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Beyond dissociation: Exploring interactions
between implicit priming and explicit recognition

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Declaration

This thesis is submitted in fulfilment of the requirements for the degree of Doctor of Philosophy at the University of Stirling. I declare that the work contained in this thesis is my own except for quotations and citations in the text, which have been duly acknowledged. I also declare that this thesis has not been submitted, either in whole or in part, for any other degree or qualification.

(Joanne Park)

Publications

The following conference presentations have been adapted from work detailed in this thesis:

Park, J.L., Allan, K. & Donaldson, D.I 'Investigating the relationship between priming and familiarity using Event-Related Potentials' Poster presented at the 19th conference of the Cognitive Neuroscience Society, Chicago, Spring 2012.

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Abstract

Over the last 30 or more years evidence has accumulated in favour of the view that memory is not a unitary faculty; rather, it can be subdivided into a number of functionally independent subsystems. Whilst dividing memory phenomena into these distinct subsystems has undoubtedly advanced our understanding of memory as a whole, the approach of studying subsystems in isolation fails to address potential interactions between them. Over the last few decades there has been a gradual increase in the number of studies attempting to move beyond dissociation by characterising functional interactions between subsystems of memory. The main aim of this thesis was to contribute to this endeavour, by examining interactions between two specific subsystems that are positioned on opposite sides of the declarative and non-declarative divide in long-term memory: priming and episodic recognition. Event-Related Potentials (ERPs) were employed to monitor neural markers of repetition priming and episodic memory during recognition tests with masked priming of test cues. In the standard procedure, half of the studied and unstudied test trials began with a brief (48ms) masked repetition of the to-be-recognized word prior to the onset of test items; the remaining unprimed trials were preceded by the word “blank”. The pattern of priming effects across experiments was reasonably consistent, with differences between experiments directly related to the intended manipulations. In contrast to priming effects, the pattern of memory effects was variable across experiments, demonstrating that the engagement of explicit recognition signals is influenced by the outcome of implicit processing, and suggesting that interactions between priming and explicit retrieval processes do occur. Taken together, results from experiments reported in this thesis indicate (1) that under certain circumstances, priming is sufficient to support accurate recognition and does not necessitate changes in memory performance, (2) that mid-frontal old/new effects indexing familiarity are not merely driven by repeated access to semantic information, and (3) that priming influences neural correlates of recollection by speeding their onset. Overall, the data clearly demonstrate that there are multiple potentially interacting routes to recognition.

Chapter 1

Memory

1.1 Introduction

Long-term memory refers to the powerful yet fragile set of cognitive abilities used by humans to retain information, reconstruct past experiences, and plan for the future (James, 1890). Memory is known to be critical to everyday functioning, and the loss of memory function is central to the devastating problems that occur during normal ageing and that result from many forms of disease ranging from dementia to alcoholism. Long-term memory is not a single entity however, and many years of research has led to clear divisions being drawn between different types of memory (e.g., Cohen & Squire, 1980; Tulving, 1985a). The majority of memory research over the past 30 or more years has focused on identifying and dissociating these different types of memory. Within long-term memory a basic division is drawn between declarative (i.e., conscious or explicit) and non-declarative (i.e., unconscious or implicit) forms of memory (e.g., Eichenbaum & Cohen, 2001; Tulving, 1989). Declarative memory is subdivided into memory

for facts (semantic knowledge about the world) and events (episodic memory of one's past). Non-declarative memory (also called procedural memory) is divided into conditioning, skill learning, non-associative learning, and priming (see Figure 1.1). Extensive evidence from a wide variety of research methods including behavioural investigations, neuropsychological studies of patients, and more recently neuroimaging studies, have lead to the conclusion that these different forms of memory each have their own functional characteristics and, in addition, each form of memory is believed to be supported by its own distinct neural system.

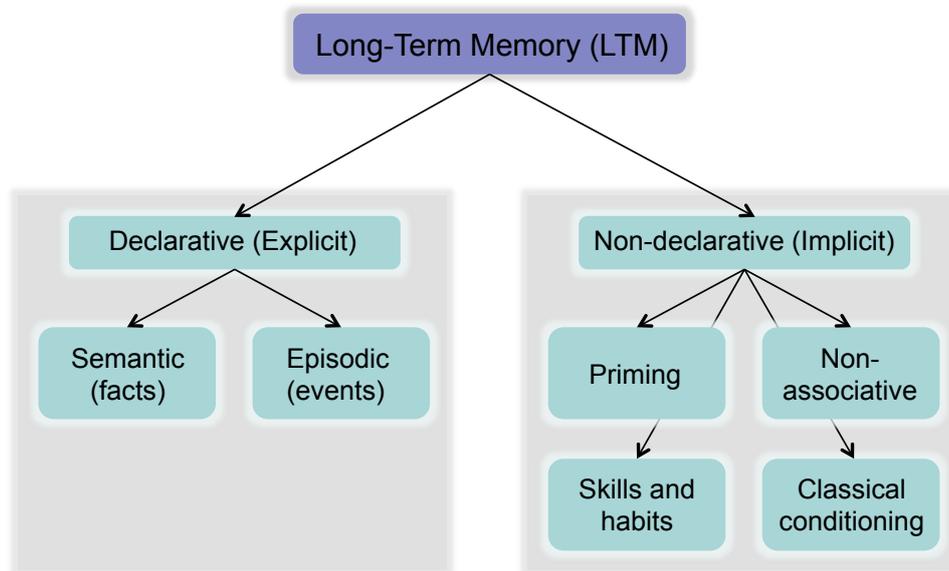


Figure 1.1: Long-term memory. Schematic illustration of sub-systems that comprise long-term memory. Declarative memory systems are explicit and allow previously encountered information to influence current behaviour via consciousness. In contrast non-declarative memory systems are implicit and allow past experience to influence current behaviour in the absence of conscious awareness (adapted from Squire, 2004).

One critical aspect of the distinction between declarative and non-declarative memory described above is that they differ in whether access to these forms of memory relies on explicit (conscious) or implicit (unconscious) forms of remembering (e.g., Graf & Schacter, 1985). The terms implicit and explicit are

essentially descriptive; the two types of memory can be differentiated by the psychological experience that accompanies the memory at the time of retrieval. For example, episodic memory is an explicit form of memory that supports the remembering of events; the retrieval of this information comes consciously to mind such that the rememberer is said to re-experience the original episode. By contrast, priming is a form of implicit memory that reflects a change in sensitivity (e.g., a faster reaction to a stimulus) that results from prior experience; this occurs without any need to re-experience the prior episode consciously, or any need for the rememberer to be aware that they are remembering.

Psychologists have argued for the existence of distinct explicit and implicit forms of memory on a number of grounds, using a variety of different methods, but largely by examining the different forms of memory in isolation from one another. The interaction between explicit and implicit forms of memory is an area of research that has received relatively little examination to date, at least in part because of the difficulties of assessing conscious versus unconscious remembering using traditional behavioural research methods. In essence, behavioural methods are not ‘process pure’ (e.g., Dunn & Kirsner, 1988; Richardson-Klavehn & Bjork, 1988; Salthouse, Toth, Hancock & Woodard, 1997), which means that they do not allow the experimenter to tap just one form of memory in isolation. By fractionating memory into functionally distinct cognitive capacities, psychologists have provided a way to move forward with empirical investigation. Episodic memory and priming have been well characterised as functionally independent subsystems, with behavioural, neuropsychological and neuroimaging evidence supporting the view that these forms of memory are dissociable.

Before providing a description of evidence demonstrating the functional independence of priming and episodic memory systems, it is necessary to understand the

logic underlying the method of dissociation, and how it has contributed to the identification of functionally separable subsystems of memory. Dissociations fall into two main categories, single and double. A single dissociation is discovered when an experimental variable influences performance on task A, but has no influence on performance in task B. A double dissociation is identified when the opposite pattern can also be observed, such that a different experimental variable influences performance on task B, but not on task A. One key assumption underlying the use of dissociations to separate mental functions is that task conditions can be effectively applied to isolate the operation of a single cognitive function, meeting the criterion for ‘process purity’ (Dunn & Kirsner, 1988), but in reality this assumption is rarely justified.

It is generally accepted that a single dissociation reflects only weak evidence of the existence of separate mental functions, as it remains plausible that the two tasks engage the same mental resource but to a different degree; producing detectable differences on only one task despite its contribution to both (Shallice, 1988). Double dissociations are generally thought to constitute stronger evidence of separate mental functions, but have also been subject to criticism on similar grounds. For example, Dunn and Kirsner (2003) proposed that double dissociations can only be reliably identified in pure neuropsychological cases, where only a single function is damaged. Despite the aforementioned limitations, the method of dissociation remains a useful tool for delineating complex cognitive systems (Baddeley, 2003), providing that interpretations and resultant theories of cognitive function are constrained by the potential limitations of this approach.

Traditionally, investigations of implicit priming and explicit recognition memory have employed distinct experimental manipulations in an attempt to isolate processing related to each form of memory. For example, priming is measured on

tasks such as word stem completion, where the operation of memory is indexed by an enhanced tendency to complete word stems with previously encountered words in the absence of a conscious retrieval attempt. By contrast, episodic memory is measured using recall or recognition tasks employing explicit retrieval conditions, where participants are required to consciously identify items from a previous study episode. However, this approach of employing distinct tasks to query these different aspects of memory cannot rule out the possibility of implicit or explicit contamination, or the presence of interactions between memory systems; in essence the tasks cannot be considered 'process pure'. For example, in word stem completion it is likely that responses on some trials are contaminated by explicit reference to the study episode (Squire, Shimamura & Graf, 1987). Equally, on explicit tests it is impossible to rule out the potential contribution of implicit memory, as items have been previously studied and are therefore by definition also primed. As a result, it is often claimed that the strongest evidence supporting the functional separation of priming and episodic memory systems is provided by neuropsychological studies.

Distinguishing cleanly between implicit and explicit memory has typically been considered easier in patient populations who have lost the ability to consciously remember. In patient populations a single dissociation is discovered when a patient or a group of patients performs well on one type of memory task but shows impaired performance on an alternative memory task. A double dissociation is discovered when there are two patients or groups of patients showing completely opposing patterns of impairment. For example, amnesic patients have been found to show severe deficits in their ability to explicitly remember recently presented information, but show intact implicit memory for aspects of the same stimuli (Monti et al., 1996). Older participants have been shown to perform more poorly

in explicit memory tasks compared to younger participants, but the two groups show comparable levels of priming on implicit tasks like picture naming (Mitchell, 1989). In addition, patients with damage to the Medial Temporal Lobe (MTL) exhibit intact priming but show impairments in episodic memory (Warrington & Weiskrantz, 1974). The opposite pattern has also been claimed; for example, damage to the occipital lobe is associated with intact episodic memory but impaired visual priming (Gabrieli, Fleischman, Keane, Reminger & Morrell, 1995). On this basis, the findings from neuropsychological studies suggest that priming and episodic memory systems are functionally and anatomically distinct.

Focusing on memory deficits clearly has significant benefits, but it also means that potential interactions between implicit and explicit memory have often been ignored because one form of memory is being examined in the absence of the other. Early behavioural work investigating priming and episodic memory in normal populations demonstrated that manipulation of specific variables had differential effects on priming and recognition, providing support for the separate systems view. For example, depth of processing at encoding has been shown to impact performance on explicit recognition tasks, with deep semantic encoding improving performance, but has no effect on implicit tasks. In contrast, changes in modality between study and test have been shown to impact performance on implicit tests, but not on explicit tests (Jacoby & Dallas, 1981). Retention interval has also been shown to differentiate between implicit priming and explicit recognition, such that recognition performance is diminished over time in explicit tests, but priming effects on word-stem completion remain unchanged (Tulving, Schacter & Stark, 1982). In addition, divided attention at encoding reduces subsequent explicit recognition, but does not impact priming effects assessed via word-stem completion (Parkin, Reid & Russo, 1990). One criticism of the pre-

ceding evidence concerns the use of different tasks to assess the contribution of implicit and explicit memory phenomena, meaning that observed effects could be contaminated by differences in task demands or retrieval strategies.

As a result of potential differences in task demands or retrieval strategies, it has been proposed that comparisons of implicit and explicit memory should be designed to meet the retrieval intentionality criterion, which requires that all factors of an experimental task are identical; only differing in the retrieval instructions provided at test (Schacter, Bowers & Booker, 1989). For example, contrasting priming and recognition should be achieved by presenting matched study lists and test cues (e.g., word stems), and participants should be instructed to complete words stems with the first word that comes to mind (implicit task), or to complete stems with words from that are remembered from the study list (explicit task). Findings from studies adopting this approach are in general agreement with those reported above, for example, demonstrating differential effects on implicit and explicit memory as a function of divided attention and levels of processing (e.g., Mulligan & Hartman, 1996; Toth, Reingold & Jacoby, 1994). While meeting the constraints imposed by the retrieval intentionality criterion appears to reduce the possibility of explicit contamination of implicit memory, it still does not completely rule out the possibility. The problem of obtaining pure measures of implicit and explicit memory in normal populations remains a challenge, and while significant progress has been made in methods applied to isolate pure implicit memory (Roediger & McDermott, 1993), it has become increasingly obvious that controlling implicit contributions to explicit memory is a far more difficult proposition.

The current section has provided an introduction to implicit and explicit memory, and a brief overview of evidence supporting the view that priming and episodic

recognition represent functionally and anatomically distinct subsystems of memory. In addition, some of the difficulties inherent in isolating and measuring the contribution of implicit and explicit memory to performance have been outlined. In normal populations, it is a standard assumption that explicit memory can contribute to performance on implicit memory tests, and moreover, there is growing evidence indicating that implicit memory can drive recognition responses during explicit memory tests (e.g., Keane, Orlando & Verfaellie, 2006; Rajaram & Geraci, 2000; Voss, Baym & Paller, 2008; Wolk, Schacter, Berman, Holcomb, Daffner & Budson, 2005). The main aim of the current thesis was to explore the nature of interactions between implicit priming and episodic recognition using Event-Related Potentials (ERPs), which allow different forms of memory to be examined directly, employing ‘neuro-signatures’ of memory related processing as a way to measure the contribution of each form of memory to performance. Before detailing evidence supporting the presence of interactions between implicit priming and explicit recognition, the following sections will provide an introduction to theories of episodic memory and priming independently.

1.2 Episodic memory

The importance of episodic memory as a defining characteristic of humans cannot be overstated, as it retains our sense of personal identity over a lifetime. This continuity of the self is claimed to set us apart from other animals, and is also thought to be an absolute requirement to make sense of any concept of moral responsibility (Sutton, 1998). Tulving (1972) first introduced the term episodic memory to describe memory phenomena that maintain temporal and spatial relations between autobiographical events or episodes. Episodic memory

is characterised by access via auto-noetic consciousness; the retrieval of information comes consciously to mind such that the rememberer is said to re-experience the original episode embedded within its particular context. Processing related to episodic memory can be further sub-divided into three distinct stages, encoding, storage and retrieval. For simplicity of explanation, these stages are analogous to the stages involved in information processing carried out by computers. The computer receives the input and translates the higher level representation into machine code, assigns this code to a storage address in main memory, then at retrieval the address is specified and the code is produced as output.

The ability to remember past events has been shown to depend upon the processing that they receive at the time of encoding. Encoding relies upon two components, first, an initial component must transform input into a representation of an event, and then, a second component must bind multiple aspects of this representation into an enduring memory trace (Paller & Wagner, 2002). An important point concerns the wide variety of information that must be integrated at encoding to form an enduring memory trace representing a specific episode or event, including sensory, semantic, temporal and spatial information. This description views memory as a storage system; each episodic memory has its own dedicated trace or representation through which it can be accessed. In the case of a computer the trace would be an address held in an array of addresses that refers to a specific location in the memory store. The exact mechanisms of storage in the human brain are not yet well understood, and cannot be manipulated directly in experiments. As a result, the bulk of research into episodic memory to date concentrates on investigation of encoding and retrieval processes. Details of encoding will not be discussed further as the focus of the current thesis is on

processes related to the retrieval; the following sections will introduce current theories of episodic retrieval.

