inferences based on latency should, however, be treated with caution. The underlying neural processes related to familiarity, for example, may differentiate between old and new items well before the Mid-Frontal old/new effect becomes significant. In addition, differences in the engagement of familiarity often manifest as amplitude differences (Rugg & Curran, 2007) rather than onset latencies – as is the case when comparing the retrieval of unitized and non-unitized stimuli (Rhodes & Donaldson, 2008; Pilgrim et al., 2012). Regardless of when familiarity is first able to differentiate between old and new items, the point at which the old/new effect becomes significant within the Compound Definition task at least implies that familiarity operates differently compared to alternative unitization tasks that result in the typical early on-setting Mid-Frontal old/new effect (as per Interactive Mental Imagery observed in Chapter 8). In essence, although Compound Definitions and Interactive Mental Imagery instructions both encourage unitization, it remains possible that one set of instructions may be more successful than the other at encouraging unitization. Whether one task is more likely to lead to a greater proportion of trials in which unitization was successful or whether unitization was encouraged to a greater extent, remains unclear.

Notwithstanding the discussion above, it is important to acknowledge that this explanation is impossible to verify without directly comparing both encoding instructions within a single group of participants. To date, it remains unclear whether different encoding manipulations of unitization, or different stimulus properties result in varying levels of unitization. A clear demonstration that one set of encoding instructions results in greater levels of unitization than another would have important implications for the development of unitization techniques as an aid for those with selective recollection deficits (see the General Discussion for a more detailed discussion of the practical implications of the current data).

9.4.4. Comparison with other studies

A secondary aim of the current experiment was to investigate the apparent inconsistency among ERP studies of unitization – namely that different ERP effects are observed under alternative unitization manipulations. In Chapter 8 we ruled out stimulus relationship (i.e., novel word pairs) as a likely explanation as to why Rhodes and Donaldson (2008) found a Mid-Frontal old/new effect during retrieval but Bader et al., (2010) observed an early Central Parietal old/new effect. In the current experiment, we go further by demonstrating that novel word pairs Compound Definitions and Sentence Frames elicited similar, although not identical, ERP effects to those observed under mental imagery instructions. The data therefore demonstrates a consistency in ERP effects across unitization studies employing novel word pairs and different encoding strategies. The data from the current experiment, however, are difficult to reconcile with a dual familiarity account proposed by Bader et al., (2010) – described in more detail in Chapter 8. If a dual familiarity account is correct, then it is unclear why under identical encoding instructions, absolute familiarity contributed to retrieval of novel associations in the Bader et al., (2010) study but relative familiarity contributed to retrieval of novel associations in the current study.

Here, we call into question the argument for a dual familiarity signal given that the only evidence that Bader et al., (2010) cite in favour for their familiarity account was a facial recognition study conducted by MacKenzie and Donaldson (2008) and thus may not be directly comparable to recognition of words. To be clear, familiarity for faces may exhibit an early parietal distribution whereas familiarity for words exhibits a frontal distribution. Instead, our data supports the conclusions of Rhodes and Donaldson, (2008) by demonstrating that unitization, regardless of how it is achieved, modulates the same underlying neural correlate of familiarity. Given the slightly later time course of the Mid-Frontal old/new effect observed for Compound Definitions in the current study, we would add that although the same neural mechanisms are engaged, it may be the case that the degree of that engagement may depend on how successfully two items become unitized.

Thus far we have effectively ruled out the use of novel associations and alternative encoding strategies as explanations for the atypical ERP effects observed by Bader et al., (2010). There are, however, still several remaining caveats of the Bader et al., (2010) study that makes interpretation of their findings difficult. For example, Bader and colleagues compared ERPs across two separate groups of participants who were presented with either the Compound Definition or Sentence Frame task. Although this experimental procedure prevents cross-contamination of experimental instructions (i.e., preventing participants from adopting one strategy over another), one cannot be certain whether the ERP differences between tasks reflect genuine retrieval effects or simply overall differences between the two populations. Furthermore, Bader et al., (2010) failed to report discrimination accuracy or response bias and therefore it is unclear whether the observed ERP differences between tasks reflected genuine episodic retrieval effects or simply different response strategies adopted by these two separate groups of participants.

9.4.5. Summary

The current experiment was conducted to assess whether conditions that manipulate unitization, other than mental imagery, were sufficient to encourage familiarity during associative retrieval. To this end, mediating sentences were employed that have previously been demonstrated to elicit unexpected ERP effects not typically associated with familiarity or recollection. In the current experiment, however, a sustained Mid-Frontal old/new effect was exhibited in the Compound Definition task but not the Sentence Frame task, albeit with a slightly later onset compared to the Mid-Frontal old/new effect observed in Chapter 8. The results provide some consistency among ERP studies of unitization by demonstrating that similar ERP effects related to familiarity and recollection are exhibited when employing different manipulations of unitization.

Chapter 10

Investigating unitization of related and unrelated word pairs

The overall goal of unitization research is to understand the optimum conditions that encourage familiarity for successful associative retrieval. From a practical perspective, understanding the necessary conditions that best facilitate unitization has important implications for those individuals with recollection deficits. One important question that arises from the literature, for instance, is whether unitization is best suited to encouraging familiarity for pre-existing relationships, or for creating novel representations from previously unrelated information. Previous studies have investigated unitization for either related or unrelated stimuli, however, no existing study has directly compared the effects of unitization between related and unrelated stimuli in the same experiment. Demonstrating that unitization has greater benefits (i.e., greater contribution of familiarity) when information is related compared to unrelated would allow us to better characterise unitization at a theoretical level, but also inform future development of unitization as a mnemonic technique to aid those with memory deficits. Therefore, the aim of the current study is to compare the benefits of unitization for related and unrelated word pairs.

10.1. Introduction

So far the current thesis has established that at a neural level of analysis, unitization enhances the neural correlate of familiarity for completely novel information (see Chapter 8) and influences the same correlate under different encoding instructions (see Chapter 9). One particularly interesting question that arises from these previous results is whether unitization is best suited to encouraging familiarity for completely novel associations, or whether unitization has a greater benefit for pre-existing associations. Unitization research has typically focused on manipulating unitization for related or unrelated information, but no study has ever compared the benefits of unitization for established and novel associations within the same experiment. Importantly, previous ERP studies of unitization suggest that unitization is modulated by word pairs sharing different types of pre-existing relationship, but it is currently unclear whether unitization has a larger impact on memory for conceptually related or completely novel word pairs. The aim of the current experiment is to therefore compare the benefits of unitization for related and unrelated pairs by employing the mental imagery manipulation of unitization (previously demonstrated to influence the Mid-Frontal old/new effect within the standard 300-500ms time window). First, however, we briefly review the previous unitization studies that suggest familiarity at retrieval is influenced by the relationship between word pairs.

In two separate studies, Rhodes and Donaldson demonstrated that the type of pre-existing relationship between word pairs influences the engagement of familiarity during associative recognition. For instance, Rhodes and Donaldson (2007) demonstrated that only word pairs sharing an associative relationship (compared to a semantic or combination of associative and semantic relationship) are encoded in a unitized fashion, giving rise to significant Mid-Frontal old/new effects during associative retrieval. The results were expanded in a later study in which Rhodes and Donaldson (2008) demonstrated that retrieval of associative pairs was not sensitive to instructions that encouraged or discouraged unitization. Semantic pairs, by contrast, exhibited improved behavioural performance and enhanced familiarity (indexed by the

Mid-Frontal old/new effect) when encoding instructions encouraged unitization. The results from Rhodes and Donaldson (2008) study therefore suggest that the benefits of encoding information with Interactive compared to Item imagery are larger when word pairs share a semantic rather than associative relationship. The results, however, say nothing about the effects of unitization between pre-existing and completely novel information. To this end, the current experiment directly compares associative recognition of related and unrelated word pairs by manipulating unitization using the mental imagery method.

Here, we manipulate unitization of conceptually related (i.e., word pairs sharing both an associative and semantic relationship[21]) and completely unrelated word pairs. Some Dual Process models predict that associative recognition can be supported by familiarity for word pairs sharing pre-existing relationships (for example, through activation of lexical nodes – see Atkinson & Juola, 1973, 1974) regardless of unitization instructions. We therefore predict that although a benefit of unitization will be observed for related word pairs, the advantage of Interactive compared to Item imagery will be smaller compared to that observed for completely unrelated pairs. To be clear, we still expect to observe a difference between encoding tasks for associative and semantically related pairs because each word in the pair is perceived as a separate representation (as opposed to a single item: see Rhodes & Donaldson, 2007). On the basis of this view, we predict that familiarity will be enhanced following Interactive imagery instructions for both relationship types, however, the benefits of unitization

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[21] Word pairs sharing both an associative and semantic relationship are conceptually related and have been found to exhibit conceptual priming effects at a behavioural level of analysis (i.e., Moss et al., 1995; Shelton & Martin, 1992). During standard associative recognition tasks, however, retrieval of associative and semantically related pairs is not believed to be supported by familiarity – as indexed by the Mid-Frontal old/new effect (i.e., Rhodes and Donaldson, 2007).

will be significantly larger for unrelated compared to related pairs. Behaviourally, a comparable pattern of results is expected for discrimination accuracy and response times (i.e., although increased accuracy and response times to Intact pairs will be present for related and unrelated word pairs, the difference in accuracy between encoding tasks will be larger for unrelated pairs). In terms of ERPs, the magnitude of the Mid-Frontal old/new effect is expected to be enhanced following Interactive compared to Item imagery for both related and unrelated pairs, although the difference in the size of the Mid-Frontal old/new effect between tasks will be largest for unrelated pairs. As with previous chapters, we do not predict that recollection will be influenced by unitization encoding instructions.

10.2. Method

10.2.1. Participants

Thirty three participants from the University of Stirling took part in the study. Data from three participants was rejected due to an insufficient number of ERP trials in at least one experimental condition and a further four were excluded due to poor behavioural performance. The remaining 26 participants (12 female) had a mean age of 22 (range: 18-29).

10.2.2. Stimuli

The stimulus properties are identical to those described in Chapter 5. To briefly reiterate, 720 word pairs were used in the current experiment; 360 Unrelated pairs randomly selected from the stimulus set used in Chapter 8, and 360 Related pairs that shared both an associative and semantic relationship. Word pairs were divided into two lists (List 1 and List 2), each comprising 180 Related and 180 Unrelated pairs. In addition to matching the stimuli across lists (described in more detail in Chapter 5), stimuli were also matched between relationship type for word length [Related mean = 5 (s.d. = 1); Unrelated mean = 5 (s.d. = 1)], word frequency [Related mean = 69 (s.d. = 52); Unrelated mean = 60 (s.d. = 49)] and imagability [Related mean = 514 (s.d. = 58); Unrelated mean = 520 (s.d. = 31)].

Both stimulus lists were divided into 10 study/test blocks and assigned to either the Interactive or Item imagery task – counterbalanced across participants. Identical to Chapters 8 and 9, the current experiment followed a blocked design, with the order of Interactive and Item imagery tasks being counterbalanced across participants – i.e., half the participants would be presented with Interactive imagery task first[22]. Across participants, the presentation order of individual study/test blocks and stimuli presented within blocks was randomised.

Each study block consisted of 24 word pairs: 12 ‘Intact’ word pairs (i.e., to be presented in the same pairing at test) and 12 ‘Recombined’ word pairs (i.e., to be presented in a different pairing at test). Each of the 12 word pairs comprised of 6 Related pairs and 6 Unrelated pairs. A single Test block consisted of 36 word pairs: 12 ‘Intact’, 12

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[22] A series of independent t-tests were carried out to assess potential task order effects. Analysis was carried out on discrimination accuracy from two groups of participants – i.e., those who were presented with either the Item or Interactive imagery task first. Comparison of the Item task between groups, and Interactive task between groups, did not reveal any significant difference for either Related or Unrelated pairs, confirming that task order did not significantly influence the overall pattern of behavioural results.

‘Recombined’ (each word repeated from study but in new pairings) and 12 ‘New’ pairs (not previously presented during study). In contrast to Chapters 8 and 9, the restricted number of stimuli meant that all Recombined words were presented at test, however, care was taken not to intermix between Relationship – i.e., a word from a Related Recombined pair was never paired with a Unrelated Recombined partner at test. Across participants, stimuli were presented equally often as either an ‘Intact,’ ‘Recombined,’ or ‘New’ pair.

The use of conceptually related word pairs in the current experiment meant the inclusion of a small proportion of pre-experimental compound words (i.e., word pairs sharing a single definition such as ‘Blackbird’). To check for compound pairs, the definition of each word pair used in the current experiment was checked using the Collins English Dictionary online (www.collinsdictionary.com/dictionary/English/). Importantly, no compound words were found for Unrelated pairs. By comparison, investigation of Related pairs revealed a small proportion of compound words in List 1 (22%) and List 2 (26%).

10.2.3. Procedure

The general experimental procedure corresponds to the one described in Chapter 5 (see Section 5.3.2). Prior to each experimental task, participants were required to complete a short practice session, comprised of 8 word pairs at study (i.e., 2 Related Intact, 2 Unrelated Intact, 2 Related Recombined and 2 Unrelated Recombined), and 12 word pairs at test (i.e., 2 Related Intact, 2 Unrelated Intact and 2 Related Recombined and 2 Unrelated Recombined, along with 2 Related New and 2 Unrelated New). Both verbal and written instructions were given to participants prior to the practice block. Immediately after the practice, participants were asked to verbally confirm that they had understood both the study and test instructions and to give examples of the mental images they had created. Participants were given the opportunity to repeat the practice if they were unsure about the task demands, or the experimenter believed the participants were not using the mental imagery instructions appropriately. The timings of the current experiment are identical to Chapter 8, albeit with the exclusion of the Remember/Know/Guess decision.

The general ERP recording procedure is identical to the one described in Chapter 5 (see Section 5.4.2). To briefly reiterate, ERPs were analysed by examining mean amplitudes (relative to the pre-stimulus baseline) during *a priori* defined time windows, aimed at capturing the neural correlate of familiarity (i.e., 300-500ms) and recollection (i.e., 500-800ms). The initial analysis was conducted to investigate whether the pattern of Mid-Frontal and Left Parietal old/new effects observed in the current study was similar to those found by Rhodes and Donaldson (2008). To this end, the pattern of old/new effects were characterised for each experimental condition (i.e., Related Item, Related Interactive, Unrelated Item and Unrelated Interactive). Analysis was carried out on fronto-central and parietal strings (see Figure 10.1, left panel) using a repeated measures ANOVA with factors of Retrieval [Hit/Correct Rejection], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Only interactions with Retrieval are reported. Once old/new effects had been defined within conditions, further subsidiary analyses were performed including topographic analyses and a comparison of the mean magnitude of Mid-Frontal and Left Parietal old/new effects between experimental conditions (analysed by averaging across a cluster of

Mid-Frontal and Left Parietal electrodes: see Figure 10.1, right panel). The mean number of trials contributing to the grand average ERPs was: Related Item [Hit (48), Correct Rejection (52)], Related Interactive [Hit (47), Correct Rejection (49)], Unrelated Item [Hit (36), Correct Rejection (51)] and Unrelated Interactive [Hit (43), Correct Rejection (50)].

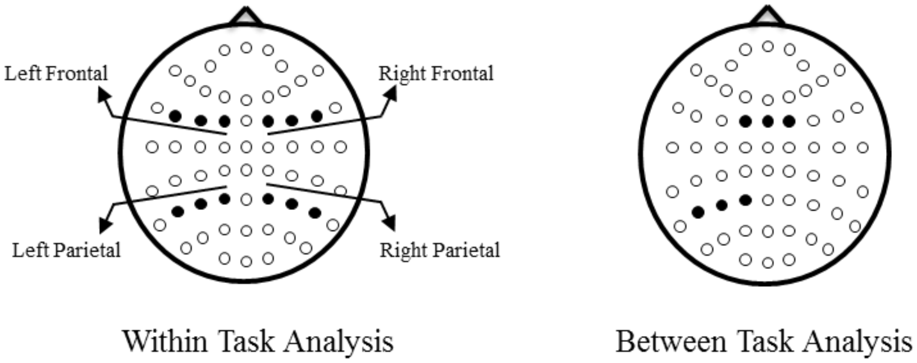

Figure 10.1: Schematic illustration of electrodes used in the ERP analysis: the within task analysis is shown on the left side, and between task analysis is shown on the right.

10.3. Results

10.3.1. Behavioural data

For Related pairs the mean Hit rate for the Item task was 81% (s.d. = 15%) and Interactive task was 84% (s.d. = 12%). For Unrelated pairs, the mean Hit rate for the Item task was 61% (s.d. = 14%) and Interactive task was 74% (s.d. = 15%). Consistent with previous chapters, False Alarms (1 - Correct Rejections) were divided among Intact and Recombined responses and therefore discrimination accuracy reflects False Alarms to Intact pairs only. The False Alarm rate was relatively small for all experimental conditions (<3%), reflecting the three-way decision task whereby the majority of False Alarms are made to Recombined pairs. From Figure 10.2 it can be observed that accuracy was greater for Related pairs compared to Unrelated pairs. Importantly, discrimination accuracy is greater following Interactive compared to Item imagery for Unrelated pairs, whereas no observable difference can be seen for Related pairs. Discrimination accuracy was analysed with a repeated measures ANVOA with factors of Relationship [Related/Unrelated] and Task [Item/Interactive]. The results revealed a significant main effect of Relationship [F(1,25) = 115.13, p < .001], a significant main effect of Task [F(1,25) = 9.10, p < .01], and a significant interaction [F(1,25) = 23.23, p < .001], reflecting the selective increase in discrimination accuracy following Interactive compared to Item imagery tasks for Unrelated pairs, but not for Related pairs.

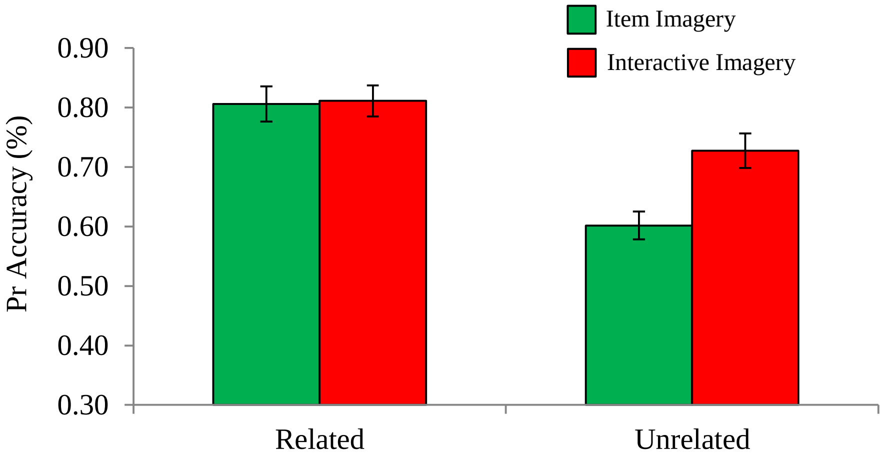

Figure 10.2: Means (and standard error) of Discrimination Accuracy (Pr) for Related and Unrelated pairs across Item and Interactive tasks, illustrating the selective benefit to Unrelated word pairs.