1.2.1 Episodic retrieval

Episodic retrieval can be assessed using a variety of experimental tasks that can be split into two main categories: recall and recognition tasks. In both tasks participants are presented with items to be studied, before memory for these items is probed during a subsequent testing phase. Recall tasks can be further subdivided into free recall and cued recall tasks; during free recall tests participants are merely instructed to recall as many items as they can from the study phase, whilst during cued recall participants are presented with cues at test to aid retrieval (e.g., a partial repetition of study items). By contrast, during recognition tests studied items are re-presented in their entirety, randomly intermixed with unstudied items, and participants are required to discriminate between studied (old) and unstudied (new) items. The distinction between recall and recognition tasks is largely driven by the amount of cue information available at retrieval, with recall tasks relying to some extent on generation of previously encountered items and recognition tasks relying on identification of previous occurrence. The research reported in this thesis employs a recognition task, and so the remainder of this section will focus on theories of recognition memory. In the literature there are two opposing accounts of the operation of recognition memory, which are broadly classified into single-process and dual-process theories.

1.2.1.1 Single-process theories

Single-process theories propose that recognition is supported by a single retrieval process that operates via assessment of memory strength at the time of retrieval. A number of single-process models of recognition memory have been proposed (e.g. MINERVA 2, Hintzman, 1988; TODAM 2, Murdock, 1997; BCDMEM, Dennis & Humphreys, 2001), and the majority of these models are based on signal detection theory (Snodgrass & Corwin, 1988). Signal detection theory asserts that the memory strength of studied and unstudied items can be represented by partially overlapping Gaussian distributions, situated along a continuum of memory strength, with studied items situated further along the continuum than unstudied items (see Figure 1.2). During recognition tests participants set a response criterion that supports discrimination of studied from unstudied items, such that items falling above the criterion will be judged as studied, and those failing to reach the criterion will be judged as unstudied.

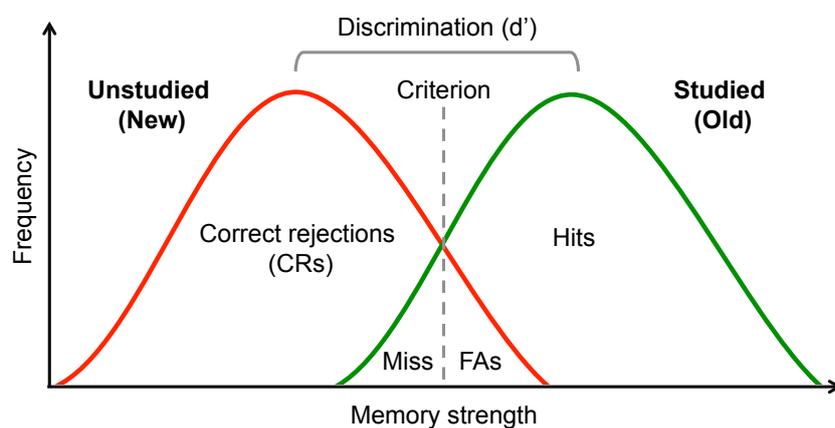


Figure 1.2: Signal detection theory. Schematic illustration of signal detection theory. Studied and unstudied items are represented by partially overlapping Gaussian distributions, situated along a continuum of memory strength, with studied items situated further along the continuum than unstudied items due to prior exposure. The distance between the means of the two distributions provides a measure of discrimination.

As can be seen in Figure 1.2, the overlapping distributions for studied and unstudied items characterise the four response types observed during recognition testing, which are classified as correct or incorrect on the basis of the response criterion. For correct responses, the hit rate describes the proportion of the distribution for studied items exceeding the response criterion, and the correct rejection rate describes the proportion of the unstudied distribution falling below the criterion. Misses describe the proportion of the distribution for studied items that fail to reach the criterion and are incorrectly classified as unstudied, and false alarms describe the proportion of the distribution for unstudied items that exceed the criterion and are incorrectly classified as studied. Signal detection models also support additional measures of memory performance by providing an index of discrimination and response bias.

Discrimination measures how easy it is to distinguish studied from unstudied items and is based on the distance between the studied and unstudied distributions, with a low degree of overlap indicating high discriminability (i.e., better discrimination). Response bias provides a measure of the likelihood that participants will classify items as studied under conditions of uncertainty, and can be liberal or conservative. Bias is directly related to the placement of the response criterion along the continuum of memory strength, with a liberal bias indicating placement at the low end and a conservative bias indicating placement toward the high end. As such, with a conservative bias items are only classified as studied when they are associated with a very high level of memory strength, and with a liberal bias even items with a low level of memory strength will be classified as studied.

Whilst attractive for their simplicity, single-process theories based on signal detection theory have been widely criticised for failure to account for a range of ex-

perimental findings without modification (Yonelinas, 2002). For example, word frequency mirror effects (i.e., the finding that low frequency words produce a higher hit rate and a lower false alarm rate than high frequency words) have been considered to represent a significant challenge to single-process accounts of recognition (e.g., Arndt & Reder, 2002; Glanzer & Adams, 1985). While debate still continues over whether purely signal detection based or dual-process models represent the best fit to account for the wealth of recognition data (e.g., Parks & Yonelinas, 2007; Wixted, 2007), in recent years dual-process theories of recognition memory have dominated the literature.

1.2.1.2 Dual-process theories

Dual-process models propose that recognition memory is supported by two separate search processes, familiarity and recollection. Recollection is typically characterized as an effortful process that can be identified as having occurred when participants are able to remember specific context details associated with an event. In contrast, familiarity has been claimed to index the degree of similarity between a current event and some event in our past experience and has been considered to be an automatic process. The qualitative difference between these two processes is often demonstrated by the common experience of recognising that someone is familiar but being unable to recollect any specific contextual details about them (Mandler, 1980). Dual-process models assert that familiarity represents a graded index of memory strength that is well described by signal detection theory, while recollection is thresholded and supports the all-or-nothing retrieval of specific contextual information related to an episode (see Yonelinas, 2002, for an extensive review).

There are a number of dual-process models of recognition (e.g., Atkinson & Juola, 1974; Jacoby, 1991; Mandler, 1980; Yonelinas, 1994), that represent slight variations on a single theme, whilst sharing key assumptions. For example, most dual process models assume that familiarity operates faster than recollection, but models differ in specifications of the exact relationship between recollection and familiarity at retrieval. Knowlton (1998) describes three potential relationships that could exist between familiarity and recollection at retrieval: exclusivity, redundancy or independence. Firstly, an exclusive relationship between familiarity and recollection posits that either process can result in retrieval, but that familiarity and recollection do not co-occur. Secondly, a redundancy view posits that recollection can only be active when familiarity is also active, and finally, the last view of the relationship between familiarity and recollection assumes that both processes contribute to retrieval independently.

A number of distinct variants of dual-process theory exist within the episodic memory literature. For example, a slightly alternative view of the relationship between familiarity and recollection is suggested by the conditional search model proposed by Atkinson and Juola (1974). The conditional search model differentiates familiarity and recollection based on the type of information that each process is thought to handle; familiarity is described as a fast acting process that assesses the degree of perceptual match between the current item and stored representations, while recollection is described as an effortful process that matches semantic information. Importantly, the model proposes that familiarity reflects the default process for recognition and that the occurrence of recollection is contingent upon the failure of familiarity, which does not fit neatly within the exclusivity, redundancy or independence view of the relationship between familiarity and recollection. While the conditional search model proposes that familiarity

and recollection operate in a serial fashion, with familiarity being completed prior to initiation of recollection, the remaining models largely assume that familiarity and recollection operate independently and are initiated in parallel at retrieval (Jacoby, 1991; Mandler, 1980; Yonelinas, 1994).

While most dual-process models are generally in agreement on a number of key issues (for example, that familiarity is faster than recollection and that both processes are initiated in parallel at retrieval) there are also key differences that continue to be controversial. Importantly for the aims of the current thesis, some dual-process theories suggest that common processes may underlie both familiarity in recognition memory and priming on implicit memory tests (see Jacoby & Dallas, 1981; Mandler, 1980). This suggestion will be discussed in more detail in Section 1.3.2, where evidence supporting interactions between priming and familiarity will be presented. The following sections will introduce the details of methods applied to measure the contribution of familiarity and recollection, before reviewing the behavioural and neural evidence supporting the existence of dissociable retrieval processes in recognition memory, on which dual-process models of recognition have been based.

Measuring familiarity and recollection

Standard old/new recognition tests (see Section 1.2.1) do not allow direct identification of the contribution of familiarity or recollection. As a result a number of methods have been developed to either isolate the contribution of one process, or to estimate the contribution of each process to retrieval. Task dissociation methods are applied to isolate a single retrieval process. For example, comparisons of item and source recognition have been used in the literature to isolate recollection, based on the dual-process assumption that only recollection supports the

retrieval of contextual information. However, recent evidence demonstrating that under certain circumstances familiarity can support associative recognition (e.g., Diana, Yonelinas & Ranganath, 2008), suggests that isolating the contribution of recollection in this way is not straightforward. In fact, examination of all methods applied to estimate the contributions of familiarity and recollection reveals limitations in each approach. The remainder of this section will introduce and critique three prominent methods that have been applied to measure the contribution familiarity and recollection; the ‘Remember/Know’ (RK) procedure, the ‘Process Dissociation Procedure’ (PDP), and ‘Receiver Operating Characteristics’ (ROC).

The RK procedure differentiates familiarity and recollection based on subjective reports of qualitative differences in memory experience at retrieval (Tulving, 1985b). In addition to making an old response, participants are required to introspect about their recognition response, and make a ‘remember’ response when retrieval is accompanied by contextual details. In contrast, a ‘know’ response is made when an item feels familiar but is not accompanied by the retrieval of contextual information about the study episode (e.g., Gardiner, Java & Richardson-Klavehn, 1996; Rajaram, 1993). One problem with the RK procedure is that responses are exclusive; items are only classified as familiar when not subsequently recollected, leading to an underestimation of the contribution of familiarity if both processes are assumed to be independent as suggested by most dual-process models. Yonelinas and Jacoby (1995) introduced the Independence Remember/Know (IRK) procedure to address this issue, which estimates familiarity by dividing the proportion of actual ‘know’ responses by proportion of possible ‘know’ responses (see Chapter 4, Section 4.5).

Another criticism of the RK procedure is that RK responses could merely capture differing degrees of memory strength rather than identifying qualitatively different memory processes, in line with single-process interpretations of recognition (e.g., Donaldson, 1996; Eldridge, Sarfatti & Knowlton, 2002). In addition, the RK procedure is highly dependent upon the accuracy of introspection, and although results from the RK procedure are largely in agreement with those obtained using other methods of estimation, it should be noted that the procedure is highly dependent on the nature of the task instructions used and can vary across participants or studies. The basic RK procedure has also been modified to include a third response option to filter out trials where participants have guessed that an item was studied, which is thought to largely contaminate estimates of familiarity (Gardiner, Ramponi & Richardson-Klavehn, 1998). An alternative modification to the RK procedure involves measuring familiarity and recollection in two separate conditions where instructions are varied to isolate each process (Montaldi, Spence, Roberts & Mayes, 2006). In the familiarity condition participants are not instructed to attempt to recollect, but to concentrate on feelings of familiarity and merely report recollection when it occurs. However, distinct disadvantages with this approach are that it fails to capture interactions between familiarity and recollection, and that memory experience cannot be assessed on a trial-by-trial basis, which is considered to be one of the key advantages of the RK procedure.

Another method commonly used to estimate familiarity and recollection is the PDP method developed by Jacoby (1991), which also relies on the premise that if an event is recollected, specific details of the event should be available (for example, when and where it was studied) and that familiarity should not show this pattern. The PDP method uses comparisons of performance across inclusion

and exclusion tasks to separate the contribution of familiarity and recollection. For example, in Jacoby's original experiment participants first studied a list of visually presented items and were then asked to listen to a second list of items. In the following inclusion task participants were instructed to give a 'yes' (old) response to items that had appeared in either study list, and in the exclusion task participants were asked to make a 'yes' (old) response only to items from the heard list. The basic idea is that in the inclusion condition correct judgements can be based on either familiarity or recollection, whereas in the exclusion task correct responses will be supported by recollection, as participants must also identify the context in which an item was studied. One criticism of PDP concerns the use of differential instructions at test causing differential engagement of familiarity and recollection across conditions. The procedure assumes that recollection will be operative in both the inclusion and exclusion conditions, but task instructions may reduce the prevalence of recollection in the inclusion task leading to a skew in parameter estimates (see Yonelinas, 2002, for a discussion).

Measuring ROCs, overcomes issues related to variability in task instructions by employing a single test procedure. Participants are required to make recognition judgements and are then asked to rate their confidence levels, to assess the impact of the response criterion. It is assumed that recollection should support high confidence responses, whereas the contribution of familiarity should be revealed by low confidence responses. ROCs relate the hit rate of correct recognition to the false alarm rate of incorrect recognition; the graph is plotted as a function of response confidence. The ROCs associated with familiarity and recollection exhibit different profiles; judgements based solely on familiarity produce a ROC that is curvilinear and symmetrical, but the added contribution of recollection causes the ROC to become asymmetrical. By examining the shape of the ROC curve,

researchers can identify the processes contributing to recognition performance. However, supporters of single process theory have argued that two processes are not required to explain the pattern of ROC curves obtained during recognition tests, and that the data can be accounted for in terms of an unequal-variance signal detection model, where the variance of the old distribution is considered to be greater than the variance for the new distribution (e.g., Glanzer, Kim, Hilford & Adams, 1999).

All of the methods described above provide different approaches to separating out the contribution of familiarity and recollection in recognition memory tests. Researchers have generally found that results obtained through one method are confirmed by the corresponding results found using the alternative methods. While a wealth of evidence indicates that familiarity and recollection are independent, it has been claimed that all of the methods used to test their independence actually start out by assuming the result, and this assumption is inherent in all of the methods of process estimation methods reported above. As a result, it has been suggested that behavioural data alone cannot be used to test the independence of the familiarity and recollection; familiarity must be measured to establish its independence from recollection, but it is necessary to assume independence to measure familiarity (Norman & O'Reilly, 2003). It seems therefore that behavioural studies could just be measuring different stages in a single recognition process and to avoid this conclusion it is necessary to provide evidence from other areas of research to truly demonstrate the independence of familiarity and recollection. As such, the following sections will provide a brief review of behavioural and neural evidence supporting dual-process theories of recognition.

Behavioural dissociations

Behavioural methods have been applied to dissociate familiarity and recollection by manipulating a wide range of variables, and measuring the impact of these different variables on familiarity and recollection. Manipulations that have been found to differentially affect familiarity and recollection include divided attention, response deadlines, processing fluency, forgetting rates and levels of processing. These manipulations can be divided into two broad categories: those that manipulate processing at encoding, and those that manipulate retrieval processing. A wealth of evidence has demonstrated that encoding manipulations influence recollection to a much greater degree than familiarity. For example, dividing attention at encoding has been shown to selectively disrupt recollection (Craik, Govoni, Naveh-Benjamin & Anderson, 1996; Yonelinas, 2001). In addition, manipulations of levels of processing at encoding have demonstrated that deep (semantic) encoding enhances recollection to a greater degree than familiarity (Gardiner et al., 1996; Rajaram, 1993; Toth, 1996; Yonelinas, 2001). Finally, administering benzodiazepines at encoding, which produce temporary amnesia-like memory impairments, also has a greater impact on recollection than familiarity (Curran, Gardiner, Java & Allen, 1993).

A wealth of evidence has also demonstrated that manipulations of retrieval processing can be applied to dissociate familiarity and recollection. For example, studies employing response deadlines at retrieval, where subjects are forced to respond within a specific time limit, have indicated that familiarity is available earlier than recollection, supporting a key assumption of dual-process theories (Yonelinas, 2002). Familiarity has also been shown to contribute to performance earlier than recollection under non-speeded test conditions (Yonelinas & Jacoby,

1994), and the contribution of recollection has been found to increase, while the contribution of familiarity remains constant, over speeded and non-speeded tests (Benjamin & Craik, 2001). The manipulations discussed so far all impact upon recollection, while leaving familiarity relatively unaffected, but manipulations of other variables have been shown to produce the opposite pattern. For example, manipulation of the retention interval between study and test has shown that levels of familiarity decrease rapidly over short retention intervals (i.e., between 8-32 intervening items), while levels of recollection remain consistent over the same period (Yonelinas & Levy, 2002). Importantly, given the aims of the current thesis, manipulations designed to increase the processing fluency of test items also selectively impact familiarity. For example, briefly flashing a word just before the start of a recognition test leads to an increase in familiarity based responses for studied and unstudied items, but does not influence recollection (e.g., Rajaram, 1993; Rajaram & Geraci, 2000).

Overall, there is a wealth of behavioural evidence suggesting that familiarity and recollection are functionally independent, but as noted above, behavioural findings based on process estimation methods generally assume this independence in advance. However, findings from neuropsychological and neuroimaging studies provide additional support for a dual-process independence account of recognition, demonstrating anatomical differences between familiarity and recollection. The following section will provide a brief review of neural evidence indicating that familiarity and recollection are supported by different brain structures, and as such, reflect functionally independent retrieval processes.

Neural dissociations

Neuropsychological studies of patients with impaired memory function have revealed dissociations between familiarity and recollection. For example, organic amnesiac patients can detect that a previously studied item is familiar, but have difficulty recollecting the context in which it was studied (Huppert & Piercy, 1976, 1978). More broadly, selective damage to the hippocampus has been specifically linked to deficits in recollection, while more extensive temporal lobe damage has been found to disrupt both processes, although recollection is always more severely impaired than familiarity (Stark & Squire, 2000). In addition, damage limited to the perirhinal cortex has been shown to selectively disrupt familiarity, while leaving recollection unaffected (Bowles, Crupi, Mirsattari, Pigot & Parent, 2007). In normal populations, studies have revealed age-related deficits in recollection that are proportionate to the age of the participant, while familiarity remains relatively unchanged across the lifespan (e.g., Lakhan & Foundation, 2006). Interestingly, however, this finding has been attributed to deterioration of the frontal lobes, suggesting that they are vital for recollection but not critical for familiarity judgements (despite patient data linking recollection to the hippocampus). Differences in findings between patient and normal populations highlight a key limitation of patient data: that findings may not always generalise to healthy populations.

There are three main reasons driving this potential lack of generalizability of findings from patient to normal populations. Firstly, neuropsychological studies are often carried out on single participants, meaning that individual differences can have a large impact upon the generalizability of results. Secondly, the brain is highly adaptive and may compensate for long-term damage by developing quali-

tatively different neural circuitry to support some of the function that has been lost. Finally, it is often difficult to identify the precise location or extent of the damage in individual patients, which is highly dependent upon the resolution and reliability of functional imaging techniques (e.g., Rempel-Clower, Zola, Squire & Amaral, 1996). Functional neuroimaging, and in particular findings from functional Magnetic Resonance Imaging (fMRI), have demonstrated a difference in the spatial location of neural generators associated with familiarity and recollection in normal populations, supporting the view that familiarity and recollection are dissociable at a neural level (for electrophysiological dissociations see Chapter 3, Section 3.1). Before describing the findings obtained via this technique, a brief overview of the fMRI technique will be provided.

The main advantage of fMRI is that it has high spatial resolution, making it possible to identify specific areas of the brain that are associated with specific cognitive functions, by measuring the haemodynamic responses related to neural activity in the brain. Briefly, neurons require energy when they are active, but they do not have their own reserves, thus the firing of neurons creates a need for more energy. Movement of blood supplies this energy, releasing oxygen to firing neurons at a higher rate than to inactive neurons, and fMRI measures the difference in magnetic susceptibility between oxygenated and deoxygenated blood to locate the firing neurons associated with specific cognitive processes (Ogawa, Kay & Tan, 1990). Studies employing fMRI to examine familiarity and recollection in normal populations are broadly consistent with the findings from patient studies.

For example, Eldridge, Knowlton, Furmanski, Bookheimer and Engel (2000) used fMRI to examine retrieval processes using the RK procedure and found that the hippocampus is essential for the retrieval of detailed episodes indexed by R

judgements, but is not necessary for recognition-based on familiarity. In another study, Henson, Rugg, Shallice and Dolan, (1999) used the same procedure and found a dissociation between the parietal and prefrontal cortices at the time of test: an increase in left parietal activity was found to index recollection, while an increase in prefrontal activity was found to index familiarity in the absence of recollection. It lies beyond the scope of this thesis to cover in detail the vast amount of fMRI data suggesting that familiarity and recollection can be dissociated, but the examples given above support the view that different patterns of brain activation are associated with familiarity and recollection.

The evidence reviewed so far broadly suggests that the hippocampus is essential for recollection but not for familiarity-based recognition. An alternative view of the involvement of the hippocampus in recognition memory comes from computational modelling (albeit based on the findings from patient populations). Norman and O'Reilly (2003) contrasted the role of the hippocampus and the MTL in recognition memory with the complementary learning systems model. In this model the hippocampal component operates via pattern separation: the incoming stimuli are assigned a distinctive pattern to allow differentiation between specific episodes. By contrast, the model proposes that the MTL component assigns similar representations to similar stimuli. When the models were tested independently, the results demonstrated that performance agreed with the data from patients studies. However, when the models were combined and tested, the assumption that familiarity and recollection are independent at retrieval was not supported by the results: the authors found that lesions to the hippocampus caused a comparable deficit in familiarity and recollection. These findings have been taken to suggest that the hippocampus is the storehouse of episodic memory traces, and that both retrieval processes are reliant on access to a single trace.

More recently, Greve, Donaldson and Van Rossum (2010) demonstrated that a computational model of a single memory store accessed by the two independent retrieval processes was consistent with a single-trace, dual-process account of recognition.

1.2.2 Summary

The preceding sections have provided an overview of episodic memory, with a particular focus on theories of recognition memory. Two main theoretical accounts compete to explain the mechanisms involved in recognition memory, but while single-process theories are attractive for their simplicity, they have largely been made redundant by the wealth of evidence supporting a dual-process account of recognition. A number of estimation procedures have been developed to investigate recognition, including the RK procedure, ROC curves and PDP estimates. Consistent results obtained across these methods have demonstrated that recognition is supported by two independent retrieval processes: familiarity and recollection. While process estimation methods have been criticised for assuming independence in order to obtain estimates of familiarity and recollection, convergent results from neuropsychological and functional imaging have supported the view that recognition is supported by two independent retrieval processes, with differing functional and anatomical characteristics.

1.3 Implicit priming

Priming is characterized by the absence of conscious awareness of retrieval from memory, and is indexed by changes in speed, bias or accuracy of stimulus pro-

cessing as a result of prior exposure to the same or a related stimulus (Graf & Schacter, 1985). Research has identified the existence of multiple forms of priming, but these forms can generally be divided into two main categories: perceptual and conceptual (Roediger & McDermott, 1993). Perceptual priming is driven by a match in the surface features of a repeated stimulus (e.g., letter case or modality), whereas conceptual priming is driven by shared aspects of stimulus meaning (e.g., category membership or frequent co-occurrence). Perceptual and conceptual forms of priming have both been shown to be preserved in amnesiac patients on implicit memory tasks (Vaidya, Gabrieli, Keane & Monti, 1995). In healthy populations, specific factors have been shown to differentiate between perceptual and conceptual forms of priming. For example, dividing attention at encoding influences conceptual priming but has no impact on perceptual priming (Mulligan & Hartman, 1996). It is important to note that perceptual and conceptual forms of priming are differentiated in the behavioural literature largely on the basis of task requirements (i.e., reliance on stimulus form vs stimulus meaning), but this does not rule out the possibility that both forms can contribute concurrently to performance during recognition testing. Traditionally, tasks most commonly used to investigate perceptual priming include lexical decision, perceptual identification and word stem completion, whereas conceptual priming has been assessed using word association and category generation tasks amongst others (see Roediger & McDermott, 1993, for further examples).

During perceptual identification tasks participants are often briefly exposed to a stimulus (e.g., for around 35ms) and have to try to identify the presented item (e.g., Jacoby & Dallas, 1981). On this task priming is indexed by a reduction in the amount of time taken to identify the item, or an increase in the accuracy of identification for presented relative to new items. On word completion

tasks participants are normally presented with a list of study words, followed by a list of word stems (e.g., squ_____ for squirrel) or word fragments (e.g., e__ph___ for elephant), and have to complete the stems or fragments with the first word that comes to mind (e.g., Roediger, Weldon, Stadler & Riegler, 1992). Priming on these tasks is indexed by an increase in the probability that stems will be completed with words from the initial study list. On word association tasks participants again study a list of words and then during the test phase are presented with a cue word related to a study item (e.g., cat-? after studying dog), and are required to provide the first related word that comes to mind (e.g., Shimamura & Squire, 1984). The current thesis aims to obtain concurrent measures of priming and recognition within the confines of a standard recognition task, and so further discussion of these priming specific tasks will be limited to a review of the evidence demonstrating the nature of priming related phenomena (see Schacter, 1987; Wagner & Koutstaal, 2002, for reviews).

Of particular interest within the current context are “repetition priming” experiments where prime-target pairings are presented separated in time, and the prime item serves to establish processing context for the upcoming target. The nature of the relationship between prime-target pairings can be manipulated, such that pairings may be semantically related (e.g., whale-dolphin), associatively related (e.g., fruit-fly), or full repetitions (e.g., garden-garden), which can then be compared to a baseline condition where prime and target items are unrelated (e.g., tree-radio) to establish the influence of different varieties of priming. The current thesis employs repetition priming to explore interactions between priming and explicit recognition, as this sort of priming would normally occur under standard recognition test conditions, where items are repeated across study and test phases. It is important to note for the purposes of this investigation that repe-

tition from study to test and between prime-target pairings means that priming could be perceptual or conceptual in nature. Initially, repetition primes were thought to provide a measure of the degree of perceptual priming (e.g., Tulving & Schacter, 1990), but more recently it has been appreciated that repetition can also produce conceptual priming, particularly when the stimuli involved are words (Voss, Schendan & Paller, 2010b), as is the case in the experiments reported in this thesis. The following section will provide an introduction to repetition priming, including an overview of the evidence and a brief description of theoretical accounts.

1.3.1 Repetition priming

Evidence related to repetition priming comes from two broadly independent areas of research: investigations concerned with the nature of lexical organization in word identification, and investigations of episodic memory (Schacter, 1987). Early evidence from word identification research suggested that repetition priming was largely supported by a perceptual representation system that operates on information about the physical features of a stimulus, but does not support access to meanings or associations between items (e.g., Schacter, 1990; Tulving & Schacter, 1990). This assertion was driven by a wealth of evidence demonstrating that priming is reduced by changes in modality (e.g., visual to auditory) or surface features (e.g., font) between study and test on data driven tasks such as word stem completion and perceptual identification (e.g., Jacoby & Dallas, 1981; Kirsner, Dunn & Standen, 1989; Roediger & Blaxton, 1987). A number of competing accounts have been proposed to account for the structure of repre-

sentations supporting word identification, which can be broadly divided into two categories: abstract lexical representations and episodic representations.

Strict abstractionist theories assert that distinct representations are formed for episodes and lexical entries, such that each word is assigned a separate abstract representation in the lexicon, which does not contain a reference to prior experience (e.g., Morton, 1969). By contrast, episodic theories assert that word identification relies on reference to specific episodes where they have been encountered previously (e.g., Jacoby & Witherspoon, 1982; Kolers & Roediger, 1984). On both views, the same representation is used to access unprimed and primed words, with recent activation of a lexical entry or a specific episodic representation producing facilitation effects for repeated items, but debate continues over which view best accounts for the wealth of data (see Bowers, 2000; Tenpenny, 1995, for discussions). In broad terms, these alternative accounts of representation have been developed to account for qualitatively different types of repetition priming observed across a range of tasks. For example, evidence draws a distinction between short-term priming effects lasting only a few seconds, and long-term priming effects that can persist for minutes, hours or even days (e.g., Rajaram & Neely, 1992).

Abstractionist views are consistent with activation accounts of repetition priming, which assert that exposure to a word produces a temporary short-term increase in the activation of a pre-existing abstract representation, lowering the threshold for subsequent access to the same entry producing facilitation (Morton, 1969), but that this temporary increase in activation decays gradually over time (McClelland & Rumelhart, 1981). Pure activation accounts of priming waned in popularity because they were unable to account for the reduction in priming induced by changes in modality or surface features from study to test, and cannot account

for long-term priming effects that persist over longer delays (Wagner & Koutstaal, 2002). While the specificity of priming effects can be readily explained by appeal to facilitation based on access to specific episodic representations, this view has been criticized for failure to account for short-term priming effects, particularly when the presentation of the prime is rapid or subliminal.

Over the last few decades there has been an increase in the use of masked priming paradigms to assess the contribution of repetition priming. Masked priming studies involve a very brief presentation of the prime item, which is obscured by the presentation of a pattern mask occupying the same visual space before and/or after the presentation of the prime; in the strongest cases prime items are usually surrounded by forward and backward masking for optimal concealment. These pattern masks usually take the form of a series of letters or symbols matched to the length of the prime item. The key benefit of this approach is that participants are usually unable to report the presence of the prime, making it possible to measure its contribution to performance on a variety of tasks in the absence of explicit engagement. Traditionally, masked and unmasked priming were thought to engage differential forms of repetition priming: masked priming was largely associated with short-lived facilitation effects as a result of repeated access to lexical entries, while unmasked priming was associated with long-term priming effects and linked to recognition memory (Forster & Davis, 1984).

More recently, it has been suggested that repetition priming may be considered a form of episodic learning, where presentation of a prime item induces changes in connection weights, or adds a distinct event to episodic memory (Bodner & Masson, 2001). But the problem remains of how to account for masked repetition priming, where prime episodes are not accessible via conscious awareness. Bodner and Masson (1997) asserted that masked primes can result in the creation of rep-

representations of specific episodes based on orthographic information, without the need for conscious accessibility. Moreover, Masson and Bodner (2003) have proposed a retrospective (retrieval based) account of masked and long-term repetition priming, based on the assumption that prime events create a memory resource, which aims to provide a framework for integration of findings from word identification and memory research, by collapsing dissociations between short-term and long-term priming. In addition, functional imaging work has supported the view that dissociations between supraliminal long-term and subliminal short-term masked priming are unwarranted, demonstrating that both forms of priming result from the same underlying processes, activating the same brain structures but to a lesser degree for masked compared to unmasked words (Dehaene et al., 2001). In reality, it is likely that lexical access and episodic theories of repetition priming are not mutually exclusive, and whether facilitation is driven largely by enhanced lexical or episodic access may be partially determined by task demands.

Evidence demonstrating that changes in surface features produce reductions in priming on data-driven tasks such as fragment completion or perceptual identification is often cited in support of a perceptual representation system account of priming, but can be challenged on the basis of task demands. For example, Graf and Ryan (1990) manipulated the font of words between study and test, finding reduced priming on word stem completion when the study task focused on perceptual features, but also finding that this reduction was eliminated when the study task focused on word meaning. This finding is in line with transfer-appropriate processing accounts of repetition priming, which assert that the magnitude of priming effects on a specific task are dependent upon the degree of match between cognitive processes engaged during an initial encounter with an item, and processes engaged during a subsequent encounter (Wagner & Koutstaal, 2002).