As can be seen in Figure 10.3, response times to Hits appear quicker for Related compared to Unrelated pairs. Furthermore, response times to Hits are quicker following Interactive compared to Item imagery for both Relationship types. Response times to Correct Rejections, by contrast, are very similar across Relationship type and Task. Analysis of Response times was performed using a repeated measures ANOVA, with factors of Relationship [Related/Unrelated], Task [Item imagery/Interactive imagery] and Retrieval [Hit/Correct Rejection]. The results revealed a significant main effect of Task [F(1,25) = 63.22, p < .001], a main effect of Retrieval [F(1,25) = 10.75, p < .01], a significant interaction between Relationship and Retrieval [F(1,25) = 39.08, p < .001], and a significant interaction between Task and Retrieval [F(1,25) = 39.08, p < .001]. The interactions reveal that response times to Hits were slower following Item imagery compared to Interactive imagery, and slower for Unrelated pairs compared to Related pairs, whereas no differences in response times were observed for Correct Rejections. Critically, further analysis revealed that the difference in response times to Intact pairs between tasks was greater for Unrelated compared to Related pairs [t(25) = 2.16, p < .05].

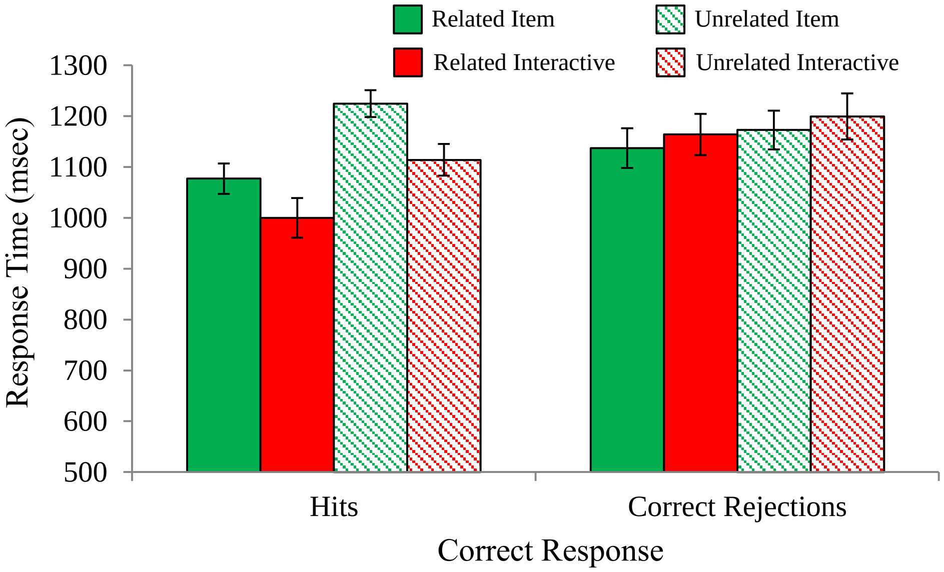

Figure 10.3: Mean reaction times (and standard error) for correctly identified Intact (Hits) and New (Correct Rejection) word pairs for Related and Unrelated pairs across Item and Interactive tasks.

10.3.2. Event Related Potentials

The Grand Average ERPs for Hits and Correct Rejections across the Related Item, Related Interactive, Unrelated Item, Unrelated Interactive conditions are shown in Figure 10.4 at representative electrodes FCZ and P3. Overall, ERPs evoked by Hits appear to be more positive going than Correct Rejections, diverging from one another around 250ms post stimulus onset. For all experimental conditions, the old/new differences at both FCZ and P3 are sustained until around 1100ms. For Related pairs, the magnitude difference between Hits and Correct Rejections across frontal and parietal electrodes appears very similar for Item and Interactive tasks. By comparison, for Unrelated pairs, there is a smaller difference between Hits and Correct Rejections following Item imagery, compared to Interactive imagery, at both frontal and parietal electrode sites.

The distribution of old/new effects (i.e., Hits - Correct Rejections) for all experimental conditions is shown in Figure 10.5. For the Related Item, Related Interactive and Unrelated Item imagery conditions, the topography of old/new effects during the 300-500ms time window exhibits a frontal maximum that is bilaterally distributed. For the Unrelated Interactive condition, the distribution is less focused over frontal electrodes and appears to extend over central and parietal locations. Within the 500-800ms time window, the Related Item, Related Interactive and Unrelated Interactive conditions exhibit a broad maximum over frontal, central and parietal electrodes. Critically, the topography of effects over parietal electrodes appears to be lateralised over the left hemisphere, which is consistent with a Left Parietal effect. By comparison, the Unrelated Item condition exhibits a reduced old/new effect, with a distribution that is maximal over frontal electrodes, with a left greater than right hemisphere asymmetry over parietal electrodes.

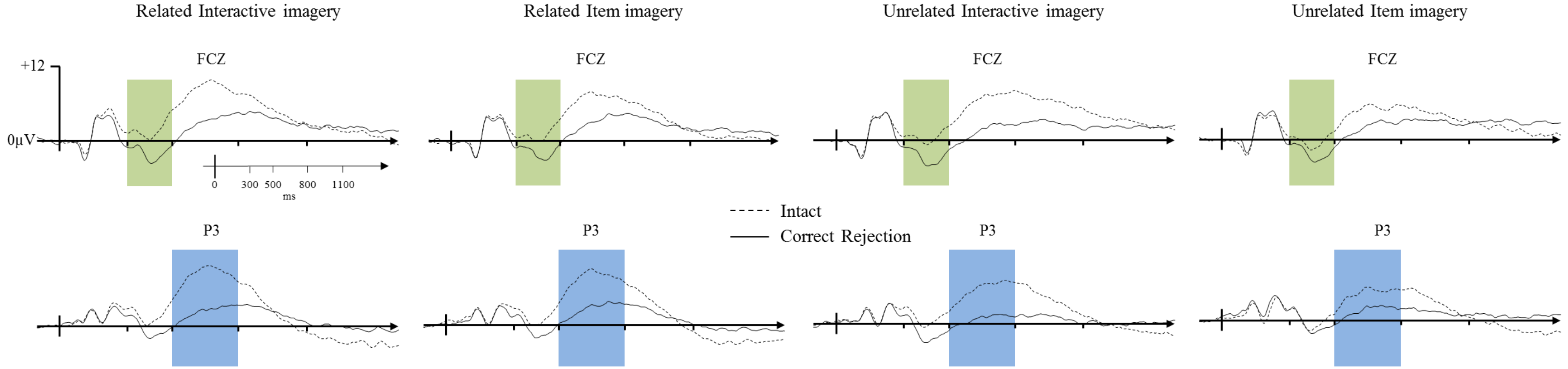

Figure 10.4: Grand averages for Hits (dotted) and Correct Rejections (solid black line). Presented at the top is the Grand Average for each experimental task at representative electrode FCZ. Presented at the bottom is the Grand Average for each experimental task at representative electrode P3. The 300-500ms time window is highlighted in green and the 500-800ms time window is highlighted in blue. Overall, the data clearly shows that the magnitude of old/new differences was greater for Related compared Unrelated word pairs. In addition, the old/new difference was larger for Interactive compared to Item tasks for Unrelated pairs, but the old/new difference was similar across tasks for Related pairs.

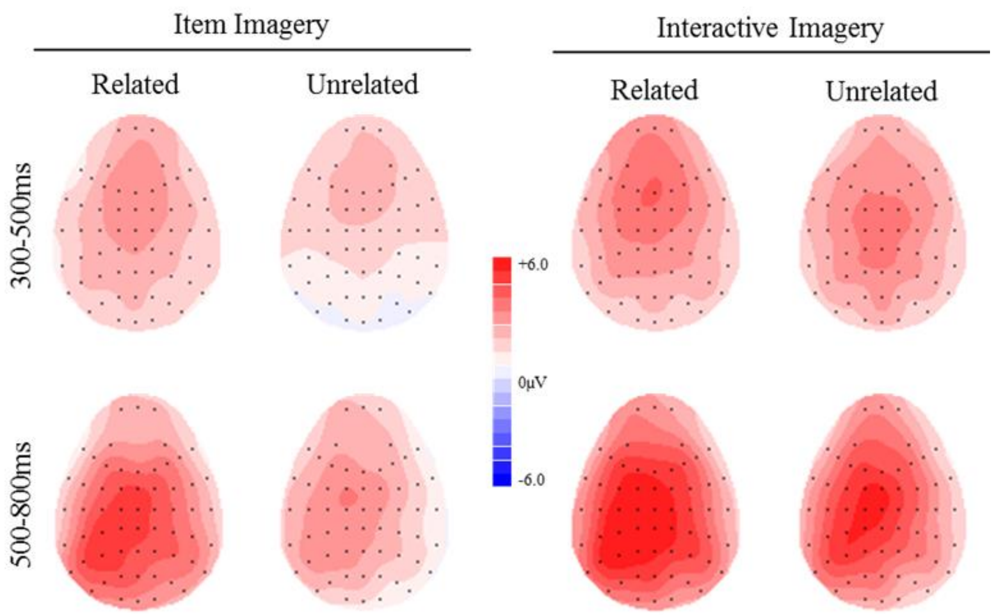

Figure 10.5: Topographic maps illustrating the distribution of old/new effects within the 300-500ms and 500-800ms time windows. The Item imagery task is shown on the left, with old/new effects for Related and Unrelated pairs presented on the left and right. The Interactive imagery task is shown on the right, which is divided between Related and Unrelated pairs on the left and right. The scale bar reflects the voltage range (μV).

10.3.2.1. The Mid-Frontal old/new effect

Analysis of the 300-500ms time window revealed significant main effects of Retrieval for the Related Item [F(1,25) = 32.22, p < .001], Related Interactive [F(1,25) = 33.01, p < .001], Unrelated Item [F(1,25) = 4.10, p = .05] and Unrelated Interactive [F(1,25) = 55.32, p < .001] imagery conditions, reflecting the more positive-going activity evoked by Hits compared to Correct Rejections. To investigate whether significant Mid-Frontal old/new effects were present, separate repeated ANOVAs were carried out within each condition and are reported below.

Analysis of the Related Item imagery condition revealed a series of significant interactions including Retrieval by Site [F(1,25) = 20.87, p < .001], Retrieval by

Location by Hemisphere [F(1,25) = 6.60, p < .05], Retrieval by Location by Site [F(1.06,26.59) = 8.00, p = .01], and a significant four-way interaction: Retrieval by Location by Hemisphere by Site [F(1.69, 42.16) = 6.78, p < .001]. The four way interaction reflects old/new effects that are maximal at the superior electrodes at the frontal location and extend over the left hemisphere at the parietal location.

Analysis of the Related Interactive imagery condition revealed significant two way interactions: Retrieval by Location [F(1,25) = 12.14, p < .001] and Retrieval by Site [F(1.06,26.14) = 22.37, p < .001], as well as a significant three way interaction: Retrieval by Location by Site [F(1.17,29.14) = 10.46, p < .001]. The results reveal that the old/new distribution was greater at the superior sites at the frontal location compared to the parietal location. The absence of any interaction with Hemisphere suggests the effect was bilaterally distributed.

Analysis of the Unrelated Item imagery condition revealed a significant Retrieval by Location interaction [F(1,25) = 5.87, p < .02], reflecting a larger old/new difference over frontal compared to parietal electrodes. The initial ANOVA also revealed a significant Retrieval by Site interaction [F(1.15,28.72) = 4.47, < .05], reflecting a larger old/new difference at superior electrodes over both locations. Again, the absence of any interaction with Hemisphere confirmed that the frontal old/new effect was bilaterally distributed.

Finally, analysis of the Unrelated Interactive condition revealed a significant two-way interaction between Retrieval and Site [F(1.08,29.97) = 30.93, p < .001], reflecting the increased old/new difference over superior electrode sites. The absence of a significant interaction with location indicates that the effect was broadly distributed over frontal and parietal locations, however, the old/new effect was numerically larger over the frontal compared to parietal location [i.e., mean frontal old/new effect = 2.99μV (s.d. = 2.39); mean parietal old/new effect = 2μV (s.d = 2.35)].

Topographic analysis

Topographic analyses were carried out to investigate potential differences in the distribution of old/new effects between conditions during the 300-500ms time window. There were two separate aims of the topographic analysis. First, we assessed potential differences in topography between Item and Interactive imagery tasks within Relationship types, by submitting subtraction data [Hits minus Correct Rejections] to a repeated measures ANOVA with factors of Task [Item/Interactive], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Secondly, we also assessed differences in topography between Related and Unrelated pairs within Tasks, by submitting subtraction data to a repeated measures ANOVA with factors of Relationship [Related/Unrelated], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Significant interactions indicating topographic differences were followed up by rescaling the subtraction data (in line with McCarthy & Wood, 1985) and resubmitting the data to analysis. The within Relationship type analysis is reported first, followed by the within Task analysis.

Within Relationship comparison

Comparison of Related Item and Interactive tasks revealed significant Task by Location by Hemisphere [F(1,25) = 5.00, p < .05] and Task by Location by Hemisphere by Site [F(1.53,38.34) = 5.16, p < .05] interactions, reflecting a left greater than right asymmetry over parietal electrodes exhibited by the Item imagery task, whereas the Interactive task exhibited a right greater than left asymmetry over frontal electrodes. As we were interested in potential differences in old/new effects at frontal electrodes, a focused analysis was carried out on frontal electrodes. The results did not reveal any significant interactions, suggesting that the topography of old/new effects over frontal electrodes did not differ.

For Unrelated pairs, a significant interaction Task by Site [F(1.11, 27.76) = 4.96, p < .05] interaction was observed. When the data was rescaled, however, the original Task by Site interaction did not reach significance, indicating that the original interaction reflected a quantitative change in mean amplitude generated from a common set of neural generators.

Comparison of Related and Unrelated Item conditions revealed significant Retrieval by Location by Hemisphere [F(1,25) = 5.01, p < .05] and Retrieval by Location by Hemisphere by Site [F(1.41,35.31) = 5.16, p < .05] interactions. The interactions reflect the left lateralised distribution over parietal electrodes exhibited by the Related Item condition, compared to the more right lateralised distribution over frontal electrodes exhibited by the Unrelated Item condition. When focused analysis was carried out on the frontal location, however, no interactions were observed, suggesting that the frontal effects found in both conditions did not differ topographically. In addition, a comparison of Related and Unrelated Interactive conditions revealed no significant main effects or interactions, again indicating that the observed old/new effects found in both conditions did not differ topographically.

Magnitude comparison

Finally, a targeted comparison of the mean magnitude of the Mid-Frontal old/new effect was carried out between tasks for both Related and Unrelated word pairs. The planned comparison was licenced by the experimental prediction of an enhancement of the Mid-Frontal old/new effect following Interactive compared to Item imagery instructions. To directly compare Mid-Frontal old/new effects for Related and Unrelated pairs, old/new differences were averaged over a cluster of Mid-Frontal electrodes (FC1,FCZ,FC2) during the 300-500ms time window. The mean magnitude difference for each condition is shown in Figure 10.6. From the figure it can be seen that the Mid-Frontal old/new effect was larger following Interactive compared to Item imagery encoding for both Related and Unrelated pairs. Importantly, the magnitude difference between Interactive and Item tasks appears greater with Unrelated (mean difference = 1.54μV) compared to Related (mean difference = .80μV) word pairs. A focused one-tailed t-test performed on the averaged cluster of electrodes revealed that the Mid-Frontal old/new effect did not statistically differ between tasks for Related pairs. By comparison, analysis of Unrelated pairs revealed that the Mid-Frontal old/new effect was statistically larger following Interactive imagery compared to Item imagery [$t(26) = 2.03$, $p = .03$]. The pattern of Mid-Frontal old/new effects suggest that familiarity was modulated by encoding instructions that manipulate unitization for Unrelated but not Related word pairs.

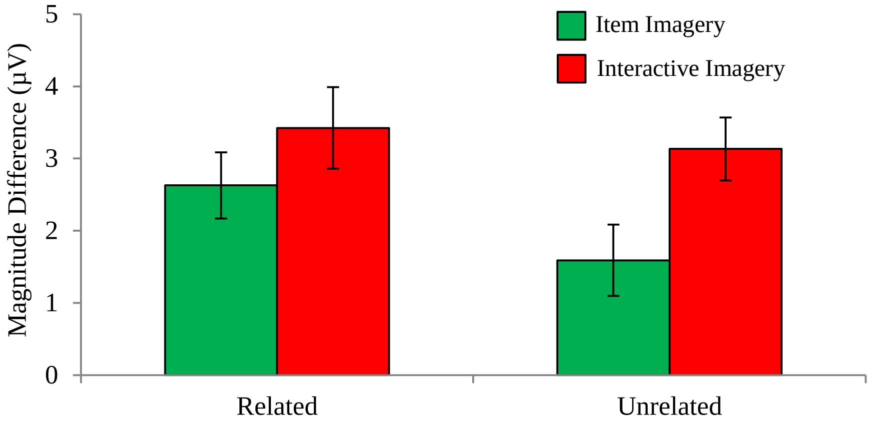

Figure 10.6: Mean magnitude (and standard error) of the Mid-Frontal old/new effect following Item and Interactive imagery tasks for Related and Unrelated word pairs, highlighting the difference in Mid-Frontal effects for Unrelated but not Related word pairs.

10.3.2.2. The Left Parietal old/new effect

Analysis of the 500-800ms time window revealed significant main effects of Retrieval for the Related Item [F(1,25) = 85.27, p < .001], Related Interactive [F(1,25) = 77.29, p < .001], Unrelated Item [F(1,25) = 18.48, p < .001] and Unrelated Interactive [F(1,25) = 67.04, p < .001] conditions, reflecting the overall greater positivity elicited by Hits compared to Correct Rejections. Separate repeated measures ANOVAs were conducted on all experimental conditions to establish whether significant Left Parietal old/new effects were present in the 500-800ms time window. Specific ANOVAs targeting Related and Unrelated word pairs are reported in turn below.