Interestingly, this account of repetition priming mirrors the encoding specificity principle in episodic memory, which states that memory for events is optimal when contextual information present during encoding is also available at retrieval (Tulving & Thomson, 1973), providing further support for an episodic representation view of repetition priming.

The transfer-appropriate processing account differentiates data-driven and conceptually driven contributions to repetition priming on the basis of task demands, but if the underlying representation is primarily episodic in nature, changes in contextual aspects between an initial encounter and a subsequent encounter should also lead to a reduction in repetition priming. Masson and Freedman (1990) demonstrated in a lexical decision task that repetition effects were reduced when the meaning of context words accompanying a repeated item was changed from study to test (see also Masson & Macleod, 1992). These findings demonstrate that repetition priming is also sensitive to conceptual aspects of a prior exposure, even when the task is primarily data-driven and perceptual in nature. In addition, differences in the time course of perceptual and conceptual contributions to data-driven tasks have been observed. For example, Weldon (1993) demonstrated that the impact of changes in surface features on priming in word fragment completion were diminished by increasing the allotted response time, and asserted that perceptual and conceptual processes may in fact contribute to word stem completion in a serial fashion.

It lies beyond the specific aims of the current thesis to differentiate between different views of how priming is supported by underlying representations, or to separate out the contribution of perceptual and conceptual aspects of repetition priming. For the current purpose, it is merely important to note that repetition priming within the confines of a standard recognition task may result from a

combination of any, or all, of these factors. However, the preceding discussion of repetition priming does provide some reasons to think that episodic memory and priming phenomena may be very closely related. The following section will introduce behavioural and neuropsychological evidence supporting the view that common processes may underlie both priming and recognition, before going on to describe the nature of potential relationships between priming, familiarity and recollection.

1.3.2 Recognition and priming

Some dual-process theories suggest that common processes may underlie recognition memory and priming on implicit memory tests (Jacoby & Dallas, 1981; Mandler, 1980). One line of evidence that supports the view that priming can influence recognition performance comes from studies investigating the impact of processing fluency. The notion of processing fluency refers to the subjective experience of the ease with which information is processed, and it has been shown to exert an influence on reasoning and judgement across a broad range of dimensions (for a review see Alter & Oppenheimer, 2009). For example, words presented in a font that makes them easy to read are subsequently rated as more familiar than those presented in a difficult font (Reber & Zupanek, 2002). In essence, any factor that makes items easier to process, results in a subjective experience of fluency, which in turn influences judgement independently of the actual content of cognition (Schwarz et al., 1991).

Before introducing evidence supporting the view that fluency induced by priming contributes to recognition, it is necessary to provide a brief overview of one method that is employed to capture the contribution of priming within the con-

finer of a standard recognition task. Repetition of items from study to test during recognition testing means that all studied items are potentially primed, making it impossible to separate out the respective contributions of priming and recognition memory. Employing masked priming during the test phase of a standard recognition task facilitates assessment of the contribution of priming in the absence of explicit engagement. Masked priming involves very brief presentation of prime items, which are obscured by the presentation of a pattern mask occupying the same visual space before and/or after the presentation of the prime. Comparison of old and new items preceded by either a matching or unrelated prime at test facilitates separation and comparison of the respective contributions of priming and recognition memory.

In the context of explicit memory experiments, fluency induced by masked priming increases the probability that a primed item will be classified as studied at test, irrespective of whether the item was actually studied, producing an increase in hit and false alarm rates. Response bias accounts of priming, based on signal detection theory, have been proposed to explain the impact of fluency in recognition tests, and assert that fluency induces a more liberal bias (e.g., Ratcliff & McKoon, 1996; Thapar & Rouder, 2001). As noted above, priming can operate on many levels of representation, facilitating performance based on an increase in fluency at orthographic, phonological, lexical or semantic levels (for a review see Alter & Oppenheimer, 2009). A growing body of evidence supports the view that fluency signals induced by different forms of priming can contribute to explicit recognition (e.g., Cleary, 2004; Jacoby & Whitehouse, 1989; Parkin et al., 2001; Westerman, Lloyd & Miller, 2002; Westerman, Miller & Lloyd, 2003; Whittlesea, Jacoby & Girard, 1990), and the remainder of this section will provide an overview of the evidence to date.

In an early behavioural study that has set the tone for research in this area, Jacoby & Whitehouse (1989) employed masked priming during an explicit recognition test, where the prime was either a repetition of the upcoming target (primed) or a different word (unprimed), and contrasted conditions where participants were aware or unaware of the presence of the prime. The authors found that the probability of an old judgement to the target word when it matched the preceding prime was increased when participants were unaware of its presence, but when participants were made aware of the presence of the prime this pattern of bias was reversed. These findings were interpreted as a misattribution of fluency created by masked repetition to the study phase when participants are unaware of the source of fluency. Moreover, the findings were taken as further support for the view that attribution of processing fluency to a prior encounter leads to the feeling of familiarity (see also Jacoby & Dallas, 1981; Jacoby & Kelley, 1987).

In line with this early study, the bulk of the evidence to date supports the view that fluency manipulations selectively impact familiarity (e.g., Rajaram, 2000; Miller, Lloyd & Westerman, 2008; Woollams, Taylor, Karayanidis & Henson, 2008). For example, Rajaram and Geraci (2000) demonstrated using the RK procedure that presenting test items in a semantically appropriate context increased familiarity but had no effect on recollection. More recently, it has been claimed that procedures used to estimate the contribution of familiarity and recollection may prevent detection of the impact of fluency manipulations on recollection (Higham & Vokey, 2004), particularly in studies employing a standard RK procedure (see Chapter 6 Section 6.1, for discussion of these issues). Some recent evidence supports this view, demonstrating that fluency manipulations can also increase the proportion of illusory recollection (e.g., see Kurilla & Westerman, 2008; Brown & Bodner, 2011).

One undesirable aspect of the findings reported above is that it is difficult to see how priming can be classified as an implicit memory phenomena *per se*, given that fluency manipulations of this sort demonstrate an increase in the proportion of illusory recognition as well as an increase in the hit rate, reducing discrimination. This difficulty can be alleviated by claiming that priming manipulations of this sort encourage reliance on fluency driven by facilitated access to abstract lexical representations of test items, rather than episodic representations. Despite this objection to the preceding evidence, there is tentative evidence to support the view that recognition on some occasions can proceed in the absence of awareness, leaving open the possibility of accurate implicit recognition that may be driven by repetition induced fluency. For example, Voss, Baym and Paller (2008) employed kaleidoscope images that were difficult to verbalize, and an attentional manipulation at encoding in a two-alternative forced choice recognition test with similar foils. The findings demonstrated that recognition was enhanced under divided attention and that highly accurate recognition (80%) at test occurred in the absence of introspective awareness of explicit retrieval. Overall, therefore these findings can be taken as support for the view that implicit recognition, based on repetition-induced perceptual fluency, can contribute to performance under certain circumstances, Importantly however the existing evidence does not provide unequivocal evidence of interactions between priming and explicit memory.

1.3.3 Summary

The preceding sections have provided a brief introduction to different forms of priming, including a description of the tasks employed to measure different varieties of priming. As the current thesis employed repetition priming, a selective

overview of the evidence and a brief description of theoretical accounts of repetition priming was then provided, before focusing on evidence demonstrating that priming can influence performance on tests of explicit recognition. Further discussion of potential relationships between priming and recognition will be postponed until after a comprehensive introduction to one specific method that has greatly contributed to their discovery - Event-Related Potentials (ERPs).

Chapter 2

Event-Related Potentials

ERPs provide a direct measure of neural activity related to a specific event and are derived from EEG (electroencephalogram), which measures the electrical activity generated by the brain from electrodes placed on the scalp (Coles & Rugg, 1995). ERPs are constructed by averaging together sections of the EEG, which are time-locked to an event, usually the presentation of a stimulus. Averaging the EEG reduces background noise and reveals the signal of interest, the ERP, which provides an index of processing related to that specific type of event. An individual ERP is a waveform showing voltage changes over a specified period of time (an epoch); in practice average waveforms are produced for multiple events of interest and then compared and analysed. By allowing comparisons between different experimental conditions, ERPs allow researchers to isolate and study the cognitive processes associated with performance on a specific task. In comparison to fMRI and PET, the spatial resolution of ERPs is poor because it is difficult to identify precisely which regions of the brain are active during processing (Luck, 2005). In contrast ERPs are particularly useful for assessing the timing of cognitive processes, providing millisecond temporal resolution. This chapter provides

a general introduction to the ERP technique from the generation of electrical fields in the brain, to recording, processing and analysing the the signal, followed by detailed discussion of the inferences that can be drawn from the resulting ERPs.

2.1 Neural origins

To gain a full understanding of the benefits and limitations of the ERP technique it is important to understand the neural origin of the signal recorded at the scalp. The electrical activity that comprises the electroencephalogram is mostly generated by underlying neural activity; however the structure of the brain and the orientation of neurons play a critical role in determining the activity that can be detected at the scalp. The following sections outline some of the key factors determining the nature of activity that can be detected by electrodes placed on the surface of the scalp.

2.1.1 Electrogenesis

Electrogenesis is the production of electrical fields from the activity of single neurons or populations of neurons in the brain. This section will describe the way in which individual neurons generate these electrical fields, before moving on to discuss limitations imposed by measuring these signals from the surface of the scalp. Figure 2.1 shows the basic structure of a typical neuron containing a cell body (soma), dendrites and an axon. Neurons are electrically excitable cells that communicate via electrical and chemical signals exchanged across a synapse, where these signals are passed from the axon terminals of the presynaptic cell

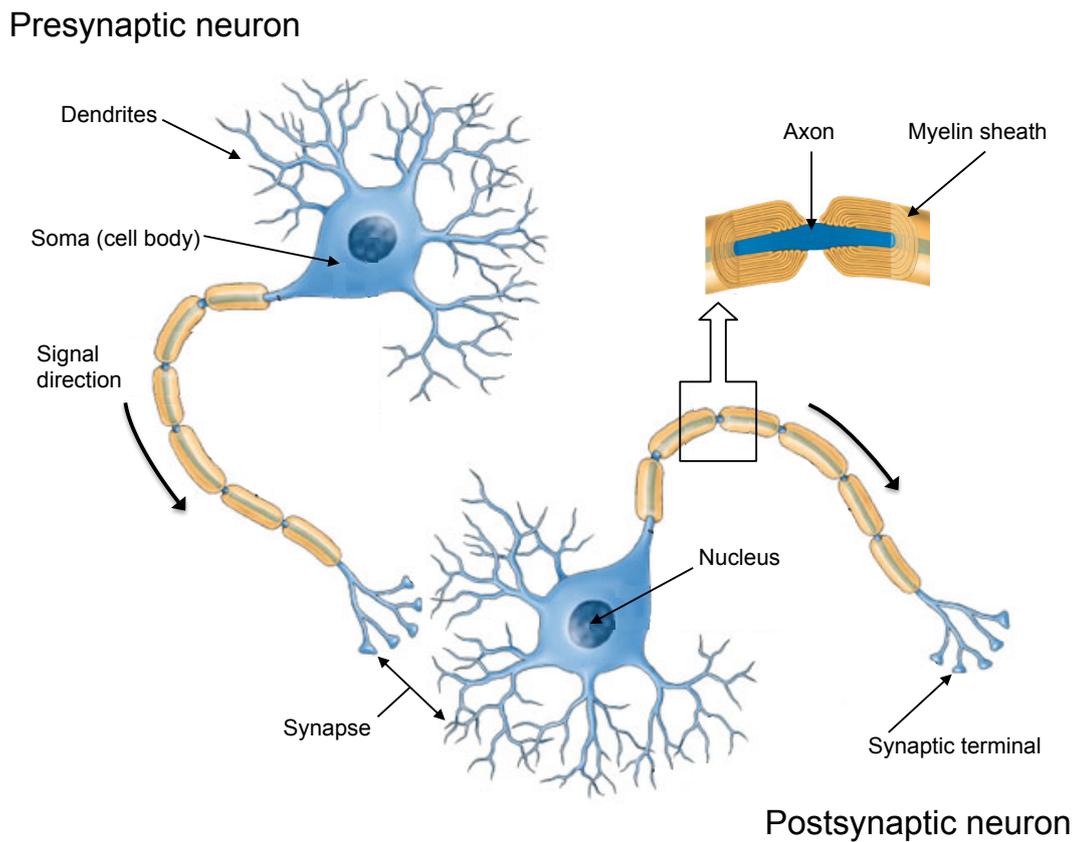


Figure 2.1: Neuron structure. Neurons comprise of a cell body, nucleus, dendrites and axon. Incoming activation is passed to the cell body via dendrites, the cell body generates an action potential that is transmitted along the axon to the synaptic terminals (adapted from Morris & Maisto, 2002).

to the dendrites of the postsynaptic cell. Action potentials play a central role in this cell-to-cell communication and are generated by voltage-gated ion channels embedded in the cell membrane. The cell membrane serves as a barrier between intracellular and extracellular fluids, controlling the flow of ions in and out of the cell, and this flow of ions determines the difference in voltage between the inside and the outside of the cell.

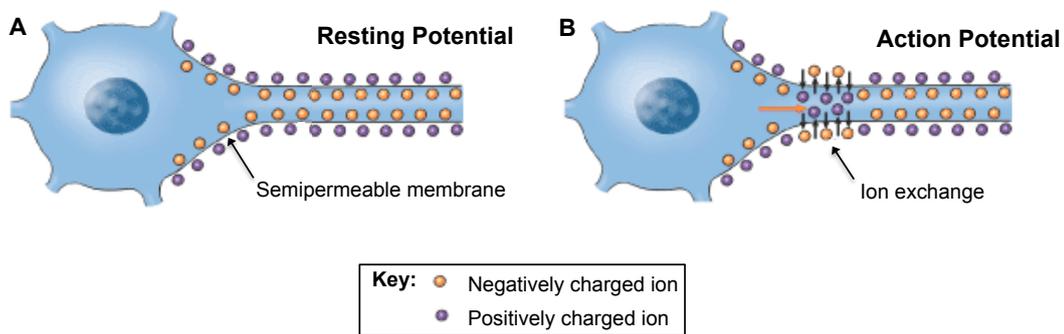


Figure 2.2: Communication within a neuron. A: Neuron in resting state with negatively charged ions in intracellular fluid. B: Excitation above threshold at the axon hillock opens ion channels creating depolarization (adapted from Morris & Maisto, 2002).

Figure 2.2 shows the resting and action potentials in an individual neuron. In resting state, separation of positive and negative charges by the cell membrane maintains an electrical potential of around -70 mV, driven by ion pumps which ensure that the concentration of positively charged sodium ions is maintained at a low level. An action potential is a rapid fluctuation of up to 100 mV in electrical potential across a cell membrane, that lasts in the order of 1 ms, before the membrane returns to resting state. When the threshold of excitation (around -55 mV) is exceeded at the axon hillock an action potential is produced, sodium channels open and allow sodium ions to enter into the negatively charged intercellular fluid. The action potential triggers a chain reaction, voltage changes in one area of the neuron will elicit changes in nearby areas, allowing the electrical current

to propagate along the axon to the synaptic terminals. When an action potential reaches the synapse, opening ion channels allow an influx of calcium ions, driving the release of neurotransmitters. These neurotransmitters bind to receptors on the postsynaptic cell and the opening of ion channels trigger postsynaptic potentials. Action potentials are intracellular, producing transfer of information within a single neuron, whereas postsynaptic potentials are extracellular and represent transfer of information between neurons.