Analysis of the Related Item condition revealed significant two way Retrieval by Hemisphere [F(1,25) = 6.51, p < .05] and Retrieval by Site [F(1,25) = 35.09, p < .001] interactions, a three way Retrieval by Location by Site [F(1.06,26.50) = 32.70, p < .001] interaction and a four way interaction between Retrieval by Location by Hemisphere by Site [F(1.98, 49.69) = 6.22, p < .001]. Subsidiary analysis breaking down this four way interaction revealed main effects of Retrieval at both frontal [F(1,25) = 49.39, p < .001] and parietal [F(1,25) = 106.65, p < .001] locations, reflecting a broad distribution of old/new effects. In addition, significant Retrieval by Site interactions were also found at both frontal [F(1.06,26.53) = 43.16, p < .001] and parietal [F(1.06, 26.58) = 10.83] locations, with a more superior distribution over frontal electrodes and an effect extending over medial electrodes across the left hemisphere at the parietal location. Analysis of the parietal location also revealed significant Retrieval by Hemisphere [F(1,25) = 12.67, p < .001] and Retrieval by Hemisphere by Site [F(1.35,33.73) = 3.82, p = .05], consistent with the presence of a Left Parietal old/new effect – i.e., a left greater than right asymmetry over parietal electrodes that is maximal at the medial site.

Analysis of the Related Interactive imagery condition revealed a number of significant interactions including Retrieval by Hemisphere [F(1,25) = 7.69, p = .01], Retrieval by Site [F(1.14, 28.60) = 52.68, p < .001] and Retrieval by Location by Site [F(1.1, 27.58) = 13.17, p < .001]. Given the experimental hypothesis regarding the presence of a Left Parietal old/new effect, the initial ANOVA was followed up with targeted ANOVAs at each location. The results revealed significant main effects of Retrieval at both the frontal [F(1,25) = 73.13, p < .001] and parietal [F(1,25) = 71.38, p < .001] locations, reflecting the broad distribution of old/new effects. In addition, Retrieval by Site interactions were also found at frontal [F(1,25) = 73.13, p < .001] and parietal [F(1,25) = 71.38, p < .001] locations, with the effect increasing towards superior electrode sites at frontal location and extending towards the medial site across the left hemisphere at the parietal location. Crucially, analysis of the parietal location also revealed significant Retrieval by Hemisphere [F(1,25) = 6.30, p < .05] and Retrieval by Hemisphere by Site [F(1.68, 42.11) = 3.80, p < .05] interactions, reflecting a left lateralised distribution, maximal over medial sites.

Analysis of the Unrelated Item imagery condition revealed significant Retrieval by Hemisphere [F(1,25) = 16.39, p < .001], Retrieval by Site [F(1,25) = 21.50, p < .001], Retrieval by Location by Site [F(1.17, 29.19) = 6.44, p = .01] and Retrieval by Hemisphere by Site [F(1.18, 29.54) = 6.44, p < .01] interactions, reflecting an overall greater left sided asymmetry over both frontal and parietal locations. Again, given the specific hypothesis about the presence of a Left Parietal old/new effect, focused ANOVAs were carried out at frontal and parietal locations separately. Main effects of Retrieval were observed at frontal [F(1,25) = 17.52, p < .001] and parietal [F(1,25) = 14.75, p < .001] locations, reflecting the broad distribution of old/new differences. A Retrieval by Site interaction was also observed over both the frontal [F(1,25) = 17.52, p < .001] and parietal [F(1.14,28.55) = 9.02,p < .05] locations, with a superior distribution over frontal electrodes and an effect extending towards the medial site over the left hemisphere over the parietal electrodes. Importantly, analysis of the parietal location revealed additional significant interactions between Retrieval by Hemisphere [F(1,25) = 14.75, p < .001] and Retrieval by Hemisphere by Site [F(1.24,30.87) = 13.30, p < .001], reflecting an old/new effect that is greater over the left hemisphere and maximal at the medial site – consistent with the presence of a Left Parietal old/new effect.

Finally, analysis of the Unrelated Interactive imagery condition revealed a number of significant interactions including a Retrieval by Hemisphere [F(1,25) = 16.88, p < .001], Retrieval by Site [F(1.09,27.27) = 45.14, p < .001], Retrieval by Location by Site [F(1.09,27.27) = 15.98, p < .001] and Retrieval by Hemisphere by Site [F(1.27,31.77) = 5.84, p < .05] interaction. These results reflect activity that is broadly distributed over the left hemisphere at both parietal and frontal locations. Crucially, a four-way Retrieval by Location by Hemisphere by Site [F(1.64,41.03) = 8.40, p < .001] interaction was also observed. Subsidiary analysis of this four way interaction revealed significant main effects of Retrieval at both frontal [F(1,25) = 73.13, p < .001] and parietal [F(1,25) = 71.38, p < .001] locations, reflecting the broad distribution of old/new effects. In addition, significant Retrieval by Site interactions were also observed at frontal [F(1.15,28.72) = 58.90, p < .001] and parietal [F(1.16,28.94) = 17.83, p < .001] locations, reflecting a the superior maxima over frontal electrodes and a medial maxima extending over the left hemisphere at parietal electrodes. Analysis of the parietal location also revealed significant Retrieval by Hemisphere [F(1,25) = 6.30, p < .05] and Retrieval by Hemisphere by Site [F(1.68,42.11) = 3.80, p < .05] interactions confirming the presence of a significant Left Parietal old/new effect.

Topographic Analysis

The logic of the topographic analysis is identical for the analysis carried out on the 300-500ms time window. Again, the within relationship type analysis is reported first, followed topographic analysis between Relationship types. Significant interactions were followed up by rescaling the subtraction data and resubmitting the data to analysis.

Comparison of the Related Item and Interactive tasks did not reveal any significant interactions suggesting that there were no topographical differences between tasks. Analysis of the Unrelated Item and Interactive tasks did reveal a significant Task by Site [F(1.12, 27.91) = 4.99, $p < .05$] interaction, reflecting the overall greater superior distribution following the Interactive compared to Item imagery task. When the data were rescaled and resubmitted to analysis, the interaction did not survive, confirming that the Task by Site interaction reflected a change in mean amplitude strength. Similarly, comparison of the same Tasks between Relationship types revealed no significant interactions, indicating similar topographic distributions between conditions within the 500-800ms time window.

Magnitude Comparison

The previous analysis confirmed that significant Left Parietal old/new effects were present in all experimental conditions. Planned comparison of the magnitude of the Left Parietal old/new effect between Tasks was carried out by averaging across a cluster of left parietal electrodes (P5,P3,P1). As can be seen in Figure 10.7, Left Parietal old/new effects appear larger following Interactive compared to Item imagery tasks for both Related and Unrelated word pairs, although the difference in magnitude between tasks is larger for Unrelated pairs compared to Related pairs. Planned pair-wise t-tests confirmed that no observable differences in the magnitude of the Left Parietal old/new effect was found between the Item [mean = 4.40μV (s.d. = 2.09)] and Interactive imagery [mean = 5.31μV (s.d. = 3.26)] tasks. By contrast, analysis of Unrelated pairs revealed that the magnitude of the Left Parietal effect was significantly larger following

Interactive [mean = 4.38µV (s.d = 2.64)] compared to Item imagery [mean = 2.48µV (s.d. = 2.51)] tasks [t(26) = 2.86, p <.01].

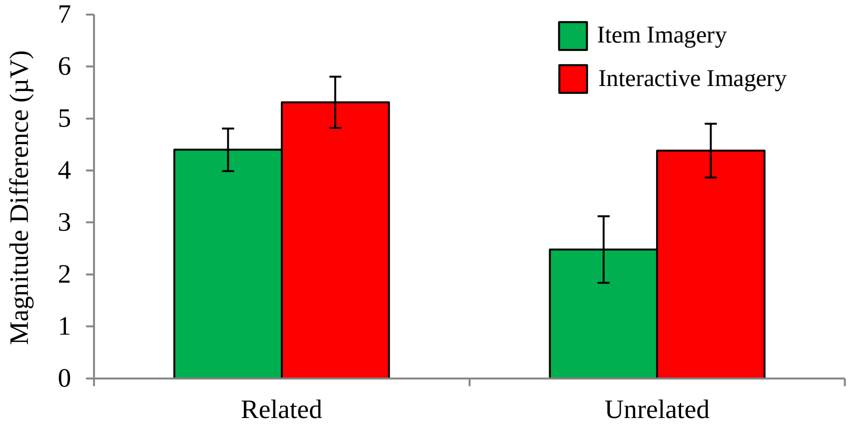

Figure 10.7: Mean magnitude (and standard error) of the Left Parietal old/new effect for Item and Interactive imagery tasks across Related and Unrelated pairs, highlighting the difference in magnitude between Item and Interactive tasks for Unrelated but not Related pairs.

10.3.2.3. Time window comparison

The previous analyses demonstrated reliable old/new differences within both the 300-500ms and 500-800ms time windows. To demonstrate that the distribution of effects changed over time for both tasks, additional analyses were conducted on subtraction data for each condition, employing an ANOVA with factors of Time [300-500ms/500-800ms], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Each experimental condition is reported in turn, with significant interactions followed up by analysis on rescaled data.

Analysis of the Related Item imagery condition revealed significant Time by Location [F(1,25) = 17.25, p < .001], Time by Site [F(1.09,27.19) = 6.73, p = .01] and Time by

Location by Site [F(1.27,31.76) = 30.32, p < .001] interactions, reflecting a change from a superior distribution over frontal electrodes in the 300-500ms time window, to a superior distribution over parietal electrodes during the 500-800ms time window. Crucially, reanalysis of the rescaled data revealed that the Time by Location interaction survived [F(1,25) = 12.06, p < .001], confirming that there was a genuine shift from a frontal distribution during the 300-500ms time window, to a parietal effect in the 500-800ms time window.

Analysis of the Related Interactive imagery condition revealed significant Time by Location [F(1,25) = 16.89, p < .001], Time by Hemisphere [F(1,25) = 6.32, p < .05] and Time by Site [F(1.08,26.99) = 14.44, p = .001] interactions, reflecting a change from a frontal to parietal distribution that is central in the 300-500ms time window and is greater over the left hemisphere compared to the right during the 500-800ms time window. Critically, when the ANOVA was resubmitted to the rescaled data, the results showed a significant Time by Location [F(1,25) = 19.39,p < .001] and Time by Hemisphere [F(1,25) = 4.12, p < .05] interaction, confirming that the initial interactions reflected qualitative change in topography rather than a quantitative change in mean amplitude strength.

Analysis of the Unrelated Item imagery condition revealed a number of significant interactions including Time by Location [F(1,25) = 12.63, p < .01], Time by Hemisphere [F(1,25) = 13.40, p = .001], Time by Site [F(1.15,28.64) = 9.19, p < .001], Time by Location by Site [F(1.13,28.29) = 13.82, p = .001], Time by Hemisphere by Site [F(1.92,29.79) = 8.10, p < .01] and Time by Location by Hemisphere by Site

[F(1.97,49.14) = 3.18, p < .05]. The pattern of interactions reflect the change in topography over time from a mid-frontal distribution that is maximal towards superior sites to a more focused left parietal distribution maximal over the medial site. When the ANOVA was resubmitted to the rescaled data, the results revealed significant Time by Location [F(1,25) = 14.23, p < .01], Time by Hemisphere [F(1,25) = 8.72, p < .01], Time by Location by Site [F(1.18,29.44) = 9.94, p < .01] and Time by Hemisphere by Site [F(1.18,29.38) = 5.82, p < .05] interactions. The reanalysis confirms that the distribution of old/new effects changed from a frontal effect to a parietal effect between time windows, and from a superior distribution in the early time window to a more medial distribution over the left hemisphere in the later time window. The data therefore supports the finding that there was a significant qualitative change in topography between the early 300-500ms and later 500-800ms time windows.

Finally, analysis of the Unrelated Interactive condition revealed a significant Time by Location by Hemisphere by Site [F(1.84,46.07) = 7.44, p < .01] interaction reflecting a change from a bilateral frontal distribution to a more focused left parietal distribution. Importantly, the four way interaction was significant after the data was rescaled [F(1.96,49.06) = 3.33, p < .05] confirming that the change in topography reflected the contribution of non-overlapping neural generators across time.

Overall, the topographic analyses reflect a change in topography between the early 300-500ms and later 500-800ms time windows for all experimental conditions. The topographic analyses confirm the contribution of non-overlapping neural generators indicating that distinct retrieval processes were engaged across time windows.

10.3.3. Subsidiary analysis: Conceptual Priming or Familiarity?

So far in this thesis, we have interpreted the modulation of the Mid-Frontal old/new effect as reflecting the contribution of familiarity. Recently, however, some researchers have argued against a familiarity account, instead arguing that Mid-Frontal activity reflects the contribution of conceptual priming (for a review see Paller, Voss & Boehm, 2007). To briefly clarify, conceptual priming refers to the facilitation of behaviour due to prior access to related meaning. According to Paller et al., (2007) most explicit tests of recognition memory are contaminated by implicit memory processes when meaningful stimuli are employed. Studies linking the Mid-Frontal old/new effect to familiarity have, therefore, done so by simply showing that the Mid-Frontal old/new effect does not reflect recollection.

To be clear, according to proponents of the conceptual priming account, demonstrating that the Mid-Frontal old/new effect is not affected by recollection does not entail that the effect is related to familiarity. Instead, Voss and Paller (2006, 2007) have argued that the Mid-Frontal old/new effect is better characterised as a frontally distributed N400 that is sensitive to the ease of semantic fluency (i.e., conceptual priming). By this view, the Mid-Frontal old/new effect is an N400, elicited by meaningful stimuli in recognition tasks, and modulated in amplitude when prior exposure facilitates meaningful processing (Voss & Paller, 2006; Voss & Paller, 2008; Voss, Lucas & Paller, 2010; Voss & Federmeier, 2011).

The conceptual priming interpretation poses a serious problem for the ERP studies that investigate the impact of unitization, by challenging the dual process account of enhanced familiarity. To date, it has proved relatively difficult to test between both conceptual priming and familiarity accounts, because studies typically employ meaningful stimuli. More specifically, studies of associative recognition, whereby the relationship between word pairs is critical to successful retrieval, will run into difficulty when employing pairs that are related. To be clear, by comparing between related word pairs, it is difficult to assess whether successful retrieval is supported by an increase in familiarity or simply enhanced conceptual fluency between pairs. As such, the Rhodes and Donaldson (2008) study cannot distinguish between a conceptual priming or familiarity account because no unrelated (i.e., word pairs that do not have a pre-existing meaningful association) baseline was employed. In the current study, however, it may be possible to indirectly test between the conceptual priming and familiarity accounts, since both conceptually related and completely novel word pairs were employed.

In theory, the conceptual priming and familiarity accounts make different predictions about the pattern ERP activity associated with successful retrieval. According to a conceptual priming account, for example, related pairs will, on average, exhibit greater levels of conceptual fluency because they map onto existing concepts (unlike unrelated pairs). In theory, therefore, related pairs should exhibit greater Mid-Frontal activity for both Hits and Correct Rejections compared to novel associations (whereby no conceptual fluency is present: see Figure 10.8, left side). By contrast, a familiarity account would only predict greater activity for Related Hits (because pre-existing pairs will carry both higher pre-experimental familiarity for the pair and additional familiarity from study), with no difference in activity predicted for Correct Rejections (as both Related and Unrelated pairs have not been previously studied: see Figure 10.8, right side).

To test between the conceptual priming and familiarity accounts, Related and Unrelated Hits and Correct Rejections were formed by collapsing across Item and Interactive tasks. Analysis directly compared both Hits and Correct Rejections separately between Related and Unrelated word pairs. The result of this analysis should discriminate between the conceptual priming and familiarity accounts of the Mid-Frontal effect (see Figure 10.9). As this subsidiary analysis was specifically an investigation of early Mid-Frontal activity, all analyses were confined to the 300-500ms time window. The mean number of trials contributing to the grand averages was: Related Hit (48), Related Correct Rejection (50), Unrelated Hit (39), Unrelated Correct Rejection (50).

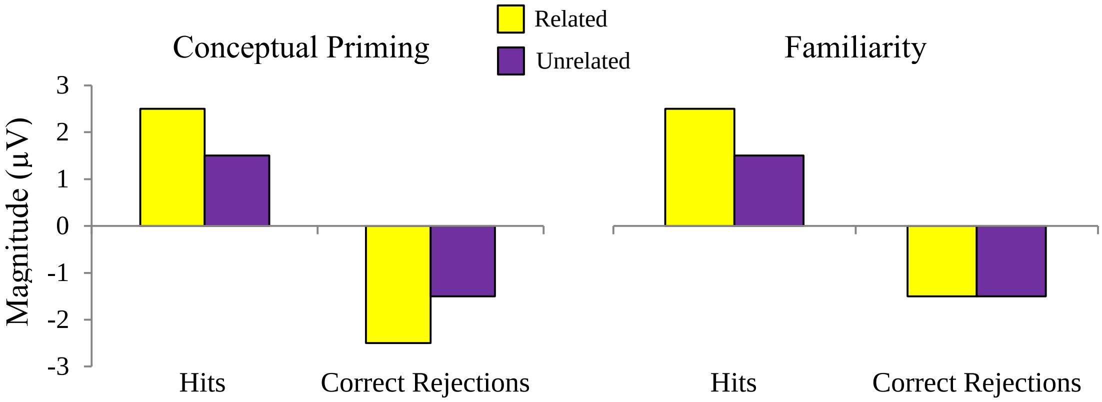

Figure 10.8: The pattern of activity for Hits and Correct Rejections predicted by the conceptual priming (left side) and familiarity (right side) accounts. Related pairs are presented in yellow and Unrelated pairs are in purple.

10.3.3.1. Comparison of Hits and Correct Rejections

The topographies of Hit and Correct Rejection contrasts between Related and Unrelated pairs within the 300-500ms time window is shown in Figure 10.9. From the figure, it can be seen that the difference in Hit activity is maximal over frontal electrodes, with a slight right sided asymmetry. By contrast, comparison of Correct Rejection activity appears to show very little difference, with no clear maxima.

The distribution of Hit/Hit differences was analysed with a repeated measures ANVOA with factors of Retrieval [Related Hit/Unrelated Hit], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior]. Analysis of Correct Rejections was carried out with an equivalent ANOVA, with factors of Retrieval [Related Correct Rejection/Unrelated Correct Rejection], Location [Frontal/Parietal], Hemisphere [Left/Right] and Site [Inferior/Medial/Superior].