While it is possible to measure action potentials directly using single-unit recordings, where micro-electrodes are inserted into the brain, these changes in potential are not generally measurable at the scalp. Basically, the parallel orientation and lack of exact synchrony of firing across neurons entails that action potentials are likely to cancel each other out, producing a signal that is too weak to be reliably detected by scalp electrodes (Luck, 2005). In contrast to action potentials, postsynaptic potentials are present in the dendrites and cell body and occur instantaneously, lasting up to hundreds of milliseconds. Specific spatial alignments of neurons allows summation of postsynaptic potentials, which can then be recorded at the scalp and this will be discussed in the following section.

2.1.2 Neural activity at the scalp

When an action potential reaches the dendrites of a postsynaptic cell, positive current flows into the dendrites, generating negativity in the extracellular fluid. This negativity causes current to flow out of the cell body, creating positivity at the cell body. Negativity at the dendrites and positivity in the cell body form a small dipole, which represents the sum of inputs to an individual neuron, rather than its output. The dipole produced by a single neuron is not measurable at the

scalp, but when synaptic input to thousands of neurons is similar and they share a specific orientation, the dipoles of these populations sum together, producing strong voltage signals at the scalp. The main determinants of the strength of measurable dipoles are the distance from the scalp and the relative configuration of the active neurons (Allison, Wood & McCarthy, 1986). It is important to note for the purposes of interpretation that there is neural activity that cannot be picked up at distance from the scalp.

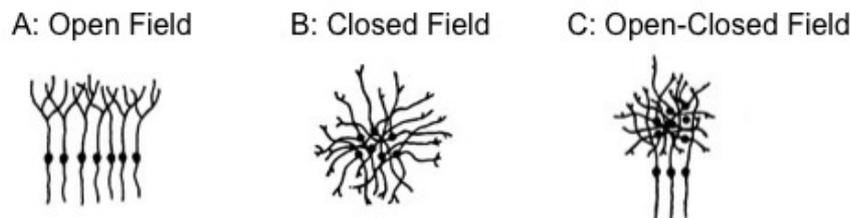


Figure 2.3: Orientation of neural populations. In an open field (A) cells are aligned in parallel allowing summation. In a closed field (B) cells are randomly oriented and have a tendency to reduce or cancel out the signal. Open-closed fields (C) fall somewhere between these orientations and can be activity dependent (adapted from Allison et al., 1986).

Figure 2.3 shows the possible orientations of populations of neurons. When neurons are aligned in parallel such that the positive and negative sides of the dipoles are oriented in the same direction, this is known as an open field and the effects will sum together to produce a relatively strong dipole. By contrast, where neurons are randomly oriented this is known as closed field. When cells are oriented more than 90 degrees with respect to each other the signal will be reduced, cancelling out completely at an orientation of 180 degrees (Luck, 2005). In reality the orientation of the cells will be somewhere between these two states, known as open-closed fields. Importantly, even a fixed set of neurons will produce different voltage patterns at the scalp depending on the activity of the individual neurons involved.

Some brain structures, such as the cerebral cortex, contain neurons that support summation of their electrical activity, sharing the same orientation and running perpendicular to the surface of the cortex. However, other structures, such as the cerebellar cortex, contain orientations of cells that make it difficult or near impossible to detect activity at the scalp (Luck, 2005). Reliance on summation to measure potentials from distant scalp electrodes determines that only a certain proportion of neural activity is detectable by EEG and it should also be clear that the absence of a difference in activity across experimental conditions does not necessitate that differences do not exist, it merely implies that they may not be measurable at the scalp (Coles & Rugg, 1995). In addition to these considerations of synchrony and orientation, the conductive properties of the brain and skull also impact the ability to accurately identify the spatial location of neural activation with scalp electrodes.

Electrical activity from dipole sources reaches the scalp because the brain, skull and scalp act as volume conductors. The skull is a less efficient conductor than brain tissue, however, leading to attenuation and spreading of potentials over the scalp (Koles, 1998). As a result it is difficult to identify the precise source of neural activation present at the scalp, which could be the result of a number of different underlying intracerebral sources. This uncertainty about the origin of the neural signal is known as the “inverse problem”, making ERPs less than ideal for establishing the anatomical structures involved in cognition. Despite this limitation, the distribution of ERP effects can still provide useful information, based on the assumption that two or more functional states cannot be associated with the same underlying physical state, which entails that the same functional state is not described by qualitatively different patterns of neural activity (Rugg & Coles, 1995). When experimental manipulations produce differences in topographic dis-

tribution, this can either reflect the engagement of different sets of neural generators, or that the same neural generators are engaged but to a different degree. It is also important to note that the absence of topographic differences does not exclude the possibility that the generators differ across conditions, it merely implies that the difference was not detectable at the scalp.

2.2 Recording ERPs

The preceding sections have described how neural activity produces changes in electrical fields in the brain and how this electrical signal propagates to the scalp. In the following section, procedures for recording these potentials will be described. The term voltage refers to the difference in electrical potential between two different points in an electrical field and ERP waveforms are a measurement of this difference between an active and a reference electrode plotted as a function of time. The recording of variation in voltage over time is called the electroencephalogram (EEG) and its amplitude varies between $\pm 100 \mu\text{V}$, with a frequency range up to 40 Hz or more (Coles & Rugg, 1995). In addition to an active electrode and a reference electrode, a ground electrode is also used, to separate background noise from the brain activity of interest. In the simplest recording, an active electrode would be positioned at the location of interest, a reference electrode would be positioned at a different location and a ground electrode could be positioned anywhere on the participant's head or body. Activity picked up at the ground electrode is eliminated by subtraction, leaving only the voltage between the active site and the reference point. Memory experiments generally employ somewhere between 16 and 128 active electrodes, all referenced

to a single electrode location. Before discussing placement of the reference, a brief description of active electrodes and their positioning will be provided.

2.2.1 Active electrodes

Scalp electrodes are small conductive metal discs attached to a wire and are normally made out of silver and have a thin silver-chloride coating (Ag/AgCl). The choice of material is driven by the need to have a metal that does not lose conductance quickly (via corrosion) and that minimises attenuation of low frequency signals (Luck, 2005). Electrodes are connected to the scalp indirectly via a conductive gel, which maintains the integrity of the signal recorded at each electrode over time. As a general rule, current flows along the path of least resistance. As a result it is critical that impedance (impediment to current flow) between the scalp and each electrode site is stable and kept to a minimum to reduce the risk of contamination from environmental noise. To achieve this the surface of the scalp is gently abraded to remove the outer layer of dead skin cells at each electrode. In the experiments reported in this thesis, impedance was reduced to below $2\text{ k}\Omega$ prior to the start of each recording phase.

To investigate the topography of ERP effects across the scalp it is necessary to record from a montage of active electrodes. The most common system for the placement and nomenclature of electrodes is the 10/20 system (Jasper, 1958). The 10/20 system assumes that the skull is symmetrical and uses cranial features to locate electrodes on the scalp (see Figure 2.4). Basically, the measured distances from nasion to inion, and between the preaurical points in front of the ears, define latitudinal and longitudinal lines across the scalp. To ensure maximal coverage, electrodes are positioned at 10% and 20% points with respect to

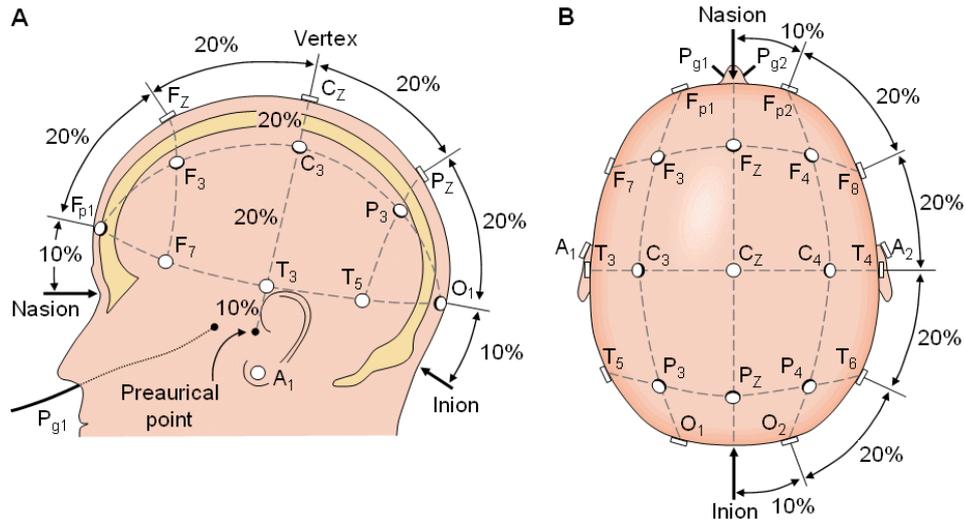


Figure 2.4: International 10/20 system. Electrode placement shown from the left (A) and above the head (B). Electrodes are positioned at 10% and 20% points with respect to latitudinal and longitudinal contours (adapted from Sharbrough et al., 1991).

these latitudinal and longitudinal contours. Advances in EEG hardware have led to an extension of this system to accommodate a larger number of electrodes, positioned at 10% points in the spaces between contours in the standard configuration. This extended version of the 10/20 system was used to record all of the data reported in this thesis. As well as defining electrode placement, the 10/20 system also provides standard naming conventions for electrodes. Each electrode is labelled with a letter that refers to location and a number to denote hemisphere. For example, in Figure 2.4 the letters F, T, C, P and O represent Frontal, Temporal, Central, Parietal and Occipital locations, even numbers denote the right hemisphere and odd numbers denote the left hemisphere, while the letter 'z' is used to label midline electrode sites.

2.2.2 Reference electrodes

As mentioned above, ERP waveforms are a measurement of the difference between active sites and a reference electrode. When recording from a montage of active electrodes, it is crucial to use a common reference point so that it contributes equally to active electrodes, ensuring that the differences between active sites will be informative (Dien, 1998). Ideally, the chosen reference site should be as neutral as possible to avoid introducing bias to the recording, although it is important to note that no reference point can really be considered electrically neutral, regardless of its distance from the head. As a result it is best to choose a site that is convenient and comfortable for the subject and that is not biased toward one hemisphere (Luck, 2005). It is common practice in memory research to place reference electrodes on the mastoid protrusion behind both ears (avoiding a hemispheric bias). This is known as a ‘linked mastoid’ reference. In practice, physically linking the left and right mastoids with a wire can distort the distribution of voltages and can reduce true hemispheric differences. As a result data are often recorded referenced to the left mastoid and then re-referenced offline using the average of the left and right mastoid sites. All of the data reported in this thesis have been referenced in this way to avoid the aforementioned issues and to allow comparison with previous memory research.

2.2.3 Amplifying, digitising and filtering

Modern research requires collection of huge amounts of data that must be digitised to allow the data to be processed and stored by computers. The raw analogue signal is amplified and transformed into a multi-level digital signal, where small changes in amplitude are measured at specific points in time. An Analog-to-

Digital Converter (ADC) samples these voltage fluctuations in the EEG, and it is crucial that the ADC device provides sufficient resolution to avoid distortion of the signal. The resolution (e.g., 12 bits) specifies the number of different voltage values (e.g., 4096) that can be produced over a range of voltages (e.g., $\pm 5V$). A key problem with digitisation is aliasing, which can occur if the signal contains high frequencies and the sampling rate is set too low, introducing low frequency artifacts. To capture all of the analogue signal, Nyquist theorem dictates that the sampling frequency should be at least twice the highest frequency obtained in the signal (Luck, 2005). To further reduce the possibility of aliasing, amplifiers typically include a low pass filter to attenuate arbitrarily high frequencies. High-pass filters are also applied to the data to attenuate low frequencies, which commonly result from gradual voltage shifts caused by skin potentials.

2.3 From EEG to ERPs

Neuronal activity related to the cognitive processing of events produces very small changes in voltage ($5-10\mu V$) and as a result are difficult to distinguish from background noise in the EEG (Kustas & Dale, 1997). Further processing is required to extract the signal of interest from this background noise. Noise in the EEG produced by muscle activity, ocular artifacts, voltage drift, environmental factors and amplifier saturation must all be dealt with to enable reliable identification of ERP effects. It is important to note that post-hoc procedures to correct for sources of noise in the EEG should never be considered a substitute for recording clean data from the outset. Most sources of background noise can be significantly reduced at recording. For example, participants can be instructed to control movements during the epoch of interest, eliminating muscle artifacts at

source. To minimise data loss due to artifacts and to reduce the amount of data correction required, critical trials in the experiments reported in this thesis were self-paced. This allowed participants some freedom to move and blink between trials as required, making them more comfortable over the duration of the experiments, and ensuring that the majority of artifacts would fall outside the epoch of interest. The following section describes the methods used to correct for artifacts remaining in the signal, despite the adoption of good data collection practices, before discussion of the averaging procedure and the signal-to-noise ratio.

2.3.1 Artifact correction

Eye movements and blinks are a major source of artifacts in EEG and distort the signal mainly at frontal electrode sites. While it is possible to ask participants to avoid moving their eyes and blinking during the epoch of interest, participants vary in their ability to control these movements and the task of monitoring them can interfere with brain activity related to the critical task. During recording Electro-Oculogram (EOG) data are collected, measuring the difference in potential between electrodes placed above and below the eye (VEOG) to capture blinks, and between electrodes placed on the outer canthi of both eyes (HEOG) to capture saccades. One way to correct the data would be to inspect these channels and remove trials containing blinks prior to averaging, but this approach would lead to a high rate of trial loss. As a result, most researchers employ EOG correction procedures based on regression techniques to remove the contribution of eye movements.

Correction procedures assume a linear relationship between EOG and EEG and compute regression coefficients for each active electrode, which are then used to

remove a proportion of EOG from each active electrode site. One limitation of this form of correction is that EOG picks up some neural activity alongside ocular activity, which will also be removed from the data (Luck, 2005). If the ERP effects of interest are observed at fronto-polar electrodes, closest to the eyes, it is also possible that this correction procedure may produce artificial data. A regression procedure was employed to correct the data reported in this thesis for ocular artifacts, but this limitation was not considered to be a significant problem due to the locations of the effects of interest. As well as the reduction of ocular artifacts, EEG data are also processed to reduce the effects of other common sources of noise in the signal. Muscle activity, tension and electrical noise from equipment can all introduce high frequency noise to the data, and while the low-pass filter attenuates some of these sources of noise, muscle activity and tension can continue to be a problem. It is common practice to inspect the raw EEG prior to epoching and to reject trials that contain excessive muscle or tension artifacts. In addition to this, epochs can also be systematically checked for artifacts by setting a limit to the amount that active electrodes may deviate from zero. For the experiments reported in this thesis, epochs were rejected when the deflection in the signal was greater than $\pm 100\mu V$.

Voltage drift is another common EEG artifact and refers to a gradual increase in voltage over time, introducing low frequency noise to the signal. A slow drift in voltage can be caused by changes in skin impedance during recording as a result of participants sweating, or when excessive movement results in a change in electrode positions. High pass filtering reduces the extent of drift picked up in the recording, but if still present in the data, drift can obscure the effects of interest. As with muscle activity and tension, epochs can be systematically checked for drift by setting an upper limit which defines when an epoch contains

excessive drift and should be rejected. In contrast to the approach applied to detect muscle artifacts, where epochs are rejected when they differ from zero by a specified amount, drift detection tracks changes in the signal within each epoch, based on the difference in amplitude between the first and last data points. For the experiments reported here, epochs were rejected when drift exceeded $75\mu\text{V}$ over each 2000ms epoch. After epochs containing artifacts have been removed, the data are ready for averaging to form ERPs and the details of the averaging procedure will be described in the next section.

2.3.2 Averaging

EEG that has been corrected for artifacts, as described above, still contains a proportion of background noise and the most commonly used technique for extracting the signal of interest from the remaining noise is averaging. To form ERPs, EEG is recorded over multiple trials time-locked to an event of interest, which is usually the presentation of a stimulus, and then the data are averaged at each time point within the epoch to produce an ERP related to a specific event. Averaging events over a large number of trials improves the signal-to-noise ratio (SNR), resulting in waveforms that provide a clearer view of the signal of interest. In essence, the SNR increases as a function of the square root of the total number of trials contributing to the average, thus adding more trials improves data quality but the benefit of adding trials reduces as the overall number increases. The experiments reported in this thesis used a minimum criterion of 16 artifact trials per participant in each condition to ensure a good signal-to-noise ratio.