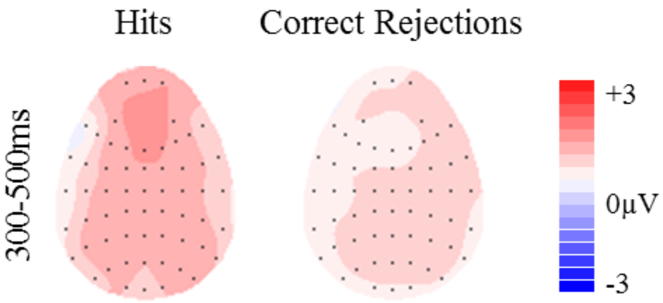

Figure 10.9: Topographic maps illustrating the distribution of Related Hit/Unrelated Hit differences (left side) and Related Correct Rejection/Unrelated Correct Rejection (right side) differences, within the 300-500ms time window

Analysis of the distribution of the Hit/Hit differences revealed a significant main effect of Retrieval [F(1,25) = 16.31, p < .001], reflecting the more positive going activity for Related Hits compared to Unrelated Hits. The results also revealed significant Retrieval by Site [F(1,25) = 6.07, p < .05] and Retrieval by Location by Site [F(1,25) = 6.34, p < .05] interactions, reflecting the more superior distribution over frontal electrodes compared to a broader distribution of activity at the parietal location. The lack of any interaction with hemisphere suggests that the Hit/Hit difference was bilaterally distributed. By contrast, analysis of Correct Rejections revealed no main effects or significant interactions.

Magnitude Comparison

Consistent with previous analyses, planned comparison of the magnitude of Hit and Correct Rejection differences was carried out on an averaged cluster of electrodes [FC1,FCZ,FC2] between 300-500ms. From Figure 10.10, it can be observed that Related pairs elicited more positive activity compared to Unrelated pairs. By contrast, activity elicited by Correct Rejection responses appears similar in magnitude across Relationship type, although activity is slightly more negative going for Unrelated pairs. Analysis of Hits [bonferroni corrected $\alpha = .03$] confirmed that the magnitude of activity elicited by Related Hits was greater than that for Unrelated Hits [$t(25) = 3.65$, $p = .001$]. By contrast, the magnitude of activity elicited Correct Rejections did not statistically differ between Related and Unrelated pairs, consistent with a pattern of activity predicted by a familiarity account.

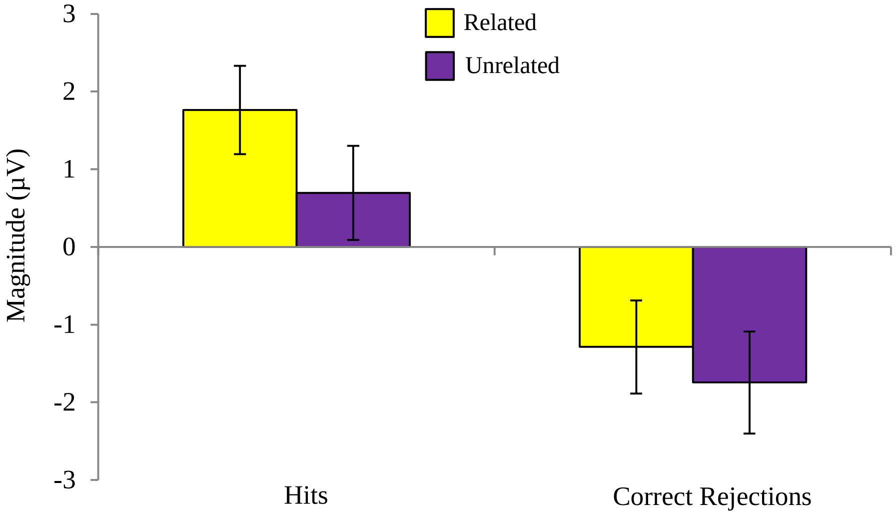

Figure 10.11: Mean (and standard error) of activity elicited by Hits and Correct Rejections between Related and Unrelated pairs. Related pairs are represented in red and Unrelated pairs in purple.

10.4. Discussion

The aim of the current experiment was to directly assess whether unitization provided clearer benefits to associative retrieval when word pairs shared either a conceptual relationship or were completely novel. Although previous studies have shown familiarity to be sensitive to unitization of word pairs sharing different types of pre-existing relationship (i.e., associative & semantic: see Rhodes & Donaldson, 2008), no direct comparison of related and unrelated word pairs has been investigated. Here, it was predicted that Interactive imagery encoding would lead to larger benefits (i.e., better behavioural performance and enhanced familiarity) compared to Item imagery when word pairs were Unrelated. The observed pattern of data was largely consistent with the experimental prediction, revealing that the difference in discrimination accuracy and the size of the Mid-Frontal old/new effect between Interactive imagery than Item imagery tasks were larger for Unrelated pairs. In the following sections, we interpret the behavioural and ERP data in turn, before considering alternative explanations and practical implications.

10.4.1. Behavioural overview

Analysis of behavioural performance revealed a pattern of results that was broadly consistent with the experimental predictions. Firstly, discrimination accuracy was significantly greater following Interactive compared to Item imagery tasks for Unrelated but not Related pairs. Secondly, response time to Intact pairs were found to be significantly quicker following Interactive compared to Item tasks for both types of word pair, whilst the difference in response time between tasks was significantly greater for Unrelated compared to Related pairs. Taken together, analysis of behavioural data supported the prediction that the improvement to retrieval between Interactive and Item imagery task would be larger when word pairs were Unrelated compared to Related.

The observed behavioural performance is broadly consistent with previous unitization studies. For Unrelated pairs, for example, the benefit to performance from Interactive encoding instructions is similar to the benefits to performance observed for novel pairs found in Chapter 8 (e.g., employing the mental imagery manipulation) and Chapter 9 (e.g., employing the lexical manipulation). The behavioural data observed for Unrelated pairs is broadly consistent with the wider unitization literature that suggests the observed benefit in behavioural performance for unitized pairs is a result of the added contribution of familiarity.

Although the results from Unrelated pairs can be adequately explained from a unitization perspective, the results for Related pairs is less clear. Analysis of discrimination accuracy of Related pairs, for example, revealed no significant differences between tasks, suggesting that Interactive imagery did not benefit discrimination accuracy for Related pairs. As observed for associative pairs under mental imagery instructions (Rhodes and Donaldson, 2008) the absence of any change in behaviour indicated that associated pairs are already perceived as being unitized and therefore do not receive any benefit from encoding instructions. Although it is possible that some of our associative and semantically related word pairs may have been perceived as a single unit, we ensured that the majority of our Related pairs did not share a common meaning. Furthermore, response times to Intact pairs were significantly quicker following Interactive imagery encoding, which is entirely consistent with the finding that familiarity is a quick and relatively automatic process. However, behavioural performance clearly reflects the contribution of both familiarity and recollection, therefore analysis of the behavioural data alone says nothing about the differential contribution of different retrieval processes. For this reason, we now turn to the ERP data that was used to index the underlying neural signals of recollection and familiarity.

10.4.2. Overview of the Left Parietal old/new effect

In the current chapter, we used ERPs to index memory retrieval, relying on the interpretation of ERP old/new effects as neural correlates of recollection and familiarity. As with previous unitization chapters, each effect is discussed in turn, beginning with the Left Parietal old/new effect. Analysis of the ERP data revealed that the Left Parietal old/new effect was present for each task and relationship type, indicating that recollection contributed to successful retrieval. Although no differences were observed between tasks for Related pairs (reflecting the equal contribution of recollection), the Left Parietal effect was significantly larger following Interactive compared to Item imagery encoding tasks for Unrelated pairs. The finding that unitization enhanced recollection for novel pairs is difficult to reconcile with previous studies.

To date, only Bader et al., (2010) have found a change in recollection when manipulating unitization – namely, an increase in parietal activity rather than reduction for non-unitized pairs, indicating that participants relied more heavily on recollection. One explanation of the current results is that unitization may influence recollection under certain circumstances, although this explanation is inconsistent with the wider unitization literature. In light of the overall poorer behavioural performance of Unrelated Item pairs, we offer an alternative explanation. For example, the inclusion of Related word pairs in the current study may have resulted in significant contrast effects. In essence, the difference in recollection for the Unrelated Item condition may have resulted from the difficulty of encoding word pairs separately – particularly in an experimental context including Related pairs and Interactive encoding instructions that both bias relational encoding. Regardless of why the Left Parietal old/new effect differed for Unrelated pairs, interpretation of the current results should be made with caution, as the overall benefit of unitization cannot be directly attributable to increased familiarity.

10.4.3. Overview of the Mid-Frontal old/new effect

Of primary interest in the current experiment was the Mid-Frontal old/new effect which is strongly associated with familiarity. Within task analysis revealed that the Mid-Frontal old/new effect was present in each experimental condition, and subsidiary topographic analysis confirmed that the distribution of the effect did not differ across frontal electrodes. Critically, the data revealed that the magnitude of the Mid-Frontal old/new effect was numerically larger following Interactive imagery for both Related and Unrelated pairs. Planned comparison of the magnitude of the Mid-Frontal old/new effect between tasks, however, revealed that the effect was significantly enhanced for Unrelated pairs but not Related pairs. To be clear, although the pattern of Mid-Frontal effects suggests that Interactive imagery resulted in a greater contribution of familiarity for both relationship types, only the Unrelated pairs resulted in a significant difference. In short, the data supports the proposal that the benefits of Interactive over Item imagery would be greater for Unrelated compared to Related word pairs.

The observed increase in the Mid-Frontal old/new effect for Unrelated pairs lends further evidence in support of unitization as an effective strategy for encouraging familiarity during associative retrieval. In addition, the enhanced effect was more clearly evident for Unrelated pairs compared to Related pairs, implying that unitization has a greater effect for previously conceptually separate stimuli. Although the results are consistent with the experimental prediction, there are multiple explanations as to why no observable differences in Mid-Frontal activity were observed for Related pairs. As discussed in Section 10.4.1., one perspective is that Related pairs in the current experiment were already perceived as a single unit. Indeed, the Related Item condition exhibited Mid-Frontal old/new effects that were comparable to the Related and Unrelated Interactive condition, implying that these pairs exhibit equivalent Mid-Frontal effects to unitized pairs. Critically, the pattern of Mid-Frontal effects between Related pairs did show a marginally greater effect for the Interactive task. The pattern of Mid-Frontal old/new effects is therefore entirely consistent with the prediction that the difference in Mid-Frontal activity between Interactive and Item tasks will be larger for Unrelated pairs.

The current data also speaks to the current debate about different familiarity signals supporting the retrieval of Related and Unrelated word pairs. To briefly reiterate, retrieval of Unrelated pairs is argued to be dependent on absolute familiarity (indexed by a parietal old/new effect), whilst retrieval of Related pairs is reliant on relative familiarity (indexed by Mid-Frontal old/new effects) – (Bader et al., 2010; MacKenzie & Donaldson, 2007; for a more detailed discussion see Chapter 8). By this dual familiarity perspective, unitization should modulate each topographically distinct effect depending on stimulus relationship. In the current experiment we intermixed both Related and Unrelated pairs, and therefore should have been able to observe these topographically distinct familiarity signals. As with Chapters 8 and 9, however, we failed to find evidence of a distinct early parietal old/new effect that would be evidence of an absolute familiarity signal. Although a detailed critique of this view has been presented in earlier chapters, it is worth noting that much like alternative accounts of the Mid-Frontal old/new effect, the dual familiarity account cannot be definitively ruled out. Instead, we argue that absolute and relative familiarity signals may both contribute to Mid-Frontal activity, as opposed to separate topographical effects.

10.4.4. Conceptual priming

Of course it is also possible that the Mid-Frontal old/new effect may not reflect familiarity. As discussed previously in this chapter, there is now a growing body of evidence indicating that the Mid-Frontal effect may instead reflect the contribution of conceptual priming (for a review see Voss & Paller, 2008). To briefly reiterate, conceptual priming is a form of repetition priming related to the repeated access to semantic representations. According to a conceptual priming account, the Mid-Frontal effect (sometimes known as an ‘FN400’) is simply an attenuated frontally distributed N400 repetition effect (Lucas, Voss, & Paller, 2010; Paller, Voss, & Boehm, 2007; Voss & Federmeier, 2011). In the current experiment, the use of Related and Unrelated pairs allowed us to indirectly assess the different predictions made by both a conceptual priming and familiarity account with regards to activity exhibited by Hits and Correct Rejections.

Overall, the pattern of results was broadly consistent with a familiarity account. To be clear, it was found that Related pairs exhibit a marginally larger Mid-Frontal old/new effect compared to Unrelated pairs, and that this difference was driven by greater activity for Hits. As previously discussed, a difference in Hits can be explained by both a conceptual priming account (i.e., increased conceptual fluency for Related pairs) and a familiarity account (i.e., the addition of pre-experimental familiarity and additional familiarity from study). The absence of any difference between Correct Rejections however, is difficult to reconcile with a conceptual priming account if it is assumed that Related non-studied word pairs will also carry a greater level of conceptual fluency than Unrelated pairs, and should therefore elicit greater ERP activity. By comparison, a familiarity account would not predict any significant difference in activity between Correct Rejections, because experimental familiarity is absent for both Related and Unrelated pairs.

Importantly, however, the comparison of Hits and Correct Rejections was an indirect test of the different predictions made by conceptual priming and familiarity accounts. As such, the current data cannot entirely rule out a conceptual priming account of Mid-Frontal old/new activity. Instead, we highlight that the pattern of activity exhibited for Hits and Correct Rejections is more consistent with a familiarity rather than a conceptual priming account. Considering the difficulty in the current literature of directly testing between the two accounts, it is conceded that a definitive conclusion about the contribution of conceptual priming and familiarity to Mid-Frontal activity is beyond the scope of the current thesis.

Recently, the conceptual priming account of the Mid-Frontal old/new effect has been challenged. For example, there is evidence that the Mid-Frontal old/new effect is graded according to familiarity strength (Stenberg, et al, 2009; Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010), that priming and familiarity elicit topographically distinct ERP effects (Yu & Rugg, 2010), and that the Mid-Frontal old/new effect can be elicited for stimuli which are argued not to contain conceptual information (Speer & Curran, 2007). Furthermore, evidence from Voss & Federmeier (2011) demonstrating that the N400 and mid-frontal old/new effect are functionally identical is questionable given that they were unable to demonstrate statistically reliable parietal and frontally distributed effects associated with the N400 and Mid-Frontal effect respectively.

Although we accept that interpretation of ERP effects are likely to change in light of new evidence, we believe the weight of current evidence supports our assumption that the Mid-Frontal old/new effect indexes familiarity.

10.4.5. Summary

The current study aimed to assess whether the benefits of Interactive imagery compared to Item imagery were sensitive to the relationship between word pairs. The analysis of behavioural performance and the early Mid-Frontal old/new effect was clear – namely, the benefits of manipulating unitization at encoding were greater when word pairs were completely novel. The current results should, however, be treated with caution considering that we also observed a difference in recollection, implying that the observed behavioural benefit cannot be attributed to an increase in familiarity. Regardless, the overall pattern of results indicates that unitization has a greater influence on successful encoding of completely unrelated word pairs – consistent with Yonelinas' (2001) assumption that unitization is an effective strategy for encouraging the learning of novel associations. Practically, the results have important implications for those with recollection deficits by demonstrating that unitization instructions may be more effective for forming completely new associations rather than strengthening memory for pre-existing relationships.

Chapter 11

General Discussion

The aim of this final Chapter is to bring together the main findings from the current thesis. The chapter will begin by summarizing the results from Chapters 6-10 in relation to the two main research questions – namely, whether the neural mechanism supporting recollection is thresholded, and whether familiarity can contribute to the retrieval of novel associative information. The theoretical implications of the current research will then be discussed before considering how the questions that have arisen from the current research can guide future research.

11.1. Summary of main findings

The overall aim of the current thesis was to explore how recollection operates and under what circumstances familiarity contributes to the recognition of novel associative information. First, this section will summarize the results of the experimental chapters that aimed to clarify the function of the neural mechanism supporting recollection. Second, this section will summarize the results from the experimental chapters investigating the contribution of familiarity towards the retrieval of novel associative recognition.

11.1.1. The function of the Left Parietal effect

The aim of Chapters 6 and 7 was to investigate the function of the neural correlate of recollection – i.e., the Left Parietal ERP effect. Chapter 6 adapted a recently developed continuous source paradigm in order to discriminate between the graded and all-or-none thresholded accounts of the Left Parietal old/new effect. Consistent with previous findings (see Harlow & Donaldson, 2013) the behavioural expression of recollection was found to fail on a subset of trials, but was variable when successful. By contrast, analysis of the Left Parietal old/new effect revealed a pattern of data that appeared graded, but this pattern of effects was not statistically significant. In Chapter 7 the continuous source paradigm was again employed, however, the old/new decision was removed to provide a more direct examination of the neural activity related to response precision. Consistent with the behavioural results, analysis of the ERP data also revealed that the magnitude of the Left Parietal effect (defined as the difference between recollected activity minus activity associated with responses over 90°) scaled with precision when recollection was successful, but was absent when recollection failed. To be clear, the magnitude of the effect was largest for high precision responses (within 10°), was significantly reduced in size for low precision trials (e.g., between 11-35°), and absent for guess responses (e.g., between 36-90°). Additional correlational analysis of fine grained bins (i.e., every 10°) confirmed that the pattern of Left Parietal effects could not be attributed to variation in guessing across bins, but instead reflected a genuine pattern of neural activity related to recollection.

11.1.2. The Mid-Frontal old/new effect and unitization

In light of the evidence suggesting that recollection could fail to provide any information from memory, it was important to investigate whether other retrieval processes could contribute to successful associative recognition. According to the DPSD model of episodic memory, encoding conditions that promote unitization should allow familiarity to contribute to the retrieval of novel associations. However, previous behavioural evidence of unitization of novel associations is heavily reliant on the assumption that curvilinear ROCs reflect familiarity (a view that has been challenged: for a greater discussion see Chapter 2). The aim of Chapters 8, 9 and 10 was therefore to provide additional evidence that unitization could encourage familiarity for novel associations by measuring changes in the magnitude of the Mid-Frontal old/new effect (i.e., the neural correlate of familiarity).

Overall, the results confirmed that instructions that encouraged unitization lead to significantly better behavioural performance (i.e., increased discrimination accuracy and quicker response times to Intact pairs), and a selective modulation of the Mid-Frontal old/new effect (i.e., familiarity), compared to instructions that discouraged unitization. Supporting the view that unitization modulates familiarity but not recollection, the Left Parietal old/new effects observed in Chapters 8 and 9 did not differ in magnitude between encoding instructions. Crucially, the ERP results from Chapters 8 and 9 suggested that encoding strategies designed to manipulate unitization may lead to different levels of familiarity at retrieval. To be clear, the Mid-Frontal old/new effect observed when word pairs were encoded with Compound Definitions was less clearly defined compared to Interactive Imagery employed in Chapter 8;

indicating that different encoding instructions may be more successful at encouraging unitization than others. Finally, the results of Chapter 10 revealed that differences in behavioural performance and modulation of the Mid-Frontal old/new effect between unitized and non-unitized instructions is greater for unrelated compared to related word pairs. In contrast to the previous studies examining unitization, the Left Parietal old/new effect was also enhanced for Interactive imagery for unrelated pairs, indicating that the behavioural data could not be attributed to a selective increase in familiarity. Regardless, the results from Chapter 10 suggest that unitization is better suited to the learning of novel associations compared to word pairs that already share a pre-existing conceptual relationship.

11.2. Implications

From a broad theoretical level, the results obtained in the current thesis provide direct support to the dual process interpretation of episodic memory. For example, the ERP correlates of familiarity and recollection were found to be independently manipulated by the two separate tasks employed in the current thesis. To be clear, the continuous source paradigm employed in Chapter 7, which was specifically designed to test recollection, revealed a selective modulation of the magnitude of the Left Parietal effect (recollection), whereas no significant Mid-Frontal effects (familiarity) were detected. By contrast, Chapters 8 and 9 found that manipulations of unitization, which influence familiarity but not recollection, selectively modulated the Mid-Frontal old/new effect, whereas the magnitude of the Left Parietal old/new effect did not differ between encoding instructions. In the following section, more specific implications regarding the observed ERP effects relating to recollection and familiarity are explored in more detail.

11.2.1. Recollection threshold

Before discussing the implications of a neural threshold, this section will briefly review the wider implications of a general recollection threshold for different models of episodic recognition. As reviewed in Chapter 4, debate about the nature of recollection has tended to centre on the issue of a threshold – that is, whether recollection can fail in a probabilistic fashion (typified by DPSD model) or is a continuous process that always returns information from memory (typified by UVSD model). The finding that recollection is both thresholded and variable, however, is difficult to reconcile with either account. For example, the evidence that recollection is thresholded is entirely consistent with the underlying assumptions of the DPSD model – i.e., recollection can fail to provide any information from memory. However, the DPSD model cannot adequately account for a variable recollection signal because the model assumes that recollection is only associated with the highest levels of memory strength – an assumption that has been recently rejected (Mickes et al., 2010; Slotnick, 2010; Yonelinas et al., 2010; Harlow & Donaldson, 2013). By contrast, the UVSD model can explain variable recollection strength (because recollection can vary from weak to strong) but cannot account for a threshold[1].

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[1] Attempts have been made to adapt the UVSD model by incorporating an encoding threshold (i.e., De Carlo, 2003; Kelly & Wixted, 2001). However, this view was recently rejected on grounds that recollection strength and probability both decay with varying study-test delays (see Harlow & Donaldson, 2013).

Alternatively, the observation that recollection is both thresholded and variable supports the view that recollection is a some-or-none process (Harlow & Donaldson, 2013; Parks & Yonelinas, 2009). Crucially, demonstrating a variable recollection signal should not be viewed as being inconsistent with a dual process account, because recollection and familiarity still reflect different retrieval processes. In essence, recollection reflects a thresholded and variable process, whereas familiarity reflects a continuous strength based process which always returns some information about the prior occurrence of a stimulus. The results from the current thesis suggest that existing dual process models (including the DPSD model) should be revised to incorporate a recollection signal that is both thresholded and variable.

11.2.2. The Left Parietal effect

The results from the current thesis provide further support to the view that the Left Parietal effect indexes processing related to recollection. For instance, the Left Parietal effect was reliably observed for recognition tasks where recollection was expected to contribute to retrieval (Chapters 6, 7, 8, 9 & 10). More specifically, the pattern of Left Parietal activity was broadly consistent with the way recollection operates under different experimental demands. In Chapters 8 and 9 (although see Chapter 10) the magnitude of the Left Parietal old/new effect did not differ between encoding tasks (i.e., unitized and non-unitized instructions), consistent with the view that unitization does not influence recollection. By contrast, during a continuous source task designed to influence recollection (Chapter 7), the magnitude of the Left Parietal effect scaled with the precision when recollection was successful, but was absent when recollection failed (e.g., for sub-threshold responses). Taken together the observed pattern of Left Parietal effects is broadly consistent with a recollection account.

Crucially, the pattern of neural data observed in Chapter 7 also has important implications for characterising the functional nature of the Left Parietal effect. As discussed in Chapter 4, two alternative functional explanations of the Left Parietal effect have been proposed – namely, the graded and all-or-none thresholded accounts. The continuous source paradigm employed in the current thesis, however, allowed us to test a third alternative account of Left Parietal activity in which the effect may operate in a some-or-none fashion. There are three main points from Chapter 7 that are relevant to the debate between different accounts of the Left Parietal effect. First, the pattern of Left Parietal effects is incompatible with a thresholded all-or-none account because the magnitude of the effect scaled with response accuracy (demonstrating a variable signal when recollection was successful). Secondly, the observed pattern of Left Parietal activity is difficult to reconcile with a Graded account because proponents of a graded Left Parietal effect make no explicit prediction about a neural threshold (Vilberg & Rugg, 2007). Lastly, the data suggests that the more nuanced some-or-none account provides a more accurate characterisation of Left Parietal activity which accommodates both a neural threshold and a variable signal that scales with the strength of recollected information.

11.2.3. Functional accounts of parietal activity

As previously discussed in Chapter 7, the findings question the usefulness of existing functional accounts of the Left Parietal effect. A number of theoretical accounts have been proposed that attempt to account for ERP and fMRI evidence of parietal retrieval success effects. For example, although both the Attention-to-Memory and Episodic Buffer perspectives can account for a thresholded and variable Left Parietal effect, neither provides an adequate explanation for why a threshold is present. By contrast, the accumulator model (Donaldson et al., 2010) may provide an explanation for why the neural signal relating to recollection is both thresholded and variable. In essence, the accumulator model proposes that a variable neural signal prompts a threshold retrieval process (Donaldson et al., 2010). Evidence of oldness is accumulated in the parietal cortex and an old decision is made when this evidence exceeds a particular threshold. By this account, the Left Parietal effect is thresholded because only memories that accumulate enough evidence to exceed the threshold will be recollected. In addition, the magnitude of the Left Parietal effect also varies in accuracy and perceived memory strength because of the varying amounts of evidence which is accumulated. The model is supported by evidence provided by Ploran et al., (2007) in which different brain regions were shown to either track the amount of mnemonic evidence, or activate in a binary (thresholded) fashion.

From a practical perspective, the separation of brain regions responsible for the accumulation of evidence and decision making processes could explain why parietal lesions result in subtle episodic memory deficits rather than amnesia (Berryhill et al., 2007; Davidson et al., 2008; Simons et al., 2009). For example, patients with parietal lobe damage exhibit poorer confidence in their decision (Simons et al., 2009), reduction in the reported richness of episodic memories (Davidson et al., 2008) or inability to produce rich, detailed memories during free recall (Berryhill et al., 2007). If the strength and rate of recollection are viewed as being independent, then it follows that patients performing tasks which require a binary decision (i.e., is the object old or new?) should not exhibit any impairment. To be clear, as long as the accumulation of evidence exceeds a particular threshold then performance should not be affected. By contrast, tasks that probe the strength of a memory would result in episodic impairment because the parietal regions are responsible for tracking the amount of mnemonic evidence. Investigating the recollection deficits experienced by patients with parietal lobe damage using the continuous source task (similar to that employed in the current thesis) would potentially clarify the function of the parietal cortex in episodic memory. A selective deficit to either recollection strength or rate would support the view that different brain regions might be involved in the tracking of recollection strength and decisional processes.

11.2.4. Does unitization enhance familiarity?

Modelling recollection as a variable process also has important implications for evidence supporting the contribution of familiarity to the retrieval of novel associations through unitization. As previously discussed in Chapter 2, behavioural and neuropsychological support for unitization has generally relied on the familiarity interpretation of curvilinear ROCs, as opposed to a variable recollection interpretation. However, the evidence presented in Chapter 7 and elsewhere (see Harlow & Donaldson, 2013; Mickes et al., 2010) supports the view that recollection varies in strength when successful. Models of episodic memory (such as the DPSD model) that therefore do not characterise recollection as being variable may incorrectly interpret recollection based retrieval as familiarity. Consequently, the DPSD model may overestimate the contribution of familiarity and underestimate the contribution of recollection. Importantly, modelling recollection as variable does not necessarily imply that familiarity is absent during associative retrieval, but it does necessitate the need to re-analyse ROC evidence, in support of unitization, by correctly characterising recollection as a variable process.

Alternatively, progress can be made by demonstrating changes in familiarity using other methods of measuring retrieval processes. For example, in the current thesis, ERPs were used to index the contribution of familiarity and recollection. The data presented in Chapters 8 and 9 demonstrated that the Mid-Frontal old/new effect (familiarity), but not the Left Parietal old/new effect (recollection: although see Chapter 10) was modulated by unitization instructions. The pattern of ERP effects is broadly consistent with the DPSD's assumption that unitization selectively encourages familiarity during retrieval of novel associative information. Furthermore, the view that unitization may simply serve to enhance recollection strength (Mickes et al., 2010) is difficult to reconcile with the finding that manipulations of unitization selectively modulated the Mid-Frontal old/new effect but not the Left Parietal old/new effect.

Crucially, the evidence provided in the current thesis in support of unitization is based on the assumption that the Mid-Frontal old/new effect is a neural correlate of familiarity (see Chapter 4 & 10). As discussed in Chapter 10, this view is contested by researchers who argue that the Mid-Frontal effect instead reflects conceptual priming. Although the data is inconsistent with a pure conceptual priming account (see Chapters 4 and 10 for a more detailed discussion) it is still theoretically possible that conceptual priming may contribute to familiarity. Explicit recognition tasks are never 'process pure' and it would be difficult to argue that there was no 'leaking in' of implicit processing (reflecting either conceptual or perceptual processing) during explicit recognition (Rugg & Curran, 2007). In addition, Wang & Yonelinas, (2012) and Wang, Ranganath, & Yonelinas, (2014) go further and argue that the same process underlies both familiarity and conceptual priming, with the critical difference being how this underlying process is tested (i.e., with an explicit or implicit memory task). Regardless, it would be unwise to argue that unitization is a mechanism that works exclusively on explicit memory considering that there are many studies demonstrating the effects of unitization on implicit memory (Dorfman, 1999; Kan et al., 2011; Graf & Schactar, 1989).

The evidence demonstrating the influence of unitization on both explicit and implicit memory is broadly consistent with the view of unitization as described by Miller (1957), whereby unitization is a general encoding strategy that operates on many different types of memory. A particularly illuminating extension of the current results would be to manipulate unitization under an experimental paradigm designed to examine the N400 effect (i.e., a word completion task). If unitization does manipulate implicit and explicit memory, we would expect the N400 effect to behave in a similar fashion to the Mid-Frontal old/new effect – i.e., larger in magnitude for unitized compared to non-unitized pairs.

11.2.5. Theoretical Implications of unitization

From a theoretical perspective, the data supporting the view that familiarity can contribute to the retrieval of novel associations (Chapters 8, 9 & 10) has important implications for dual process theories. As highlighted in Chapter 2, there is disagreement among dual process theories regarding the role of familiarity during recognition of novel associations. For example, the Atkinson and Juola (1973, 1974) model assumes that familiarity cannot contribute to the retrieval of novel information because familiarity reflects the retrieval of pre-existing lexical nodes. Similarly, the Mandler (1980) model characterises familiarity as reflecting item but not associative activation (Mandler, 1980). By contrast, the DPSD model (Yonelinas, 1994) predicts that under conditions that promote unitization, familiarity can support retrieval of novel associations because unitized pairs are encoded as single items. The finding that unitization instructions modulated the Mid-Frontal old/new effect, but not the Left Parietal old/new effect, is therefore in agreement with the assumptions held by the DPSD model.

The evidence in support of unitization also has implications beyond that for dual process theories of episodic recognition. For example, Henke (2010) has proposed a model of episodic memory that is based on the way information is processed. From this view, memory systems should be distinguished based on processing operations rather than the traditional distinction between declarative (explicit) and non-declarative (implicit) memory. According to Henke's model, the type of processing and cognitive operations performed at encoding will determine subsequent retrieval processes, similar to the transfer-appropriate processing and levels of processing theories. Unitization is described as one of three important processing modes and is specifically responsible for the rapid encoding of rigid item information after a single exposure. Since the level of consciousness is no longer a defining variable for distinguishing memory systems, Henke's model has the advantage of being able to account for evidence of unitization from both the explicit and implicit literature (Graf and Schacter, 1985, 1989; Dorfmann, 1999; Kann et al., 2011; Light et al., 1996). Although the processing mode account for describing memory systems is one of many several ways of characterising memory, it demonstrates the growing importance of unitization in shaping our current understanding of memory.

11.3. Future directions and impact

The findings from the current thesis also raise important questions that will inform future research. This section will begin by discussing the questions raised by the finding that recollection is thresholded and variable, before detailing the questions that arise from the finding that familiarity can contribute to the retrieval of novel associations. The section will conclude by discussing the impact of the current findings with regards to our understanding of memory decline as a result of ageing, disease and disorder, as well as how the current research can inform future behavioural interventions.

11.3.1. Can the rate and strength of recollection be dissociated?

One interesting question arising from the current data is whether manipulations of recollection affect its rate or strength. In Chapter 6 and 7, the distribution of responses was most accurately characterised by a threshold model with two free parameters of precision (i.e., strength) and rate. Theoretically, the strength and rate of recollection could be independently manipulated, resulting in a pattern of results where trials associated with weaker recollection strength are recollected more frequently, and stronger trials are recollected less frequently. There does appear to be some evidence in support of this prediction. For example, Onyper et al., (2010) have observed weaker but more frequent recollection derived from ROCs for travel scenes, although the reverse pattern of stronger trials recollected less frequently has yet to be demonstrated. Another critical question is whether the Left Parietal effect indexes changes in retrieval rate independent of strength – i.e., would equivalent changes in the magnitude of the Left Parietal effect be found if the rate of recollection was manipulated within participants? ERPs provide a useful tool for investigating at a neural level the influence of experimental manipulations on the rate and strength of recollection.

11.3.2. Identifying the neural substrates of recollection

Although the results from the current thesis demonstrate that the underlying neural mechanism supporting recollection is thresholded and variable, localization difficulties inherent in ERP methodology (Luck, 2005) means it is difficult to identify the underlying neural generator(s) responsible. An important extension of the current results would be to investigate whether or not the regions within the VPC (which have been shown to be sensitive to the amount of recollection; for a review see Vilberg & Rugg, 2007) are also sensitive to precision during the continuous source paradigm. A positive result would strengthen the association between the Left Parietal effect and activity within the VPC; which would further clarify the specific neural generators responsible for recollection.

If the VPC is found to track the precision of recollected information, then it is also possible that other regions may operate in a thresholded fashion (as per the accumulator model: see Donaldson et al., 2010). Neuroimaging studies using fMRI have shown that recollection involves a wider set of cortical regions, notably medial and lateral inferior parietal cortex (Vilberg & Rugg, 2012; Henson et al., 1999; Duarte et al., 2006; Wheeler & Buckner, 2004), which together with the hippocampus form a ‘core recollection network’ (Johnson & Rugg, 2007; Hamaya et al., 2012). Employing neuroimaging methods such as fMRI will be crucial in identifying the brain regions that are sensitive to the strength and rate of recollection. Not only would such findings add to our understanding of episodic memory, but by identifying the specific regions responsible for recollection failure could potentially allow researchers to better characterise why memory declines among the elderly and those suffering from disease and disorders.

11.3.3. Defining unitization

From a broad theoretical level, unitization is defined as the encoding of a number of discrete units of information into a single novel unit (Graf & Schacter, 1989). By this account, unitization should be observed across multiple stimulus materials, across different encoding strategies and at different levels of processing. However, current evidence attempting to characterise unitization has proved limited. First, the evidence that unitization occurs across multiple stimulus materials is mixed. To be more specific, although there is now sufficient evidence that lexical stimuli can be sufficiently unitized (Rhodes & Donaldson, 2007, 2008; Quamme et al., 2007; Haskins et al., 2008; Giovanello et al., 2006; also see Chapters 8, 9 & 10), the evidence for unitization of non-lexical stimuli is less clear. For example, the two behavioural studies demonstrating unitization of facial features (Yonelinas et al., 1999) and word-colour associations (Diana et al., 2008) both relied on the DPSD interpretation of curvilinear ROCs. As previously mentioned in Section 11.2.3, these studies need to be reanalysed by accurately modelling recollection as variable in order to confirm that familiarity contributes significantly to associative retrieval.

Evidence for unitization of non-lexical stimuli from ERP studies is also relatively weak. For example, Diana et al., (2011) used ERPs in a replication of their earlier source recognition study of word-colour associates. In this study, Diana et al., (2011) failed to observe the typical ERP effects related to either familiarity or recollection, although familiarity estimates (derived from ROC analysis) were again found to be larger for the Unitized compared to Non-Unitized tasks. To demonstrate that unitization occurs frequently in everyday life, future studies must test whether different non-lexical stimuli can be successfully unitized. It may be that different materials vary in their level of unitization, with some becoming more unitized than others. Discovering which stimuli are most likely to become unitized will not only add to our understanding of unitization more generally, but will also allow us to develop more effective behavioural interventions for those patients with selective memory deficits.

Secondly, it is important to determine the most effective encoding strategies that facilitate unitization. In the current thesis, the results suggest different encoding strategies may be more successful in encouraging unitization than others. To be clear, the difference in time course and magnitude of the Mid-Frontal old/new effect was more clearly defined between unitized and non-unitized instructions under the mental imagery manipulation compared to the lexical manipulation. However, as stated in Chapter 9, as no direct comparison was made between encoding manipulations it is difficult to make any strong conclusions. A potentially useful follow up study would be to compare different unitization manipulations directly within groups, to determine which strategies may be more successful than others. Such a study would be useful for testing the ‘levels of unitization hypothesis’ in which stimuli can become more or less unitized as opposed to an all-or-none process (Yonelinas et al., 2010).