Two important assumptions support the signal averaging technique. Firstly, it is assumed that noise present in the signal is random and uncorrelated with the

signal of interest. Secondly, it is assumed that the signal of interest is identical across individual trials (Luck, 2005). In reality, both of these assumptions are rarely supported. For example, it is likely that the signal of interest could be absent on some trials if participants failed to attend to the stimulus presentation. In practice, variability in amplitude across trials does not present a real problem because the pattern of voltage over time is plotted relative to activity over a pre-stimulus baseline (usually 100-200ms), and as a result, differences between conditions can still be considered informative. A more difficult problem to address is a difference in the latency of the signal of interest between trials (known as jitter), which can reduce the amplitude of peaks and distort average waveforms. It is important to note that the onset time of a difference in an average represents the earliest onset time from all contributing waveforms, and may not be representative. The impact of latency jitter can be minimised by using the mean amplitude over a specified time window to perform analyses, provided that the chosen time window captures the entire duration of the effect of interest (Luck, 2005), and this approach was adopted for all ERP analyses reported in this thesis.

2.4 Inferences from ERPs

Once the data have been corrected for artifacts, it must be interpreted in light of the limitations imposed by the recording procedure and the post-hoc corrections applied. A fully processed ERP waveform consists of a series of peaks and troughs, which reflect the summation of underlying components that contribute to processing the event of interest. Detecting components in ERP waveforms relies on the assumption that there is some form of one-to-one mapping between

patterns of neural activity and cognitive functions (Rugg & Coles, 1995). Components have traditionally been characterized by their polarity, amplitude, latency and distribution over the scalp, but peak components related to specific cognitive functions can be difficult to isolate due to the fact that multiple cognitive operations often proceed in parallel. An alternative approach is to carefully design experiments to isolate the process of interest by subtraction, where the component is defined as the difference in activation patterns between two or more experimental conditions. This approach has clear advantages in situations where component overlap is likely, but is supported by assumptions that must be fully understood to facilitate interpretation.

The subtraction method requires that the latency of equivalent components in separate conditions of interest are identical. Differences in the latency of the same components would produce separate peaks in the waveform, incorrectly suggesting that the underlying functions differ qualitatively (Coles & Rugg, 1995). It is also critical when adopting this approach to ensure that experiments are designed in a way that allows the principle of ‘pure insertion’ to be met. In essence, this principle dictates that cognitive processes are additive and do not interact (Sternberg, 1969). In reality, this principle is often violated in brain imaging research (Friston et al., 1996); however it is important to note that comparisons of behavioural measures also depend on this principle. The experiments reported in this thesis were carefully designed to isolate the processes of interest (see chapter 4), and findings were interpreted in light of potential limitations. The following sections discuss the types of inference that can be drawn from ERPs. Inferences can be drawn about the degree of engagement, timing and functional equivalence of cognitive processing, based on between condition differences in amplitude, time course and the distribution of effects over the scalp (Otten & Rugg, 2005).

2.4.1 Amplitude, latency and topographic differences

When ERP waveforms differ only in amplitude or magnitude across experimental conditions, it can be inferred that the experimental manipulation has engaged the same cognitive process across conditions but to a different strength or degree. It is important, when observing a change in the degree of engagement, to ensure that this difference is not being driven by an unequal proportion of trials, or differences in timing, across conditions. As noted above latency jitter, if present in one condition to a greater degree, could lead to a spurious difference in peak amplitude, but area measures are less likely to be affected, provided that the time window chosen captures the full extent of the effect. The assessment of differences in onset latency takes advantage of the high temporal resolution of ERPs, and can provide an upper-bound estimate of the time it takes the brain to differentiate between two or more experimental conditions. However, it is important to note that earlier differences may be present but not be measurable at the scalp (Otten & Rugg, 2005). Qualitative differences in the topographic distribution of effects between conditions reflect the operation of distinct cognitive processes, based on the aforementioned assumption that specific cognitive processes are associated with invariant underlying patterns of neural activity. However, the absence of a difference in topography does not imply the engagement of identical cognitive processes because voltages at the scalp can be compatible with an infinite number of possible underlying neural generators. In addition, it remains possible that differences in the underlying neural generators are present, but cannot be detected at the scalp.

2.5 Analysis of ERPs

This section provides an overview of statistical analyses used to assess the reliability of the ERP data reported in this thesis. After visually identifying differences in the waveforms, the data were quantified by calculating the mean amplitude of the difference over the time windows of interest, relative to the pre-stimulus baseline (100ms). Although the best statistical test to use is entirely dependent upon the design of the experiment, the most common test applied is the repeated measure analysis of variance (ANOVA), which was used in the current thesis and will be described in the following section.

2.5.1 Analysis of Variance ANOVA

Repeated measures ANOVA is a parametric test used to compare means from the same participants (within-subject) across experimental conditions. Repeated measures testing assumes quantitative data that are normally distributed and that the data does not violate the assumption of sphericity. The assumption of sphericity requires that the variances in different independent variables are equal and that correlations between variables are also equal. In practice, ERP data often violate this assumption of sphericity, because data from adjacent electrodes are inherently more correlated than data from more distant electrodes. Violation of the assumption produces spuriously low p-values, inflating the probability of type I error and leading to false rejection of the null hypothesis. However, violations of the sphericity assumption can be dealt with for ERP data by applying a Greenhouse-Geisser correction, which reduces the chance of Type I error by decreasing the degrees of freedom and as a result increasing the p-value (Greenhouse & Geisser, 1959).

2.5.2 Amplitude and topographic analyses

The ANOVA model calculates p-values for each factor included in the analysis, and as a result, increasing the number of factors inflates the probability that a factor will reach significance by chance. One approach to counter the large number of electrode factors in ERP research is to compute an average collapsed across a number of individual sites. However, for amplitude or magnitude analyses, electrode sites are normally sub-divided into factors representing different brain regions. For example, electrodes could be grouped into factors of location (frontal, central, parietal), hemisphere (left, right) and site (superior, mid, inferior) to facilitate characterization of effects and to guide follow-up analyses. Where initial analyses suggest the presence of differences in amplitude or magnitude it is critical to establish whether this change is driven by equivalent or distinct cognitive processes, by testing for differences in topographic distribution.

Topographic analyses of ERP data using repeated measures ANOVA are not straightforward. In essence, the ANOVA model is additive (assumes a constant change in factors) whereas ERP data are multiplicative (factors change unevenly). As a result, an interaction between condition and electrode can be produced by a change in the magnitude of a single generator, rather than activation of different underlying generators. Therefore, before submitting ERP data for topographic testing by ANOVA, the data must be rescaled to correct for amplitude differences across conditions, whilst preserving the relative pattern of activity between conditions to avoid this issue. The most common method used to rescale ERP data is the max/min method, which operates by identifying the maximum and minimum value for each condition across subjects, then subtracting the minimum

from each data point and dividing it by the difference between minimum and maximum values (McCarthy & Wood, 1985).

Some authors argue that the max/min procedure fails to address variance between conditions and can lead to an increase in type II errors (Urbach & Kutas, 2002). In essence, the objection is that the max/min rescaling method may be too conservative. It has been argued that rescaled data can be used to check for the existence of differences in scalp distribution, but that these effects should be characterized by referring to the original data (Wilding, 2006). The data in this thesis were rescaled using the max/min method, accepting that the approach may be conservative, and characterization of effects was limited to the original data.

2.6 Summary

ERPs reflect neural activity associated with the processing of a stimulus and are extracted from continuous EEG recorded from electrodes placed on the scalp. Prior to averaging, the data must be amplified, digitised, filtered and corrected for the contribution of unwanted artifacts. ERP waveforms can then be characterized in terms of their amplitude, latency and distribution over the scalp, providing information about the neural processing related to specific cognitive events. The preceding sections have introduced the ERP technique, from the neural origins of the signal, to the inferences that can be drawn from the data, paying special attention to the limitations inherent in measuring scalp potentials. The following sections will provide a review of findings from the ERP technique pertaining to explicit recognition and implicit priming, before setting out the aims of the current thesis in detail.

Chapter 3

Recognition and ERPs

ERPs allow different forms of memory to be examined directly, employing ‘neuro-signatures’ of memory-related processing as a way to measure the contribution of each form of memory to performance. Early electrophysiological investigations largely proceeded in the same way as behavioural and neuropsychological research, focusing on identifying neural correlates of explicit recognition and priming by examining these forms of memory in isolation. More recently, however, there has been a growing appreciation in the field of the need to move beyond this approach, and to characterize how multiple memory signals contribute to recognition performance (e.g., Voss & Paller, 2008). Importantly, it has been claimed that the operation of implicit memory during explicit memory tests presents a significant confound for ERP investigations of recognition, limiting theoretical progress by contaminating neural correlates of explicit retrieval (Voss & Paller, 2007). The following sections will provide an overview of findings from studies investigating recognition in isolation, before providing a review of the evidence from studies that have attempted to move beyond this approach, by obtaining concurrent measures of implicit priming and explicit recognition.

3.1 Explicit retrieval

To isolate the contribution of retrieval processes, ERP studies of recognition often draw upon comparisons between the activity elicited by items correctly classified as ‘old’ (i.e. studied) and items correctly classified as ‘new’ (i.e., unstudied). Activity elicited by correctly rejected new items acts as a baseline; new items that have not been studied cannot elicit retrieval as they have not been encoded. The difference in activity between the baseline new items and the retrieval of old items provides an index of the neural activity associated with successful retrieval, including the processes of recollection and familiarity. The ERP old/new effect is characterised by the waveforms for correctly recognised old items showing greater positivity than the waveforms for correctly rejected new items. By making comparisons between different experimental conditions, and using different manipulations of memory, ERPs can be used to examine the pattern of cognitive processes associated with performance during normal functioning. ERP studies using this method to assess recognition memory have largely demonstrated that the neural correlates associated with familiarity and recollection are distinct in function, spatial location and time course.

A large number of studies report an early onsetting frontal old/new effect that has been related to familiarity, followed by a parietal old/new effect that has been related to recollection (for reviews see Friedman & Johnson, 2000; Rugg & Curran, 2007). The mid-frontal old/new effect (also known as the FN400 effect) is represented by more positive-going waveforms for hits compared to correct rejections, an effect that is maximal bi-laterally at frontal sites, with an onset time of around 300ms, and has been found to vary with recognition judgements based upon familiarity. In contrast to familiarity, recollection is associated with a

positive going waveform, that onsets later, from around 500ms post stimulus presentation, and that is maximal over left parietal sites, known as the left-parietal old/new effect. As such, the key features that allow dissociation of the neural signatures of familiarity and recollection are that they differ in distribution across the scalp and in their respective timing. Importantly, ERP evidence suggests that the putative correlates of familiarity and recollection respond differently to the same experimental manipulations that have been used to dissociate familiarity and recollection in behavioural work.

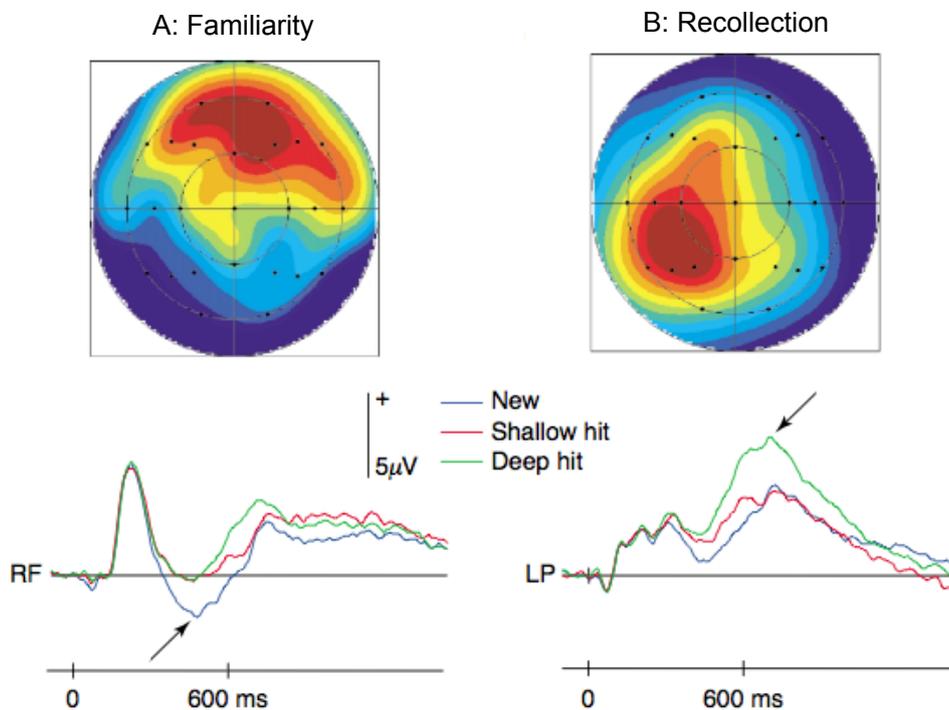


Figure 3.1: Neural correlates of familiarity and recollection. A: ERP waveforms and topographic distribution for the early mid-frontal old/new effect (300-500ms), which has been associated with familiarity. B: ERP waveforms and topographic distribution for the later left-parietal old/new effect (500-800ms), which has been previously associated with recollection (adapted from Rugg & Yonelinas, 2003).

Manipulations that have been found to differentially engage neural correlates of familiarity and recollection include divided attention, response deadlines, pro-

cessing fluency, forgetting rates and levels of processing. For example, Curran and Friedman (2004) manipulated the retention interval between study and test; they found that the left-parietal old/new effect was retained over longer intervals than the FN400, which decreases in activity as a function of time. Rugg et al. (1998) manipulated levels of processing at encoding and compared ERPs elicited at retrieval for stimuli that had been encoded via shallow and deep processing. The authors found that the FN400 effect was elicited in both conditions, while the left parietal old/new effect was only present in the deep processing condition (for a similar pattern see Figure 3.1). In another study employing a single word recognition test, Woodruff, Hayama and Rugg (2006) found that the words participants reported to be familiar in absence of recollection were associated with mid-frontal activity but no parietal activity. In contrast, words reported to be recollected were associated with the left-parietal old/new effect. The preceding section has introduced the neural correlates of familiarity and recollection; the following sections will provide a brief overview of additional ERP findings relating to each process independently, and an introduction to late onsetting right-frontal old/new effects that have also been reported in the recognition literature.

3.1.1 Recollection

As noted earlier, recollection is characterized as an effortful thresholded process that supports retrieval of contextual information associated with a prior event. In line with behavioural evidence, ERP studies employing the RK procedure have demonstrated that ‘remember’ responses are associated with larger left-parietal old/new effects than ‘know’ responses (e.g., Duarte, Ranganath, Winward, Hayward & Knight, 2004). Stronger evidence supporting a link between recollection

and the left-parietal effect comes from studies investigating the quality and degree of contextual retrieval associated with correct recognition. For example, Vilberg, Moosavi and Rugg, (2006) demonstrated that the size of the left-parietal effect was modulated by the amount of recollected information, with larger amplitudes associated with retrieval of a greater amount of contextual details. A similar pattern of results has emerged from source memory tasks, which allow separation of retrieval processing based on whether retrieval of contextual information is successful or unsuccessful.