Finally, it is also possible that unitization may operate on other domains of cognition. For example, Staresina and Davachi (2010) found that unitization may influence neural activity that is downstream from memory. More specifically, unitization was found to modulate neural activity in the visual cortical regions, whereas no such activity was found in the PRc. According to Staresina and Davachi (2010) object unitization may occur during processing stages related to perception before information is processed in memory. It is important to note, however, that the definition of unitization used by Staresina and Davachi (2010) referred to the creation of a perceptually intact object, as opposed to the creation of a novel conceptual representation. Regardless, it would be interesting to investigate the degree of similarity at a behavioural and neural level of analysis between perceptual unitization (e.g., conjunctions of stimulus features are chunked together to form a novel single unit: see Czerwinski, Lightfoot & Shiffrin, 1992) and conceptual manipulations of unitization. From a practical perspective, demonstrating that perceptual or conceptual manipulations of unitization are more effective for encouraging familiarity during associative recognition tests would have important implications for the development of behavioural interventions for patients with selective memory deficits.

11.2.5. Practical Impact

Finally, the current thesis has considerable impact on our understanding of memory decline in ageing, disease and disorder. As made clear in Chapter 2, cognitive decline among the elderly as well as patients suffering from Alzheimer's and Schizophrenia often exhibit a selective impairment in their ability to form and retrieve episodic associations. These deficits can be mediated by the development of appropriate behavioural interventions. These interventions, however, can only be effective if our understanding of why recollection is damaged is accurate. The findings in this thesis contribute to this understanding by demonstrating that the neural signal supporting recollection is thresholded in that some information fails to be retrieved from memory. One important goal of future research is to investigate memory decline in clinical populations by employing continuous recognition tasks (as in the current thesis). Such studies may begin to illuminate whether the memory deficits experienced by clinical populations are caused by the complete absence of memory (i.e., below threshold responses) or simply reduced strength in recollection. As such, behavioural interventions could then be tailored to either encourage associative recognition in the absence of recollection (see below) or to increase the strength of recollection during retrieval.

The results in the current thesis suggest that unitization could be an effective strategy for encouraging successful associative retrieval in the absence of recollection among patients with selective memory deficits. To this end, the current thesis suggests that not only is unitization effective at encouraging familiarity for novel associations, but that different encoding strategies may be more successful than others. In addition, the current results also suggest that unitization benefits the retrieval of novel associations to a greater extent rather than strengthening the relationship between pre-existing related pairs. Although there are limited studies (i.e., Giovanello et al., 2006; Quamme et al., 2007) focusing on the influence of unitization among amnesic populations, there has been little attempt (although see Bastin, Diana & Collete, 2013) to investigate unitization among the elderly. As such, future research must be focused on investigating associative retrieval among older populations in order to tailor stimulus materials and encoding strategies that encourage unitization to best mediate their memory deficits.

11.4. Conclusion

The goal of the current thesis was to explore the contribution of recollection and familiarity towards successful associative recognition. Two main themes were explored – namely, characterising the function of the neural mechanism supporting recollection and investigating whether familiarity could contribute to the retrieval of novel associations. Using associative and source recognition tasks to examine the ERP correlates of familiarity and recollection, the findings from the current thesis demonstrate that recollection occurs when a threshold is exceeded and familiarity is enhanced during successful associative retrieval when separate stimuli have become sufficiently unitized. The observation that the Mid-Frontal and Left Parietal ERP effects, which index familiarity and recollection respectively, could be independently manipulated also provides further support to the dual process model of episodic memory. Finally, the results have important practical implications for our understanding of memory decline associated with ageing and disease as well as laying the foundations for the development of behavioural interventions that could mediate specific recollection deficits.

References

Aggleton, J. P., McMackin, D., Carpenter, K., Hornak, J., Kapur, N., Halpin, S., Wiles, C. M., Kamel, H., Brennan, P., Carton, S., & Gaffan, D. (2000). Differential cognitive effects of colloid cysts in the third ventricle that spare or compromise the fornix. *Brain*, *123*(**4**), 800-815.

Aggleton, J. P., Vamm, S. D., Denby, C., Dix, S., Mayes, A. R., Roberts, N., & Yonelinas, A. P. (2005). Sparing of the familiarity component of recognition memory in a patient with hippocampal pathology. *Neuropsychologia*, *43*(**12**), 1810-1823.

Aggleton, J. P., & Brown, M. W. (2006). Interleaving brain systems for episodic and recognition memory. *Trends in Cognitive Sciences*, *10*(**10**), 455-463.

Allison, T., Wood, C. C., & McCarthy, G. (1986). The Central Nervous System. In E. Donchin, S. W. Porges, M.G.H. Coles (Eds.), *Psychophysiology: Systems, Processes & Applications* (pp. 5-26). Gulidford Press N.Y.

Atkinson, R. C.,, & Juola, J. F. (1973). Factors influencing speed and accuracy of word recognition. In S. Kornblum (Ed.), *Fourth International Symposium on Attention & Performance* (pp. 583-611). New York: Academic Press.

Atkinson, R. C., & Juola, J. F. (1974). Search and decision processes in recognition memory. In D. H. Krantz., R. C. Atkinson., R. D. Luce., & P. Suppes (Eds.), *Contemporary Developments in Mathematical Psychology* : *Vol. 1. Learning, Memory & Thinking* (pp. 243-293). San Francisco: Freeman.

Atkinson, R.C. & Shiffrin, R. M. (1968). Human memory: A proposed systems and its control processes. In G. H. Bower & J. T. Spence (Eds.), *The Psychology of Learning & Motivation: Advances in Research and Theory* (pp. 89-195). New York: Academic Press.

Azimian-Faridani, N., & Wilding, E. (2006). The influence of criterion shifts on electrophysiological correlates of recognition memory. *Journal of Cognitive Neuroscience, 18*(**7**), 1075-1086.

Baddeley, A. (2000). The episodic buffer: A new component of working memory?. *Trends in Cognitive Sciences*, *4*(**11**), 417-423.

Bader, R., Mecklinger, A., Hoppstädter, M., & Meyer, P. (2010). Recognition memory for one-trial-unitized word pairs: Evidence from event-related potentials. *Neuroimage*, *50*(**2**), 772-781.

Bastin, C., Van der Linden, M., Schnakers, C., Montaldi, D., & Mayes, A. R. (2010). The contribution of familiarity to within-and between-domain associative recognition memory: Use of a modified remember/know procedure. *European Journal of Cognitive Psychology*, *22*(**6**), 922-943.

Bastin, C., Diana, R. A., Simon, J., Collette, F., Yonelinas, A. P., & Salmon, E. (2013). Associative memory in aging: The effect of unitization on source memory. *Psychology & Aging*, *28*(**1**), 275-283.

Benjamin, A. S. & Craik, F. I. M. (2001). Parallel effects of aging and time pressure on memory for source: Evidence from the spacing effect. *Memory & Cognition*, *29*(**5**), 691-697.

Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: Bilateral damage causes impaired free recall of autobiographical memory. *The Journal of Neuroscience*, *27*(**52**), 14415-14423.

Bodner, G. (2003). Remembering and knowing in context. *Journal of Memory & Language*, *48*(**3**), 563-580.

Bower, G. H. (1970). Imagery as a relational organizer in associative learning. *Journal of Verbal Learning & Verbal Behavior*, *9*(**5**), 529-533.

Bowles, B., Crupi, C., Mirsattari, S. M.m Pigott, S. E., Parrent, A. G., Pruessner, J. C., Yonelinas, A. P., & Köhler, S. (2007). Impaired familiarity with preserved recollection after anterior temporal-lobe resection that spares the hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(**41**), 16382-16387.

Brown, M. W., & Aggleton, J. P. (2001). Recognition memory: What are the roles of the perirhinal cortex and hippocampus?. *Nature Reviews Neuroscience*, *2*(**1**), 51-61.

Bröder, A., & Schütz, J. (2009). Recognition ROCs are curvilinear — or are they? On premature arguments against the two-high-threshold model of recognition. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *35*(**3**), 587-606.

Bridger, E. K., Bader, R., Kriukova, O., Unger, K., & Mecklinger, A. (2012). The FN400 is functionally distinct from the N400. *Neuroimage*, *63*(**3**), 1334-1342.

Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience*, *9*(**8**), 613-625.

Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, *12*(**1**), 1-47.

Cabeza, R., Mazuz, Y. S., Stokes, J., Kragel, J. E., Woldorff, M. G., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2011). Overlapping parietal activity in memory and perception: Evidence for the attention to memory model. *Journal of Cognitive Neuroscience*, *23*(**11**), 3209-3217.

Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex*, *12*(**10**), 1048-1056.

Carlson, N.A. (1992). *Foundations of Physiological Psychology*. Simon & Shuster.

Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex*, *12*(**10**), 1048-1056.

Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, *46*(**7**), 1828-1851.

Clark, S. E., & Burchett, R. E. (1994). Word frequency and list composition effects in associative recognition and recall. *Memory & Cognition*, *22*(**1**), 55-62.

Clayson, P. E., Baldwin, S. A., & Larson, M. J. (2013). How does noise affect amplitude and latency measurement of event-related potentials (ERPs)? A methodological critique and simulation study. *Psychophysiology*, *50*(**2**), 174-186.

Coltheart, M. (1981). The MRC psycholinguistic database. *The Quarterly Journal of Experimental Psychology*, *33*(**4**), 497-505.

Comerchero, M. D., & Polich, J. (1999). P3a and P3b from typical auditory and visual stimuli. *Clinical Neurophysiology*, *110*(**1**), 24-30.

Corkin, S. (1968). Acquisition of motor skill after bilateral medial temporal-lobe excision. *Neuropsychologia*, *6*(**3**), 255-265.

Corkin, S., Amaral, D. G., González, R. G., Johnson, K. A., & Hyman, B. T. (1997). HM’s medial temporal lobe lesion: Findings from magnetic resonance imaging. *The Journal of Neuroscience*, 17(**10**), 3964-3979.

Craik, F. I., & Lockhart, R. S. (1972). Levels of processing: A framework for memory research. *Journal of Verbal Learning & Verbal Behavior*, *11*(**6**), 671-684.

Craik, F. I., & Tulving, E. (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology: General*, *104*(**3**), 268-294.

Craik, F. I. M., Govoni, R., Naveh-Benjamin, M., & Anderson, N. D. (1996). The effects of divided attention on encoding and retrieval processes in human memory. *Journal of Experimental Psychology: General*, *125*(**2**), 159-180.

Curran, T. (2004). Effects of attention and confidence on the hypothesized ERP correlates of recollection and familiarity. *Neuropsychologia*, *42*(**8**), 1088-1106.

Curran, T., & Cleary, A. M. (2003). Using ERPs to dissociate recollection from familiarity in picture recognition. *Cognitive Brain Research*, *15*(**2**), 191-205.

Curran, T., DeBuse, C., Woroch, B., & Hirshman, E. (2006). Combined pharmacological and electrophysiological dissociation of familiarity and recollection. *The Journal of Neuroscience*, *26*(**7**), 1979-1985.

Curran T, Tepe KL, Piatt C (2006) ERP explorations of dual processes in recognition memory. In H.D. Zimmer., A. Mecklinger., & U. Lindenberger (Eds.), *Binding in Human Memory: A Neurocognitive Approach*, (pp. 467-491). Oxford University Press: Oxford.

Czerwinski, M., Lightfoot, N., & Shiffrin, R. M. (1992). Automatization and training in visual search. *The American Journal of Psychology*, *105*(**2**), 271-315.

Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences*, *100*(**4**), 2157-2162.

Davidson, S. R. P., Anaki, D., Ciaramelli, E., Cohn, M., Kim, S. S. A., Murphy, J. K., Troyer, A., Moscovitch, M., & Levine, B. (2008). Does lateral parietal cortex support episodic memory? Evidence from focal lesion patients. *Neuropsychologia*, *46*(**7**), 1743-1755.

Dawson, G. D. (1947). Cerebral responses to electrical stimulation of peripheral nerve in man. *Journal of Neurology, Neurosurgery & Psychiatry*, *10*(**3**), 134-141.

Deese, J. (1959). On the prediction of occurrence of particular verbal intrusions in immediate recall. *Journal of Experimental Psychology*, *58*(**1**), 17-22.

DeCarlo, L. T. (2003). An application of signal detection theory with finite mixture distributions to source discrimination. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *29*(**5**), 767-778.

De Renzi, E., Liotti, M., & Nichelli, P. (1987). Semantic amnesia with preservation of autobiographic memory: A case report. *Cortex*, *23*(**4**), 575-597.

Dien, J. (1998). Issues in the application of the average reference : Review, critiques, and recommendations. *Behavior Research Methods, Instruments, & Computers*, *30*(**1**), 34-43.

Dewhurst, S. A., Holmes, S. J., Brandt, K. R., & Dean, G. M. (2006). Measuring the speed of the conscious components of recognition memory: Remembering is faster than knowing. *Consciousness & Cognition*, *15*(**1**), 147-162.

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, *11*(**9**), 379-386.

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2008). The effects of unitization on familiarity-based source memory: Testing a behavioural prediction derived from neuroimaging data. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *34*(**4**), 730-740.

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2010). Medial temporal lobe activity during source retrieval reflects information type, not memory strength. *Journal of Cognitive Neuroscience*, *22*(**8**), 1808-1818.

Diana, R. A., Van den Boom, W., Yonelinas, A. P., & Ranganath, C. (2011). ERP correlates of source memory: Unitized source information increases familiarity-based retrieval. *Brain Research, 1367*, 278-286.

Diana, R. A., & Ranganath, C. (2011). Recollection, familiarity and memory strength: Confusion about confounds. *Trends in Cognitive Sciences*, *15*(**8**), 337-338.

Dobbins, I. G., Rice, H. J., Wagner, A. D., & Schacter, D. L. (2003). Memory orientation and success: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia*, *41*(**3**), 318-333.

Donaldson, W. (1996). The role of decision processes in remembering and knowing. *Memory & Cognition*, *24*(**4**), 523-533.

Donaldson, D. I., & Rugg, M. D. (1998). Recognition memory for new associations: Electrophysiological evidence for the role of recollection. *Neuropsychologia, 36*(**5**), 377-395.

Donaldson, D, I., Wheeler, M, E., & Petersen, S., E. (2010). Remember the source: Dissociating frontal and parietal contributions to episodic memory. *Journal of Cognitive Neuroscience*, *22*(**2**), 377-391.

Donders, F. C. (1868/1969). On the speed of mental processes. In W. G. Koster, *Attention and Performance II* (pp. 412-431). Amsterdam: North Holland.

Dorfman, J. (1999). Unitzation of sublexical components in implicit memory for novel words. *Psychological Science*, *10*(**5**), 387-392.

Doyle, M. C., & Rugg, M. D. (1998). Word repetition within-and across-visual fields: An event-related potential study. *Neuropsychologia*, 36(**12**), 1403-1415.

Duarte, A., Ranganath, C., Trujillo, C., & Knight, R. T. (2006). Intact recollection memory in high-performing older adults: ERP and behavioral evidence. *Journal of Cognitive Neuroscience*, *18*(**1**), 33-47.

Düzel, E., Yonelinas, A. P., Mangun, G. R., Heinze, H. J., & Tulving, E. (1997). Event related brain potential correlates of two states of conscious awareness in memory. *Proceedings of the National Academy of Sciences of the United States of America,* 94, 5973-5978.

Düzel, E., Picton, T. W., Cabeza, R., Yonelinas, A. P., Scheich, H., Heinze, H. J., & Tulving, E. (2001). Comparative electrophysiological and hemodynamic measures of neural activation during memory-retrieval. *Human Brain Mapping*, *13*(**2**), 104-123.

Ecker, U. K., Zimmer, H. D., & Groh-Bordin, C. (2007). Color and context: An ERP study on intrinsic and extrinsic feature binding in episodic memory. *Memory & Cognition*, *35*(**6**), 1483-1501.

Eichenbaum, H., Otto, T., & Cohen, N. J. (1994). Two functional components of the hippocampal memory system. *Behavioral & Brain Sciences*, *17*(**3**), 449-472.

Eichenbaum, H., Yonelinas, A. R., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, *30*, 123-152.

Eldridge, L. L., Knowlton, B. J., Furmanski, C. S., Bookheimer, S. Y., & Engel, S. A. (2000). Remembering episodes: A selective role for the hippocampus during retrieval. *Nature Neuroscience*, *3*(**11**), 1149-1152.

Eldridge, L. L., Engel, S. A., Zeineh, M. M., Bookheimer, S. Y., & Knowlton, B. J. (2005). A dissociation of encoding and retrieval processes in the human hippocampus. *Journal of Neuroscience*, *25*(**13**), 3280-3286.

Finnigan, S., Humphreys, M. S., Dennis, S., & Geffen, G. (2002). ERP 'old/new'effects: Memory strength and decisional factor(s). *Neuropsychologia*, *40*(**13**), 2288-2304.

Ford, J. H., Verfaellie, M., & Giovanello, K. S. (2010). Neural correlates of familiarity-based associative retrieval. *Neuropsychologia*, *48*(**10**), 3019-3025.

Friedman, D., & Johnson, R. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research & Technique*, *51*(**1**), 6-28.

Friston, K. J., Price, C. J., Fletcher, P., Moore, C., Frackowiak, R. S., & Dolan, R. J. (1996). The trouble with cognitive subtraction. *NeuroImage*, *4*(**2**), 97-104.

Gallo, D. A., Meadow, N. G., Johnson, E. L., & Foster, K. T. (2008). Deep levels of processing elicit a distinctiveness heuristic: Evidence from the criterial recollection task. *Journal of Memory & Language*, *58*(**4**), 1095-1111.

Gardiner, J. M. (1988). Functional aspects of recollective experience. *Memory & Cognition*, *16*(**4**), 309-313.

Gardiner, J. M., & Parkin, A. J. (1990). Attention and recollective experience in recognition memory. *Memory & Cognition*, *18*(**6**), 579-583.

Gardiner, J. M. & Gregg, V. H. (1997). Recognition memory with little or no remembering: Implications for a detection model. *Psychonomic Bulletin & Review*, *4*(**4**), 474-479.

Gardiner, J. M., Ramponi, C., & Richardson-Klavehn, A. (1998). Experiences of remembering, knowing, and guessing. *Consciousness & Cognition*, *7*(**1**), 1-26.

Geraci, L., McCabe, D. P., & Guillory, J. J. (2009). On interpreting the relationship between remember-know judgments and confidence: The role of instructions. *Consciousness and Cognition*, *18*(**3**), 701-709.

Guiilund, G., & Shiffrin, R. M. (1984). A retrieval model for both recognition and recall. *Psychological Review*, *91*(**1**), 1-67.

Giovanello, K. S., Verfaellie, M., & Keane, M. M. (2003). Disproportionate deficit in associative recognition relative to item recognition in global amnesia. *Cognitive, Affective, & Behavioral Neuroscience*, *3*(**3**), 186-194.

Giovanello, K. S., Keane, M. M., & Verfaellie, M. (2006). The contribution of familiarity to associative memory in amnesia. *Neuropsychologia*, *44*(**10**), 1859-1865.

Glanzer, M. & Adams, J. K. (1985). The mirror effect in recognition memory. *Memory & Cognition*, *25*(**2**), 500-513.

Glanzer, M. & Adams, J. K. (1990). The mirror effect in recognition memory: Data and theory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *16*(**1**), 5-16.

Graf, P., & Schacter, D. L. (1985). Implicit and explicit memory for new associations in normal and amnesic subjects. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *11*(**3**), 501-518.

Graf, P., & Schacter, D. L. (1987). Selective effects of interference on implicit and explicit memory for new associations. J*ournal of Experimental Psychology: Learning, Memory, & Cognition*, *13*(**1**), 45-53.

Graf, P., & Schacter, D. L. (1989). Unitization and grouping mediate dissociations in memory for new associations. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *15*(**5)**, 930-940.

Grasha, A. F. (1970). Detection theory and memory processes: Are they compatible? *Perceptual & Motor Skills, 30*(**1**), 123-135.

Green, D. M. & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Gregg, V. H., & Gardiner, J. M. (1994). Recognition memory and awareness: A large effect of study-test modalities on ’know’ responses following a highly perceptual orienting task. *European Journal of Cognitive Psychology*, *6*(**2**), 137-147.

Gregg, A. G. (1971). Word Frequency, recognition and recall. In J.Brown (Ed), *Recall and Recognition*. London: Wiley.

Groh-Bordin, C., Zimmer, H. D., & Mecklinger, A. (2005). Feature binding in perceptual priming and in episodic object recognition: Evidence from event-related brain potentials. *Cognitive Brain Research*, *24*(**3**), 556-567.

Groh-Bordin, C., Zimmer, H. D., & Ecker, U. K. (2006). Has the butcher on the bus dyed his hair? When color changes modulate ERP correlates of familiarity and recollection. *Neuroimage*, *32*(**4**), 1879-1890.

Gronlund, S. D., Edwards, M. B., & Ohrt, D. D. (1997). Comparison of the retrieval of item versus spatial position information. *Journal of Experimental Psychology. Learning, Memory, & Cognition*, *23*(**5**), 1261-1274.

Guillaume, F., & Tiberghien, G. (2001). An event-related potential study of contextual modifications in a face recognition task. *NeuroReport*, *12*(**6**), 1209-1216.

Hamann, S., & Squire, L. (1997). Intact priming for novel perceptual representations in amnesia. *Journal of Cognitive Neuroscience*, *9*(**6**), 699-713.

Hannula, D. E., Libby, L. A., Yonelinas, A. P., & Ranganath, C. (2013). Medial temporal lobe contributions to cued retrieval of items and contexts. *Neuropsychologia*, *51*(**12**), 2322-2332.

Harlow, I. M., MacKenzie, G., & Donaldson, D. I. (2010). Familiarity for associations? A test of the domain dichotomy theory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *36*(**6**), 1381-1388.

Harlow, I. M., & Donaldson, D. I. (2013). Source accuracy data reveal the thresholded nature of human episodic memory. *Psychonomic Bulletin & Review*, *20*(**2**), 318-325.

Haskins, A. L., Yonelinas, A. P., Quamme, J. R., & Ranganath, C. (2008). Perirhinal cortex supports encoding and familiarity-based recognition of novel associations. *Neuron*, *59*(**4**), 554-560.

Hayes, S. M., Salat, D. H., & Verfaellie, M. (2012). Default network connectivity in medial temporal lobe amnesia. *The Journal of Neuroscience*, *32*(**42**), 14622-14629.

Hattori, M., & Hagiwara, M. (1996). Episodic associative memories. *Neurocomputing*, *12*(**1**), 1-18.

Hayama, H. R., Vilberg, K. L., & Rugg, M. D. (2012). Overlap between the neural correlates of cued recall and source memory: Evidence for a generic recollection network?. *Journal of Cognitive Neuroscience*, *24*(**5**), 1127-1137.

Healy, S. D., de Kort, S. R., & Clayton, N. S. (2005). The hippocampus, spatial memory and food hoarding: A puzzle revisited. *Trends in Ecology & Evolution*, *20*(**1**), 17-22.

Heckers, S., Rauch, S., Goff, D., Savage, C., Schacter, D., Fischman, A., & Alpert, N. (1998). Impaired recruitment of the hippocampus during conscious recollection in schizophrenia. *Nature Neuroscience*, *1*(**4**), 318-323.

Henke, K. (2010). A model for memory systems based on processing modes rather than consciousness. *Nature Reviews Neuroscience*, *11*(**7**), 523-532.

Henson, R. N., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *The Journal of Neuroscience*, *19*(**10**), 3962-3972.

Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, *287*(**5456**), 1269-1272.

Henson, R., Hornberger, M., & Rugg, M. (2005). Further dissociating the processes involved in recognition memory: An FMRI study. *Journal of Cognitive Neuroscience, 17*(**7**), 1058-1073.

Herron, J. E., Henson, R. N., & Rugg, M. D. (2004). Probability effects on the neural correlates of retrieval success: An fMRI study. *Neuroimage*, *21*(**1**), 302-310.

Hintzman, D. L. (1988). Judgments of frequency and recognition memory in a multiple-trace memory model. *Psychological Review*, *95*(**4**), 528-551.

Hintzman, D. L., & Curran, T. (1994). Retrieval dynamics of recognition and frequency judgments: Evidence for separate processes of familiarity and recall. *Journal of Memory & Language*, *33*(**1**), 1-18.

Hirshman, E., & Master, S. (1997). Modelling the conscious correlates of recognition memory: Reflections on the remember-know paradigm. *Memory & Cognition, 25*(**3**), 345-351.

Hockley, W. E. & Consoli, A. (1999). Familiarity and recollection in item and associative recognition. *Memory & Cognition*, *27*(**4**), 657-664.

Hockley, W. E., & Cristi, C. (1996). Tests of encoding tradeoffs between item and associative information. *Memory & Cognition*, *24*(**2**), 202-216.

Holdstock, J. S., Gurnikov, S. A., Gaffan, D., and Mayes, A. R. (2000). Perceptual and mnemonic matching-to-sample in humans: Contributions of the hippocampus, perirhinal and other medial temporal lobe cortices. *Cortex*, *36*(**3**), 301-322.

Hopkins, S. J., & Rothwell, N. J. (1995). Cytokines and the nervous system I: Expression and recognition. *Trends in Neurosciences*, *18*(**2**), 83-88.

Hoppstädter, M., King, A. V., Frölich, L., Wessa, M., Flor, H., & Meyer, P. (2013). A combined electrophysiological and morphological examination of episodic memory decline in amnestic mild cognitive impairment. *Frontiers in Aging Neuroscience*, *5*(**51)**, 1-12.

Inoue, C., & Bellezza, F. S. (1998). The detection model of recognition using know and remember judgments. *Memory & Cognition*, *26*(**2**), 299-308.

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory & Language*, *30*(**5**) 513-541.

Jacoby, L. L., & Kelly, C. M. (1992). Unconscious influences of memory: Dissociations and automaticity. In A. D. Milner, & M. D. Rugg (Eds.), *The Neuropsychology of Consciousness* (pp. 201-233). San Diego: Academic Press.

Jacoby, L. L., & Dallas, M. (1981). On the relationship between autobiographical memory and perceptual learning. *Journal of Experimental Psychology: General*, *110*(**3**), 306-340.

Jäger, T., Mecklinger, A., & Kipp, K. H. (2006a). Intra- and inter-item associations doubly dissociate the electrophysiological correlates of familiarity and recollection. *Neuron*, *52*(**3**), 535-545.

Johansson, M., Mecklinger, A., & Treese, A. C. (2004). Recognition memory for emotional and neutral faces: An event-related potential study. *Journal of Cognitive Neuroscience*, *16*(**10**), 1840-1853.

Johnson, J. D., & Rugg, M. D. (2007). Recollection and the reinstatement of encoding-related cortical activity. *Cerebral Cortex*, *17*(**11**), 2507-2515.

Kan, P. I., Keane, M., Martin, E., Parks-Stamm, J. E., Lewis, L., & Verfaellie, M. (2011). Implicit memory for novel associations between pictures: Effects of stimulus uniitzation and aging. *Memory & Cognition*, *39*, 778-790.

Kelley, R., & Wixted, J. T. (2001). On the nature of associative information in recognition memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *27*(**3**), 701-722.

Kinsbourne, M., & George, J. (1974). The mechanism of the word-frequency effect on recognition memory. *Journal of Verbal Learning & Verbal Behaviour*, *13*(**1**), 63-69.

Kirwan, C. B., & Stark, C. E. (2004). Medial temporal lobe activation during encoding and retrieval of novel face-name pairs. *Hippocampus*, *14*(**7**), 919-930.

Kiss, G. R., Armstrong, C. A., & Milroy, R. (1972). *An associative thesaurus of English*. Medical Research Council, Speech and Communication Unit: University of Edinburgh.

Knowlton, B. J. and Squire, L. R. (1995). Remembering and knowing: Two different expressions of declarative memory. J*ournal of Experimental Psychology: Learning, Memory, & Cognition*, *21*(**3**), 699-710.

Kobayashi, Y., & Amaral, D. G. (2003). Macaque monkey retrosplenial cortex: II. Cortical afferents. *Journal of Comparative Neurology*, *466*(**1**), 48-79.

Koen, J. D., Aly, M., Wang, W. C., & Yonelinas, A. P. (2013). Examining the causes of memory strength variability: Recollection, attention failure, or encoding variability? *Journal of Experimental Psychology: Learning, Memory & Cognition, 39*(**6**), 1726-1741.

Koen, J. D., & Yonelinas, A. P. (2014). The effects of healthy aging, amnestic mild cognitive impairment, and Alzheimer’s disease on recollection and familiarity: A meta-analytic review. *Neuropsychology Review*, *24*(**3**), 332-354.

Koles, Z. J. (1998). Trends in EEG source localization. *Electroencephalography & Clinical Neurophysiology*, *106*(**2**), 127-137.

Logan, G. D. (1990). Repetition priming and automaticity: Common underlying mechanisms?. *Cognitive Psychology, 22*(**1**), 1-35.

Light, L. L., Kennison, R., Prull, M. W., La Voie, D., & Zuelling, A. (1996). One-trial associative priming of nonwords in young and older adults. *Psychology & Aging, 11*(**3**), 417-430.

Luck, S. J., & Kappenman, E. S. (Eds.). (2011). *The Oxford Handbook of Event-Related Potential Components*. New York: Oxford university press.

MacKenzie, G., & Donaldson, D. I. (2007). Dissociating recollection from familiarity: Electrophysiological evidence that familiarity for faces is associated with a posterior old/new effect. *Neuroimage*, *36*(**2**), 454-463.

Malmberg, K. J. (2002). On the form of ROCs constructed from confidence ratings. *Journal of Experimental Psychology: Learning, Memory & Cognition*, *28*(**2**), 380-387.

Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review*, *87*(**3**), 252-271.

Mangels, J. A., Picton, T. W., & Craik, F. I. (2001). Attention and successful episodic encoding: An event-related potential study. *Cognitive Brain Research*, *11*(**1**), 77-95.

Manns, J. R., Hopkins, R. O., Reed, J. M., Kitchener, E. G., & Squire, L. R. (2003). Recognition memory and the human hippocampus. *Neuron*, *37*(**1**), 171-180.

Mark, R. E., & Rugg, M. D. (1998). Age effects on brain activity associated with episodic memory retrieval. An electrophysiological study. *Brain*, *121*(**5**), 861-873.

Mayes, A. R., Holdstock, J. S., Isaac, C. L., Hunkin, N., & Roberts, N. (2002). Relative sparing of item recognition memory in a patient with adult-onset damage limited to the hippocampus. *Hippocampus*, *12*(**3**), 325-340.

Mayes, A. R., Holdstock, J. S., Isaac, C. L., Montaldi, D., Grigor, J., Gummer, A., Cariga, P., Downes, J. J., Tsivlis, D., Gaffan, D., Quiyong Gong, Norman, K. A. (2004). Associative Recognition in a patient with selective hippocampal lesions and relatively normal item recognition. *Hippocampus*, *14*(**6**), 763-784.

Mayes, A., Montaldi, D., & Migo, E. (2007). Associative memory and the medial temporal lobes. *Trends in Cognitive Sciences*, *11*(**3**), 126-135.

McCarthy, G., & Wood, C. C. (1985). Scalp distribution of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *62*(**3**), 203-208.

McGee, R. (1980). Imagery and recognition memory: The effects of relational organization. *Memory & Cognition*, 8(**5**), 394-399.

Mecklinger, A. (2000). Interfacing mind and brain: A neurocognitive model of recognition memory. *Psychophysiology*, *37*(**5**), 565-582.

Mecklinger, A., von Cramon, D. Y., & Matthes-von Cramon, G. (1998). Event-related potential evidence for a specific recognition memory deficit in adult survivors of cerebral hypoxia. *Brain*, *121*(**10**), 1919-1935.

Mickes, L., Wixted, J. T., & Wais, P. E. (2007). A direct test of the unequal-variance signal detection model of recognition memory. *Psychonomic Bulletin & Review*, *14*(**5**), 858-865.

Mickes, L., Wais, P. E., & Wixted, J. T. (2009). Recollection is a continuous process: Implications for dual-process theories of recognition memory. *Psychological Science*, *20*(**4**), 509-515.

Mickes, L., Johnson, E. M., & Wixted, J. T. (2010). Continuous recollection versus unitized familiarity in associative recognition. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *36*(**4**), 843.

Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review*, 63(**2**), 81-97.

Montaldi, D., & Mayes, A. R. (2010). The role of recollection and familiarity in the functional differentiation of the medial temporal lobes. *Hippocampus*, *20*(**11**), 1291-1314.

Mosher, J. C., & Leahy, R. M. (1998). Recursive MUSIC: A framework for EEG and MEG source localization. *IEEE Transactions on Bio-Medical Engineering*, *45*(**11**), 1342-54.

Moss, H. E., Ostrin. R. K., Tyler, L. K., & Marslen-Wilson, W. D. (1995). Accessing different types of lexical semantic information: Evidence from priming. *Journal of Experimental Psychology: Learning, Memory & Cognition*, *21*(**4**), 863-883.

Murdock, B. B. (1974). *Human memory: The theory and data*. Oxford: Lawrence Elbaum.

Murdock, B. B. (1982). A theory for the storage and retrieval of item and associative information. *Psychological Review*, *89*(**6**), 609-626.

Naveh-Benjamin, M. (2000). Adult age differences in memory performance: Tests of an associative deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *26*(**5**), 1170-1187.

Naveh-Benjamin, M., Guez, J., Hara, Y., Brubaker, M. S., & Lowenschuss-Erlich, I. (2014). The effects of divided attention on encoding processes under incidental and intentional learning instructions: Underlying mechanisms?. *The Quarterly Journal of Experimental Psychology,* (ahead-of-print), 1-15.

Nessler, D., & Mecklinger, A. (2003). ERP correlates of true and false recognition after different retention delays: Stimulus and response related processes. *Psychophysiology*, *40*(**1**), 146-159.

Nessler, D., Mecklinger, A., & Penney, T. B. (2001). Event related brain potentials and illusory memories: The effects of differential encoding. *Cognitive Brain Research*, *10*(**3**), 283-301.

Norman, K. A., & O'Reilly, R. C. (2003). Modelling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review*, *110*(**4**), 611-646.

Nyhus, E., & Curran, T. (2009). Semantic and perceptual effects on recognition memory: Evidence from ERP. *Brain research*, *1283*, 102-114.

Olichney, J. M., Van Petten, C., Paller, K. A., Salmon, D. P., Iragui, V. J., & Kutas, M. (2000). Word repetition in amnesia Electrophysiological measures of impaired and spared memory. *Brain*, *123*(**9**), 1948-1963.

Onyper, S. V., Zhang, Y. X., & Howard, M. W. (2010). Some-or-none recollection: Evidence from item and source memory. *Journal of Experimental Psychology: General*, *139*(**2**), 341-364.

Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology*, *112*(**4**), 713-719.

Opitz, B., & Cornell, S. (2006). Contribution of familiarity and recollection to associative recognition memory: Insights from event-related potentials. *Journal of Cognitive Neuroscience*, *18*(**9**), 1595-1605.

Paller, K. A., Voss, J. L., & Boehm, S. G. (2007). Validating neural correlates of familiarity. *Trends in Cognitive Sciences*, 11(**6**), 243-250.

Parks, C. M. (2007). The role of noncriterial recollection in estimating recollection and familiarity. *Journal of Memory & Language*, *57*(**1**), 81-100.

Park, H., Abellanoza, C., Schaeffer, J., & Gandy, K. (2014). Source recognition by stimulus content in the MTL. *Brain research*, *1553*, 59-68.

Parks, C. M., & Yonelinas, A. P. (2007). Moving beyond pure signal-detection models: Comment on Wixted (2007). *Psychological Review*, *114*(**1**), 118-201.

Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson, R., & Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. *Psychophysiology*, *37*(**2**), 127-152.

Pilgrim, L. K., Murray, J. G., & Donaldson, D. I. (2012). Characterizing episodic memory retrieval: Electrophysiological evidence for diminished familiarity following unitization. *Journal of Cognitive Neuroscience*, *24*(**8**), 1671-1681.

Ploran, E. J., Nelson, S. M., Velanova, K., Donaldson, D. I., Petersen, S. E., & Wheeler, M. E. (2007). Evidence accumulation and the moment of recognition: Dissociating perceptual recognition processes using fMRI. *The Journal of Neuroscience*, *27*(**44**), 11912-11924.

Poldrack, R. A. (2000). Imaging brain plasticity: Conceptual and methodological issues – a theoretical review. *Neuroimage*, *12*(**1**), 1-13.

Postma, A. (1999). The influence of decision criteria upon remembering and knowing in recognition memory. *Acta Psychologica*, *103*(**1**), 65-76.

Quamme, J. R., Yonelinas, A. P., & Norman, K. A. (2007). Effect of unitization on associative recognition in amnesia. *Hippocampus*, *17*(**3**), 192-200.

Rajaram, S. (1993). Remembering and knowing: Two means of access to the personal past. *Memory & Cognition*, *21*(**1**), 89-102.

Ranganath, C., & Paller, K. A. (2000). Neural correlates of memory retrieval and evaluation. *Cognitive Brain Research*, *9*(**2**), 209-222.

Rempel-Clower, N. L., Zola, S. M., Squire, L. R., & Amaral, D. G. (1996). Three cases of enduring memory impairment after bilateral damage limited to the hippocampal formation. *The Journal of Neuroscience*, *16*(**16**), 5233-5255.