For example, Wilding (2000) investigated whether the magnitude of the left-parietal effect was modulated by the number of accurate source judgements, and found that correct recognition accompanied by two correct source judgements exhibited larger left-parietal effects than those only receiving one correct source judgement. One of a number of potential problems with source memory tasks is that the absence of a correct source decision does not necessitate that recollection has not occurred (e.g., Montaldi & Mayes, 2011). Participants may fail to identify the intended source but may still recollect other contextual details associated with the study episode, this is known as “non-criterial recollection” (Yonelinas & Jacoby, 1996). Notwithstanding issues with source memory tasks, a wealth of evidence supports the view that links between recollection and the left-parietal effect are reasonably well founded (although see Yovel & Paller, 2004), but links between the FN400 old/new effect and familiarity are currently more controversial.

3.1.2 Familiarity

In contrast to recollection, familiarity has been claimed to index the degree of similarity between a current event and some event in our past experience, and is generally considered to be an automatic graded process. The difficulty in understanding the nature of familiarity and the FN400 is in part driven by the range of differential descriptions of the phenomena posited by dual-process models. For example, familiarity has been described as an implicit memory phenomenon that assesses the degree of processing fluency (Jacoby & Dallas, 1981), an assessment of the strength of activation in lexical nodes (Atkinson & Juola, 1974), and a quantitative assessment of memory strength based on signal detection theory (Yonelinas, 2002). While there are subtle differences in dual-process descriptions of familiarity, strength based accounts all suggest that neural signals of familiarity should not only be present for previously encountered items, but also for similar lures. Studies contrasting ERPs for studied items and similar lures have identified the presence of comparable mid-frontal old/new effects, and this is often cited as the strongest evidence supporting a familiarity interpretation of the FN400.

For example, Curran (2000) compared ERPs elicited by studied words and plurality changed lures (i.e., truck vs trucks), based on the assumption that recollection would be required to accurately discriminate between studied words and similar lures, but that studied words and lures would both be more familiar than new words. In line with this assumption, Curran found that mid-frontal old/new differences for correctly classified studied words and incorrectly classified lures were equivalent in magnitude and distribution (also see Curran & Cleary, 2003, for similar findings with pictures). However, these findings are not entirely inconsis-

tent with a very different theoretical interpretation, namely, a perceptual priming account of the FN400. In essence, the high degree of perceptual overlap between studied words and plurality reversed lures would be expected to be conducive to perceptual priming, based on evidence demonstrating that perceptual priming is strongest when physical features match between presentations (e.g., Schacter, 1990; Tulving & Schacter, 1990).

In response to this potential confound, Curran and Dien (2003) attempted to differentiate between perceptual priming and amodal global-matching accounts of familiarity in a follow up study by manipulating the modality of words between study and test (auditory, visual). They identified distinct old/new effects for perceptual aspects of recognition and familiarity. The authors found an early onsetting fronto-polar old/new effect (176-260ms) that was only present following visual study, suggesting that this early effect was dependent upon the degree of perceptual similarity. By contrast, mid-frontal old/new effects were equivalent across study modalities, supporting an amodal global-matching view of the FN400. While these findings tentatively suggest that the FN400 does not merely reflect perceptual priming, they do not rule out a conceptual priming account, as conceptual priming is thought to be largely insensitive to changes in modality between study and test, operating at a higher level of abstraction (Wagner & Koutstaal, 2002).

Studies employing conceptually related lures have also demonstrated that mid-frontal old/new effects were comparable in magnitude for correctly classified studied words and incorrectly classified lures. For example, Nessler, Mecklinger and Penney (2001) demonstrated that mid-frontal effects were equivalent in size for accurate and false recognition. In addition, the authors demonstrated that the presence of mid-frontal old/new effects for false recognition was contingent upon

the nature of the encoding task, with encoding focused on item specific rather than conceptual features eliminating mid-frontal effects for related lures. These findings suggest that familiarity signals are largely influenced by conceptual rather than perceptual fluency. In a later study, Nessler, Mecklinger and Penny (2005) attempted to differentiate neural signals related to perceptual fluency, semantic familiarity and recognition-related familiarity using famous and non-famous faces. The authors demonstrated that mid-frontal old/new effects were present between 300-450ms for semantic and recognition related familiarity, while perceptual fluency was associated with a centro-parietal old/new difference during the same time window, suggesting that mid-frontal old/new effects are sensitive to conceptual and not perceptual processing.

3.1.3 Right-frontal old/new effect

In addition to mid-frontal and left-parietal old/new effects associated with familiarity and recollection, a number of studies have reported the presence of a late onsetting right-frontal old/new effect during recognition memory experiments (e.g., Hayama et al., 2008; Schloerscheidt & Rugg, 2004; Wilding & Rugg, 1996; Woodruff et al., 2006). The right-frontal effect onsets around 800ms post-stimulus and often continues until the end of the recording epoch (see Figure 3.2). Right-frontal effects were first reported in source memory experiments, where late onsetting right-frontal effects were found to be larger for correct than for incorrect source judgements (e.g. Wilding & Rugg, 1996), suggesting that the effect was involved in the retrieval of contextual information. However, more recent evidence has suggested that right-frontal effects are not directly related to the retrieval of source information or retrieval accuracy. A number of studies have

failed to find right-frontal effects for correct source judgements (e.g. Cycowicz & Friedman, 2003; Wilding & Rugg, 1997), and right-frontal effects have been found in studies with no requirement for the retrieval of source information (e.g. Düzel et al., 1997; Trott et al., 1999).

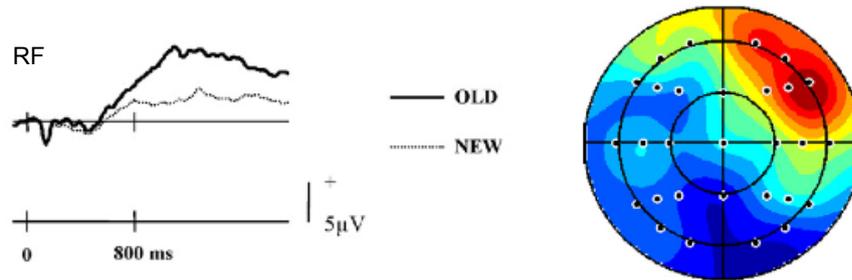


Figure 3.2: Right-frontal old/new effect. ERP waveforms and topographic distribution for the late right-frontal old/new effect (around 800ms onwards), which has been associated with monitoring the products of retrieval. (adapted from Hayama et al., 2008).

An alternative account of the functional significance of the right-frontal old/new effect suggests that it reflects evaluation or monitoring of the products of retrieval. For example Curran et al. (2001) contrasted good and poor performers during a false memory study and found that right-frontal effects were only evident for good performers, who also exhibited longer reaction times, indicating more careful and deliberate decision making. More recently, Hayama et al. (2008) contrasted right-frontal effects for recognition and semantic judgement tasks, demonstrating that right-frontal effects were not necessarily linked to monitoring the products of retrieval from memory. The presence of right-frontal effects for the semantic judgement task led the authors to suggest that the right-frontal effect reflects generic monitoring or decision making processes. While the exact functional significance of the right-frontal effect remains a matter of debate, there is general agreement that the right-frontal effect should be considered an index of post-retrieval evaluation and monitoring processes.

3.1.4 Summary

The preceding sections have provided an overview of findings from ERP studies investigating familiarity and recollection in recognition memory. Whilst the relationship between recollection and the left-parietal old/new effect appears reasonably well founded on the basis of the evidence reported above, the relationship between FN400 old/new effect and familiarity remains contested. Importantly, differential descriptions of processing thought to support familiarity by dual-process models suggests that feelings of familiarity can perhaps be multiply determined by the outcome of implicit processing, and in particular by perceptual and conceptual fluency resulting from prior exposure. Recently, it has even been suggested that both perceptual and conceptual information can in fact combine to support familiarity based recognition (Groh-Bordin, Zimmer & Ecker, 2006). It is clear, given current uncertainty, that adequately characterizing the contribution of implicit processing to recognition is vital for theoretical progress. The remainder of this chapter will focus on evidence from ERP studies obtaining concurrent measures of implicit priming and explicit recognition, before setting out the aims of the current thesis in detail.

3.2 Recognition and priming

Over the last fifteen years, the number of studies employing ERPs to isolate the contributions of implicit priming and explicit recognition has grown exponentially. This growth was initially inspired by a study published in *Nature*, demonstrating that it was possible to isolate neural correlates of implicit and explicit memory within the confines of a single experimental paradigm. Rugg et al. (1998) ma-

nipulated the levels of processing at encoding and operationalized recollection by comparing deep hits (correctly recognized old items from the deep task) and shallow hits (correctly recognized old items from the shallow task). Familiarity was operationalized by comparing shallow hits and shallow misses (old items from the shallow task that were not recognized). Finally, implicit memory was operationalized by comparing the activity elicited by shallow misses and correct rejections (new items correctly identified as new), based upon the assumption that studied items that are not recognized at test do not engage explicit memory.

The authors found that compared to new words, recently studied words elicited activity in three functionally distinct neural populations. Conscious retrieval of the stimuli was associated with ERP signals that are very similar to the neural correlates of familiarity and recollection, identified in previous research. Around 300-500ms after the onset of the stimulus, ERPs were more positive at mid-frontal sites for recognized words compared to new words and old words misclassified as new, indexing familiarity. Between 500-800ms, ERPs were more positive at left-parietal sites for deeply studied words compared to both new and shallowly studied words, indexing recollection. By contrast, a distinct and earlier onsetting (300-500ms post-stimulus) parietal ERP effect was associated with implicit memory. Critically, this effect was equivalent in size for deeply and shallowly encoded stimuli, and was present regardless of whether or not the test item was consciously recognized. Overall therefore, this early study demonstrated that employing ERPs to examine implicit and explicit memory provides the potential to control contamination and identify effects that overlap in time course and spatial location during normal function.

Despite demonstrating the potential of ERPs to assess implicit and explicit contributions to recognition concurrently, this early study is not beyond critique.

While there is a wealth of evidence to suggest that one presentation of a word is enough to change the way it is subsequently processed (Graf & Schacter, 1985), it cannot be assumed that implicit memory was operative for all repeated stimuli (Voss & Paller, 2008). Rugg et al. (1998) failed to employ a behavioural measure of priming, and as a result, there is no way to directly relate the parietal correlate reported to index priming specifically; it could reflect some other form of pre-retrieval processing rather than implicit memory *per se*. As noted earlier, implicit memory was operationalized by comparing the activity elicited by shallow misses and correct rejections, which again relies upon the assumption that priming will be operative for all repeated stimuli. This assumption is particularly problematic for recognition misses as some evidence has suggested that unconscious priming is dependent upon temporal attention (Naccache et al., 2002). It could be argued that recognition misses comprised of trials where attention was not appropriately oriented, and as such that priming would also be absent on this subset of trials, weakening any potential link between parietal activation and implicit memory. However, while Rugg et al. (1998) may not have avoided some of the pitfalls of measuring implicit and explicit memory concurrently, by demonstrating the possibility, this study has undoubtedly inspired a new and exciting direction in memory research.

In recent years, the majority of work in this area has focused on isolating and examining potential pre-cursors to recognition memory. In particular, research has focused on separating out the contribution of conceptual priming, based on the proposal that differences between old and new items in recognition tests can potentially be driven by repeated access to semantic information, calling into question links between mid-frontal old/new effects and familiarity (Paller, Voss & Boehm, 2007). For example, Yovel and Paller (2004) reported the absence of mid-

frontal old/new effects for familiarity during a face recognition task. This finding led the authors to propose that the use of verbal semantically meaningful stimuli in recognition tests elicit conceptual priming, and as such, that studies employing verbal stimuli do not provide a pure measure of familiarity. Following on from this proposition, a number of studies have demonstrated that the mid-frontal old/new effect is absent in conditions that do not support access to conceptual information (see Figure 3.3 for a schematic illustration). For example, Voss, Schendan and Paller (2010b) contrasted ERPs for geometric squiggles that were given high or low meaningfulness ratings, and found that mid-frontal old/new effects were only apparent for shapes given a high meaningfulness rating.

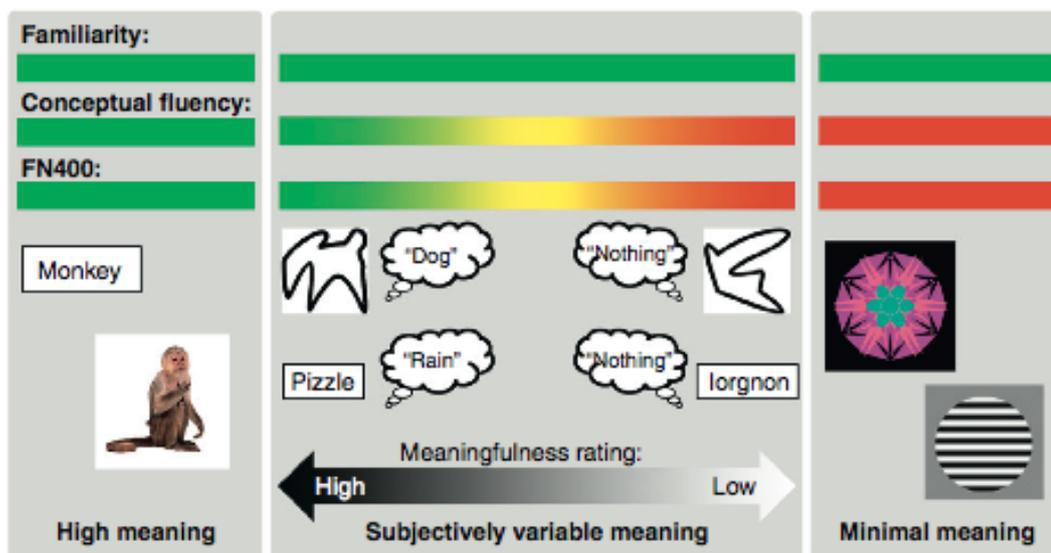


Figure 3.3: Schematic illustration of the effect of stimulus meaning. The strength of the relationship between familiarity, conceptual fluency and the FN400 is shown in the bars at the top of the diagram (green indicates strong and red indicates weak), and the bottom of the diagram illustrates the degree of meaning associated with specific stimuli in relation to these effects (adapted from Voss et al., 2012).

Voss, Paller and colleagues have also demonstrated a similar pattern of results when contrasting recognition for famous faces accompanied or unaccompanied by matching biographical information (Voss & Paller, 2006), and for uncommon En-

glish words that varied in meaningfulness (Voss, Lucas & Paller, 2010a). However, these findings are difficult to reconcile with studies showing mid-frontal old/new effects for meaningless stimuli, including pseudo-words (Curran, 1999), nonsense figures (Groh-Bordin et al., 2006), novel faces (Curran & Hancock, 2007), and two-dimensional polygons (Curran, Tanaka & Weiskopf, 2002), which do not have pre-existing conceptual representations. In addition, Sternberg, Hellman, Johansson and Rosén (2009) examined neural correlates of recognition using famous and non-famous names that also varied in frequency; the authors found that only frequency modulated the mid-frontal old/new effect, while fame modulated parietal old/new effects. Based on the assumption that famous faces should elicit a higher degree of conceptual priming due to pre-existing representations, these findings support the view that familiarity is not related to conceptual priming. More importantly, in a follow-up behavioural experiment the effect of conceptual priming on reaction times was only observed for famous names, again suggesting that the mid-frontal old/new effect reflects familiarity and not conceptual priming (although see Lucas *et al.*, 2010, for a critique; and Stenberg *et al.*, 2010, for a response).

In essence, debate still continues over whether the mid-frontal old/new effect is a generic marker of familiarity, or whether it is more closely related to conceptual implicit memory (for a recent discussion of these issues see Voss, Lucas & Paller, 2012). More generally, a number of authors have commented on the possibility that the qualitative experience of familiarity may be supported by more than one source of evidence, and that both perceptual and conceptual priming may serve as pre-cursors to explicit recognition (e.g., Groh-Bordin et al., 2006; Rugg & Curran, 2007). It is important to note that nearly all of the studies reported above have focused upon manipulation of stimulus properties to attempt to de-

lineate implicit and explicit contributions to recognition, and have not set out to directly manipulate (or even in some cases, to measure) the degree of priming. As noted earlier, behavioural evidence supporting the view that priming can influence recognition performance largely comes from studies investigating the impact of processing fluency induced by repetition. Surprisingly, this is an area that has received little attention in the ERP literature to date; the remainder of this section will outline in detail the findings from studies that have adopted this approach, as they are highly relevant to the focus of the current thesis.