Rennie, C. J., Robinson, P. A., & Wright, J. J. (2002). Unified neurophysical model of EEG spectra and evoked potentials. *Biological Cybernetics*, *86*(**6**), 457-471.

Rhodes, S. M., & Donaldson, D. I. (2007). Electrophysiological evidence for the influence of unitization on the processes engaged during episodic retrieval: Enhancing familiarity based remembering. *Neuropsychologia, 45*(**2**), 412-424.

Rhodes, S. M., & Donaldson, D. I. (2008). Electrophysiological evidence for the effect of interactive imagery on episodic memory: Encouraging familiarity for non-unitized stimuli during associative recognition. *NeuroImage*, *39*(**2**), 873-884.

Roediger, H. L., & McDermott, K. B. (1995). Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *21*(**4**), 803-814.

Roediger, H. L., Buckner, R. L., & McDermott, K. B. (1999). Components of processing. In J. K. Foster & M. Jelicic (Eds.), *Memory: Systems, processes, or function?* (pp. 31-65). Oxford: Oxford University Press.

Rosenbaum, R. S., Köhler, S., Schacter, D. L., Moscovitch, M., Westmacott, R., Black, S. E., & Tulving, E. (2005). The case of KC: Contributions of a memory-impaired person to memory theory. *Neuropsychologia*, 43(**7**), 989-1021.

Rotello, C. M. Heit. E. (2000). Associative recognition: A case of recall-to-reject processing. *Memory & Cognition*, *28*(**6**), 907-922.

Rotello, C. M., Macmillan, N. A., Reeder, J. A., & Wong, M. (2005). The remember response: Subject to bias, graded, and not a process-pure indicator of recollection. *Psychonomic Bulletin & Review*, *12*(**5**), 865-873.

Rugg, M. D., Fletcher, P. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1996). Differential activation of the prefrontal cortex in successful and unsuccessful memory retrieval. *Brain*, *119*(**6**), 2073-2083.

Rugg, M. D., Mark, R. E., Walla, P., Schloerscheidt, A. M., Birch, C. S., & Allan, K. (1998). Dissociation of the neural correlates of implicit and explicit memory. *Nature*, *392*(**6676**), 595-598.

Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences*, 11(**6**), 251-257.

Sadeh, T., Ozubko, J. D., Winocur, G., & Moscovitch, M. (2014). How we forget may depend on how we remember. *Trends in Cognitive Sciences*, 18(**1**), 26-36.

Sanquist, T. F., Rohrbaugh, J. W., Syndulko, K., & Lindsley, D. B. (1980). Electrocortical signs of levels of processing: Perceptual analysis and recognition memory. *Psychophysiology*, *17*(**6**), 568-576.

Senkfor, A. J., & Van Petten, C. (1998). Who said what? An event-related potential investigation of source and item memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *24*(**4**), 1005-1025.

Sauvage, M. M., Fortin, N. J., Owens, C. B., Yonelinas, A. P., & Eichenbaum, H. (2007). Recognition memory: Opposite effects of hippocampal damage on recollection and familiarity. *Nature Neuroscience*, **11**(**1**), 16-18.

Sauvage, M. M., Beer, Z., & Eichenbaum, H. (2010). Recognition memory: Adding a response deadline eliminates recollection but spares familiarity. *Learning & Memory*, *17*(**2**), 104-108.

Schacter, D. L. (1990). Perceptual representation systems and implicit memory. *Annals of the New York Academy of Sciences*, *608*(**1**), 543-571.

Schacter, D. L. (1992). Priming and multiple memory systems: Perceptual mechanisms of implicit memory. *Journal of Cognitive Neuroscience*, *4*(**3**), 244-256.

Schacter, D. L. & Tulving, E. (1994). What are the memory systems of 1994? In D. L. Schacter & E. Tulving (Eds), *Memory Systems of 1994*. Cambridge: MIT Press.

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, & Psychiatry*, *20*(**1**), 11-21.

Shelton, J. R., & Martin, R. C. (1992). How semantic is automatic semantic priming? *Journal of Experimental Psychology: Learning, Memory & Cognition, 8*, 3373-3378.

Simons, J. S., Peers, P. V., Hwang, D. Y., Ally, B. A., Fletcher, P. C., & Budson, A. E. (2008). Is the parietal lobe necessary for recollection in humans?. *Neuropsychologia*, *46*(**4**), 1185-1191.

Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2009). Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex*, *20*, 479-485.

Skinner, E. I., & Fernandes, M. A. (2007). Neural correlates of recollection and familiarity: A review of neuroimaging and patient data. *Neuropsychologia*, *45*(**10**), 2163-2179.

Slotnick, S. D. (2010). “Remember” source memory ROCs indicate recollection is a continuous process. *Memory*, *18*(**1**), 27-39.

Slotnick, S. D. (2013). The nature of recollection in behavior and the brain. *Neuroreport*, *24*(**12**), 663-670.

Slotnick, S. D., & Dodson, C. S. (2005). Support for a continuous (single-process) model of recognition memory and source memory. *Memory & Cognition*, *33*(**1**), 151-170.

Smith, M. (1993). Neurophysiological manifestations of recollective experience during recognition memory judgments. *Journal of Cognitive Neuroscience, 5*(**1**), 1-13.

Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: applications to dementia and amnesia. *Journal of Experimental Psychology. General*, *117*(**1**), 34–50.

Speer, N. K., & Curran, T. (2007). ERP correlates of familiarity and recollection processes in visual associative recognition. *Brain Research*, *1174*, 197-109.

Spiers, H. J., Maguire, E. A., & Burgess, N. (2001). Hippocampal amnesia. *Neurocase*, *7*(**5**), 357-382.

Sponheim, S. R., Steele, V. R., & McGuire, K. A. (2004). Verbal memory processes in schizophrenia patients and biological relatives of schizophrenia patients: Intact implicit memory, impaired explicit recollection. *Schizophrenia Research*, *71*(**2**), 339-348.

Squire, L. (1992). Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. *Journal of Cognitive Neuroscience*, *4*(**3**), 232-243.

Staresina, B. P., Cooper, E., & Henson, R. N. (2013). Reversible information flow across the medial temporal lobe: The hippocampus links cortical modules during memory retrieval. *The Journal of Neuroscience, 33*(**35**), 14184-14192.

Staresina, B., & Davachi, L. (2008). Selective and shared contributions of the hippocampus and perirhinal cortex to episodic item and associative encoding. *Journal of Cognitive Neuroscience, 20*(**8**), 1478-1489.

Staresina, B. P., & Davachi, L. (2010). Object unitization and associative memory formation are supported by distinct brain regions. *The Journal of Neuroscience*, *30*(**29**), 9890-9897.

Starns, J. J., & Ratcliff, R. (2014). Validating the unequal-variance assumption in recognition memory using response time distributions instead of ROC functions: A diffusion model analysis. *Journal of Memory & Language*, *70*, 36-52.

Stark, C. E., & Squire, L. R. (2000). Recognition memory and familiarity judgments in severe amnesia: No evidence for a contribution of repetition priming. *Behavioral Neuroscience*, *114*(**3**), 459-467.

Stenberg, G., Hellman, J., Johansson, M., & Rosen, I. (2009). Familiarity or conceptual priming: Event-related potentials in name recognition. *Journal of Cognitive Neuroscience*, *21*(**3**), 447-460.

Strack, F., & Förster, J. (1995). Reporting recollective experiences: Direct access to memory systems?. *Psychological Science*, *6*(**6**), 352-358.

Tendolkar, I., Schoenfeld, A., Golz, G., Fernández, G., Kühl, K. P., Ferszt, R., & Heinze, H. J. (1999). Neural correlates of recognition memory with and without recollection in patients with Alzheimer's disease and healthy controls. *Neuroscience Letters*, *263*(1), 45-48.

Tsivilis, D., Otten, L. J., & Rugg, M. (2001). Context effects on the neural correlates of recognition memory: An electrophysiological study. *Neuron*, *31*(**3**), 497-505.

Toth, J. P. (1996). Conceptual automaticity in recognition memory: Levels-of-processing effects on familiarity. *Canadian Journal of Experimental Psychology*, *50*(**1**), 123-138.

Trott, C. T., Friedman, D., Ritter, W., Fabiani, M., & Snodgrass, J. G. (1999). Episodic priming and memory for temporal source: Event-related potentials reveal age-related differences in prefrontal functioning. *Psychology & Aging*, 14(**3**), 390-431.

Troyer, A. K., Winocur, G., Craik, F. I., & Moscovitch, M. (1999). Source memory and divided attention: Reciprocal costs to primary and secondary tasks. *Neuropsychology*, *13*(**4**), 467-474.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology*, *26*(**1**), 1-12.

Tulving, E. (1991). Concepts of human memory. In L. Squire, G. Lynch, N. M. Weinberger, & J. L. McGaugh (Eds.), *Memory: Organisation & Locus of Change* (pp. 3-32). New York: Oxford University Press.

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science, 247*(**4940**), 301-306.

Tulving, E., Schacter, D. L., & Stark, H. A. (1982). Priming effects in word-fragment completion are independent of recognition memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *8*(**4**), 336-342.

Uncapher, M. R., Otten, L. J., & Rugg, M. D. (2006). Episodic encoding is more than the sum of its parts: An fMRI investigation of multifeatural contextual encoding. *Neuron*, *52*(**3**), 547-556.

Urbach, T. P., & Kutas, M. (2006). Interpreting event-related brain potential (ERP) distributions: Implications of baseline potentials and variability with application to amplitude normalization by vector scaling. *Biological Psychology*, *72*(**3**), 333-343.

Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W., & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science*, *277*(**5324**), 376-380.

Ventouras, E. M., Ktonas, P. Y., Tsekou, H., Paparrigopoulos, T., Kalatzis, I., & Soldatos, C. R. (2010). Independent component analysis for source localization of EEG sleep spindle components. *Computational Intelligence & Neuroscience*, *2010*(**15**). 1-12.

Verleger, R. (1991). The instruction to refrain from blinking affects auditory P3 and N1 amplitudes. *Electroencephalography & Clinical Neurophysiology*, *78*(**3**), 240-51.

Vilberg, K. L., Moosavi, R. F., & Rugg, M. D. (2006). The relationship between electrophysiological correlates of recollection and amount of information retrieved. *Brain research*, *1122*(**1**), 161-170.

Vilberg, K. L., & Rugg, M. D. (2007). Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia*, *45*(**10**), 2216-2225.

Vilberg, K. L., & Rugg, M. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*, *46*(**7**), 1787-1799.

Vilberg, K. L., & Rugg, M. (2009). Functional significance of retrieval-related activity in lateral parietal cortex: Evidence from fMRI and ERPs. *Human Brain Mapping*, *30*(**5**), 1490-1501.

Vilberg, K. L., & Rugg, M. D. (2012). The neural correlates of recollection: Transient versus sustained fMRI effects. *The Journal of Neuroscience*, *32*(**45**), 15679-15687.

Voss, J. L., & Paller, K. A. (2006). Fluent conceptual processing and explicit memory for faces are electrophysiologically distinct. *The Journal of Neuroscience*, *26*(**3**), 926-933.

Voss, J. L., & Paller, K. A. (2007). Neural correlates of conceptual implicit memory and their contamination of putative neural correlates of explicit memory. *Learning & Memory*, *14*(**4**), 259-267.

Voss, J. L., Lucas, H. D., & Paller, K. A. (2010). Conceptual priming and familiarity: Different expression of memory during recognition testing with distinct neurophysiological correlates. *Journal of Cognitive Neuroscience*, *22***(11)**, 2638-2651.

Voss, J. L., & Federmeier, K. D. (2011). FN400 potentials are functionally identical to N400 potentials and reflect semantic processing during recognition testing. *Psychophysiology*, *48*(**4**), 532-546.

Vul, E., Hanus, D., & Kanwisher, N. (2009). Attention as inference: Selection is probabilistic; Responses are all-or-none samples. *Journal of Experimental Psychology: General*, *138*(**4**), 546-560.

Wagner, A. D., Gabrieli, J. D., & Verfaellie, M. (1997). Dissociations between familiarity processes in explicit recognition and implicit perceptual memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *23*(**2**), 305-323.

Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, *9*(**9**), 445-453.

Wais, P. E., Wixted, J. T., Hopkins, R. O., & Squire, L. R. (2006). The hippocampus supports both the recollection and the familiarity components of recognition memory. *Neuron*, *49*(**3**), 459-466.

Wang, W. C., & Yonelinas, A. P. (2012). Familiarity and conceptual implicit memory: Individual differences and neural correlates. *Cognitive Neuroscience*, *3*(**3-4**), 213-214.

Wang, W. C., Ranganath, C., & Yonelinas, A. P. (2014). Activity reductions in perirhinal cortex predict conceptual priming and familiarity-based recognition. *Neuropsychologia*, *52*, 19-26.

Warren, L. R. (1980). Evoked potential correlates of recognition memory. *Biological Psychology*, *11*(**1**), 21-35.

Warrington, E. K., & Shallice, T. (1969). The selective impairment of auditory verbal short-term memory. *Brain: A Journal of Neurology*, *92*(**4**), 885-896.

Warrington, E. K., & Weiskrantz, L. (1968). A study of learning and retention in amnesic patients. *Neuropsychologia*, *6*(**3**), 283-291.

Wickelgren, W. A. (1968). Sparing of short-term memory in an amnesic patient: Implications for strength theory of memory. *Neuropsychologia*, *6*(**3**), 235-244.

Wickelgren, W. A. (1977). Speed-accuracy tradeoff and information processing dynamics. *Acta psychologica*, 41(**1**), 67-85.

Wiegand, I., Bader, R., & Mecklinger, A. (2010). Multiple ways to the prior occurrence of an event : An electrophysiological dissociation of experimental and conceptually driven familiarity in recognition memory. *Brain Research*, *1360*, 106-118.

Westerman, D. L. (2001). The role of familiarity in item recognition, associative recognition, and plurality recognition on self-paced and speeded tests. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *27*(**3**), 723-732.

Wheeler, M. E., & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *Neuroimage*, *21*(**4**), 1337-1349.

Wilding, E. L. (2000). In what way does the parietal ERP old/new effect index recollection?. *International Journal of Psychophysiology*, *35*(**1**), 81-87.

Wilding, E. L. (2006). The practice of rescaling scalp-recorded event-related potentials. *Biological Psychology*, *72*(**3**), 325-332.

Wilding, E. L., Doyle, M. C., & Rugg, M. D. (1995). Recognition memory with and without retrieval of context: An event-related potential study. *Neuropsychologia, 33*(**6**), 743-767.

Wilding, E. L., & Rugg, M. D. (1996). An event-related potential study of recognition memory with and without retrieval of source. *Brain*, *119*(**3**), 889-905.

Wilding, E. L., & Rugg, M. D. (1997). Event-related potentials and the recognition memory exclusion task. *Neuropsychologia*, *35*(**2**), 119-128.

Wilding, E. L., & Ranganath, C. (2011). Electrophysiological correlates of episodic memory processes. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford Handbook of ERP Components*, (pp. 373-396). Oxford University Press: New York.

Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, *114*(**1**), 152-176.

Wixted, J. T., Mickes, L., & Squire, L. R. (2010). Measuring recollection and familiarity in the medial temporal lobe. *Hippocampus*, *20*(**11**), 1195-1205.

Wixted, J. T., & Squire, L. R. (2011). The medial temporal lobe and the attributes of memory. *Trends in Cognitive Sciences*, *15*(**5**), 210-217.

Wolk, D. A., Manning, K., Kliot, D., & Arnold, S. E. (2013). Recognition memory in amnestic-mild cognitive impairment: Insights from event-related potentials. *Frontiers in Aging Neuroscience*, *5*(**89**), 1-15.

Woodruff, C. C., Hayama, H. R., & Rugg, M. D. (2006). Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Brain Research*, *1100*(**1**), 125-135.

Xiang, J. Z., & Brown, M. W. (2004). Neuronal responses related to long-term recognition memory processes in prefrontal cortex. *Neuron*, *42*(**5**), 817-829.

Yasuda, K., Watanabe, O., & Ono, Y. (1997). Dissociation between semantic and autobiographic memory: A case report. *Cortex*, *33*(**4**), 623-638.

Yonelinas, A. P. (1994). Receiver-operating characteristics in recognition memory: Evidence for a dual-process model. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *20*(**6**), 1341-1354.

Yonelinas, A. P. (1997). Recognition memory ROCs for item and associative information: The contribution of recollection and familiarity. *Memory & Cognition*, *25*(**6**), 747-763.

Yonelinas, A. P. (2001). Components of episodic memory: The contribution of recollection and familiarity. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *356*(**1413**), 1363-1374.

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory & Language*, *46*(**3**), 441-517.

Yonelinas, A. P., Kroll, N. E. A., Dobbins, I. G., & Soltani, M. (1999). Recognition memory for faces: When familiarity supports associative recognition judgments. *Psychonomic Bulletin & Review*, *6*(**4**), 654-661.

Yonelinas, A. P., & Jacoby, L. L. (1995). The relation between remembering and knowing as bases for recognition: Effects of size congruency. *Journal of Memory & Language*, 34(**5**), 622-643.

Yonelinas, A. P., & Jacoby, L. L. (1996). Noncriterial recollection: Familiarity as automatic, irrelevant recollection. *Consciousness & Cognition*, 5(**1**), 131-141.

Yonelinas, A. P., Kroll, N. E., Dobbins, I., Lazzara, M., & Knight, R. T. (1998). Recollection and familiarity deficits in amnesia: Convergence of remember-know, process dissociation, and receiver operating characteristic data. *Neuropsychology*, *12*(**3**), 323-339.

Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *The Journal of Neuroscience*, *25*(**11**), 3002-3008.

Yonelinas, A. P., & Parks, C. M. (2007). Receiver operating characteristics (ROCs) in recognition memory: A review. *Psychological Bulletin*, *133*(**5**), 800-832.

Yonelinas, A. P., Aly, M., Wang, W. C., & Koen, J. D. (2010). Recollection and familiarity: Examining controversial assumptions and new directions. *Hippocampus*, *20*(**11**), 1178-1194.

Yovel, G., & Paller, K. A. (2004). The neural basis of the butcher-on-the-bus phenomenon: when a face seems familiar but is not remembered. *Neuroimage*, *21*(**2**), 789-800.

Yu, S. S., & Rugg, M. D. (2010). Dissociation of the electrophysiological correlates of famialirty strength and item repetition. *Brain Research*, *1320*, 74-84.

Zola-Morgan, S., & Squire, L. R. (1986). Memory impairment in monkeys following lesions limited to the hippocampus. *Behavioral Neuroscience*, *100*(**2**), 155-160.