Woollams et al. (2008) employed a masked priming paradigm, enhancing the fluency of test cues (50% primed, 50% unprimed), to identify and dissociate the neural correlates of repetition priming and recognition within a single experimental task. Consistent with previous research, the behavioural findings indicated that masked priming selectively increased familiarity and decreased response times for hits. The data evidenced the presence of four distinct ERP effects: mid-frontal old/new effects were present between 300-500ms (R hits, K hits > CRs), and a centro-parietal positivity present between 500-800ms was associated with recollection (R hits > K hits, CRs). In addition, the authors identified a long-term repetition effect from the study exposure in the same time window as the FN400 (misses > CRs), but with a posterior distribution similar to the repetition effect reported by Rugg et al. (1998). Masked priming of test cues was associated with a positivity for primed words between 150-250ms that was maximal over central sites for all response types (R hits, K hits, CRs), and continued into the 300-500ms time window. In addition, a difference in the latency of parietal old/new effects was found, with effects for R hits onsetting 50ms earlier in the primed condition. Surprisingly, despite finding a behavioural increase in reported familiarity, the ERP data suggest that fluency induced by masked primes influenced

neural correlates of recollection, speeding their onset. However, this change in latency roughly matches the duration of the prime, and as no backwards masking procedure or measure of prime awareness was employed, this finding is less than convincing, as it could be argued that retrieval was consciously initiated in response to the prime rather than the target.

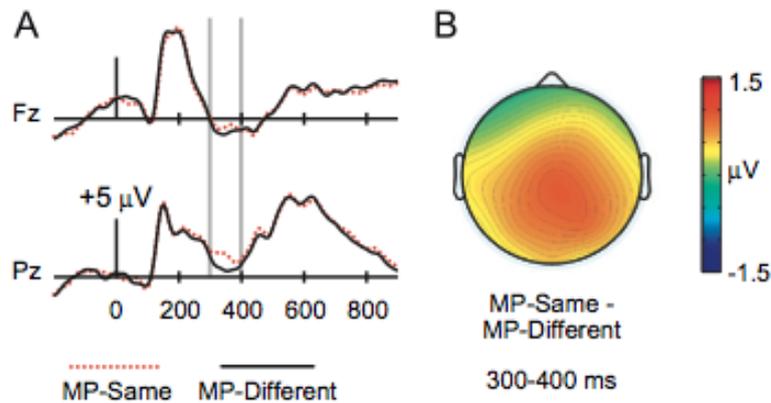


Figure 3.4: N400 masked priming effect. A: ERP waveforms for primed (MP-Same) and unprimed (MP-Different) words at test, collapsed across response types, at electrodes Fz and Pz. B: Distribution of the difference between primed and unprimed words (adapted from Lucas et al., 2012).

In a more recent study, Lucas, Taylor, Henson and Paller (2012) also employed masked repetition of test cues in two experiments that were designed to contrast neural correlates of repetition induced fluency and familiarity. In the first experiment, the behavioural data evidenced a very slight but largely non-significant increase in the percentage of R and K false alarms for primed compared to unprimed words (response time data were not reported). The ERP data demonstrated the presence of mid-frontal old/new effects between 300-500ms (K hits > misses), and parietal old/new effects between 500-800ms (R hits > K hits). Priming was associated with modulation of the N400 component between 300-400ms over posterior sites, which was topographically dissociable from mid-frontal old/new effects present during the same time period (see Figure 3.4). Moreover, masked prim-

ing effects were present for all response types (R hits, K hits, CRs), but were not significant when tested in isolation, making it difficult to assert that priming selectively influenced familiarity. The second experiment was designed to address this issue, focusing on false recognition by doubling the ratio of new to old words to encourage a more liberal response bias, to provide a clearer view of the relationship between masked priming and familiarity.

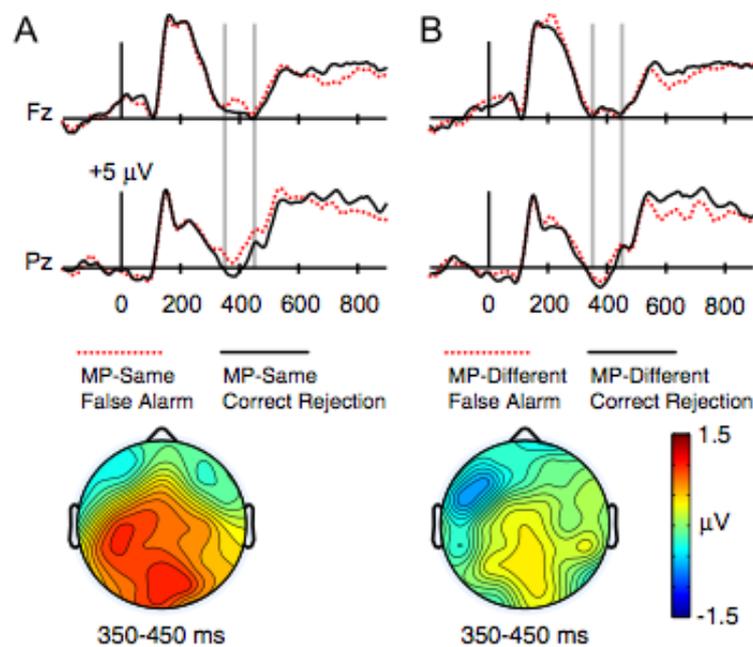


Figure 3.5: False alarm contrast. A: ERP waveforms for false alarms and correct rejections for the primed condition (MP-Same) at electrodes Fz and Pz, and the distribution of the difference between false alarms and correct rejections. B: ERP waveforms for false alarms and correct rejections for the unprimed condition (MP-Different) at electrodes Fz and Pz, and the distribution of the difference between false alarms and correct rejections (adapted from Lucas et al., 2012).

The behavioural results of Lucas et al's follow up study revealed a significant increase in the percentage of false alarms for primed compared to unprimed words, evidencing the impact of fluency on false recognition. When collapsed across response types the ERP data exhibited a similar pattern as in the previous experiment, with primed words being more positive going than unprimed words

between 350-450ms over posterior sites. Comparison of unstudied primed words revealed more positive going activity for false alarms than for correct rejections between 350-450ms, and this effect was absent in the waveforms for unprimed words (see Figure 3.5). The authors interpreted this posterior N400 effect as an index of both fluency and familiarity. As noted earlier with respect to behavioural masked priming studies, this general approach makes it difficult to see how priming can be classified as an implicit memory phenomenon, when the focus is entirely on illusory recognition (which is presumably giving rise to a conscious experience of oldness, hence the participants respond old). Notwithstanding criticisms, the findings of Woollams et al. (2008) and Lucas et al. (2012) suggest that masked priming of test cues is a useful method for measuring repetition priming, familiarity and recollection within a single experimental task - particularly if behavioural and neural measures are combined.

In summary, the majority of work in this area has focused on separating out the contribution of conceptual priming during recognition tests, based on the proposal that differences between old and new items in recognition tests can potentially be driven by repeated access to semantic information. A number of the studies outlined above have identified a neural correlate of priming maximal over posterior locations that is consistent with the timing and distribution of N400 potentials (see Kutas & Federmeier, 2011, for a review). However, despite this finding debate still continues over whether the mid-frontal old/new effect is a generic marker of familiarity, or whether it is more closely related to conceptual implicit memory. The evidence reviewed above supports the view that there are multiple processes that could potentially support recognition, but by continuing to focus on dissociation, progress in understanding how these different forms of memory contribute to recognition has been limited.

3.3 Thesis aims

Despite a wealth of research employing ERPs to dissociate multiple potential contributions to recognition, less attention has been paid to potential interactions between priming and recognition, and as such the relationship between these implicit and explicit forms of memory remains unclear. Combining masked priming with a standard recognition test makes it possible to carry out ‘interaction studies’ that are designed to manipulate implicit memory, using the ERP neuro-signatures to examine the consequence of implicit priming for explicit memory. The main aim of this thesis was to adopt this approach to explore the nature of interactions between priming and episodic memory, in the hope of gaining a better understanding of the respective contributions of implicit and explicit processing to recognition.

Research questions:

1. Do implicit priming and explicit recognition interact?
2. What is the relationship between priming, familiarity and recollection?

The research questions outlined above represent the broad questions that the experimental work reported in this thesis set out to address, and were identified based on gaps in knowledge within the existing literature. A series of four experiments will be reported in this thesis, each one designed to address a specific question (outlined in the relevant chapters). The first two experiments reported sought to provide answers to these broad questions, while the later experiments were specifically designed to address additional questions that arose over the course of the experimental work.

Chapter 4

General methods

The previous chapters have provided an overview of the theoretical and experimental background against which the experimental work reported in this thesis has been conducted. The focus now shifts to reporting the specifics of the four ERP experiments that will constitute the remainder of the thesis. The current chapter details the basic methods that apply to all of the EEG experiments described in this thesis, including an overview of the participants, stimulus materials, experimental procedures and behavioural analyses, along with details of the EEG recording procedure, data processing and analysis strategies. Where methodological factors deviate from this basic method for individual experiments, specific details are provided in the relevant chapters.

4.1 Participants

Participants were recruited from the University of Stirling and were right-handed native English speakers, between the ages of 18 and 35, with no known neu-

rological problems and normal or corrected-to-normal vision. Informed consent was obtained in line with University of Stirling ethics procedures and participants were provided with information about the EEG procedure prior to giving consent. Participants were compensated at a rate of £5 (Experiments 1 and 2) or £7.50 (Experiments 3 and 4) per hour for taking part, and Psychology students had the option of receiving payment for the first hour of participation in course credits. All participants were fully debriefed at the end of the experimental sessions.

4.2 Materials

The words used in all experiments were selected from the MRC Psycholinguistic database (Coltheart, 1981), and were medium frequency concrete nouns between 4-9 letters in length. Words had a mean written frequency of 23 (± 11) occurrences per million (Kučera & Francis, 1967), and the mean concreteness rating was 555 (± 48). Concreteness ratings in the MRC Database are based on an expansion of the norms from Paivio, Yuille and Madigan (1968) and are expressed as integer values between 100 and 700 (min 158; max 670; mean 438). Based on the mean rating for the database, only words with a rating higher than 438 were sampled, producing a list of 524 words. These words were then split into two groups to allow for an equal proportion of ‘yes’ and ‘no’ responses during the shallow encoding task (see below for details), before 480 words were randomly selected to form critical lists (240 from each list). From the remaining pool of words, 12 were used for the practice block and 32 were selected to act as fillers to be shown at the start of study and test phases.

The 480 critical words were divided into 4 blocks matched on word length, concreteness and frequency, and the factors of study response (yes, no), test status

(old, new) and condition (unprimed, primed) were fully counterbalanced across participants. All stimuli were displayed in white on a black background using Courier New 18 point font. Study and target words were displayed in uppercase, and prime words were presented in lowercase. Prime and target words are commonly presented in different cases during masked priming paradigms to ensure that resulting effects cannot merely be attributed to visual rather than lexical processing. Despite early research suggesting that repetition priming is highly sensitive to changes in case, more recent research on visual word recognition has clearly demonstrated case-independent priming under subliminal presentation conditions (Dehaene et al., 2001, 2004). Words presented at study and test subtended a vertical visual angle of 0.5° and a maximum horizontal visual angle of 5.2° .

4.3 Experimental procedure

During the performance of all memory tasks, participants were seated in a testing cubicle approximately one meter away from a 17-inch LCD monitor. The experiments were implemented using the E-Prime software package (www.pstnet.com: version 1.2), running on a desktop computer in an adjacent room, and participants were monitored via a video link between rooms for the duration of the experiments. The screen refresh rate for all experiments was 16ms, and the accuracy of critical display durations was verified using the Black Box Toolkit (www.blackboxtoolkit.com). In particular, it was ensured that the display duration of prime words and the distance between the onset of prime and the onset of target words at test remained consistent across trials and experiments. Responses were recorded using a five button PST Serial Response Box (www.pstnet.com)

resting on the desk in front of participants. Left and right index fingers were used to make all responses and the mapping of buttons for multiple response options was fully counterbalanced across participants.

An initial practice block was used to acquaint participants with the procedure, and to allow the experimenter to assess their understanding of the written and verbal instructions. Participants were never told about the presence of the prime words, and the practice block also provided the experimenter with the opportunity to exclude participants if they reported being aware of prime words at this stage. Over the course of the four experiments, this only occurred three times, and these participants were excluded on this basis. The practice block consisted of 6 study words and 12 test words (6 old, 6 new), and included a prompt screen instructing participants to respond faster if they failed to respond within the allotted time limit. In cases where participants performed poorly (i.e., failed to make a response on more than 50% of trials indicating that they had not adjusted to the response speed required over the duration of the practice block), clarification was provided and the practice block was repeated until response timing was satisfactory, before commencing the experimental blocks.

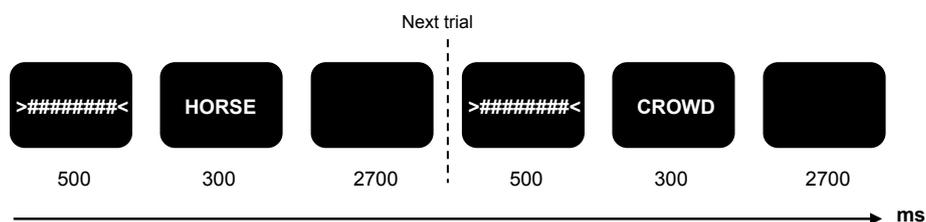


Figure 4.1: Study procedure. Every study trial started with a fixation cue, shown in the centre of the screen for 500ms, matching the mask to be used for priming during the test phase, followed by a word displayed for 300ms, before a blank screen was shown for 2700ms to allow time for participants to respond.

Experimental blocks commenced with a study list of 60 words, preceded by 4 fillers to allow participants to settle into the task and to control for primacy effects. Each study trial started with a warning signal (>#####<), shown in the centre of the screen for 500ms, followed by a single word displayed for 300ms; then a blank screen was shown for 2700ms to allow time for a response to be made (see Figure 4.1). The masking symbols used at test to occlude the prime were also employed at study to reduce the salience of the masking procedure, and were always described as a “warning signal” denoting that a word was about to appear. Experiments 1, 3 and 4 employed a shallow encoding task, where participants were required to report if the first and last letters of the presented words were in alphabetical order (responding yes or no by button press). Experiment 2 employed two deep encoding tasks in a between-participant design; participants were either asked to read each word out loud, or to fit each one into a short sentence. For the deep encoding tasks, participants were monitored via a microphone placed in the testing cubicle to ensure that the tasks were being performed satisfactorily.

To control for recency effects, at the end of the study phase participants were required to count backwards from 50, in increments of 3, for a duration of 2 minutes. This was implemented by a timed screen detailing the instructions for the task, and the test phase commenced automatically once this time had elapsed. Test lists comprised of 60 studied (old) words and 60 unstudied (new) words. Half of the studied and unstudied test trials began with a brief masked repetition of the to-be-recognized word prior to the onset of the target word. On the remaining unprimed trials target onset was preceded by the word “blank”. The word “blank” was chosen as a neutral prime, as previous research has demonstrated that it is a suitable baseline for ERP investigations of priming (Dien, Franklin

& May, 2006). It is common practice in priming research to use unrelated words as an unprimed baseline, but unrelated words still carry meaning and therefore cannot be considered truly neutral. While the word “blank” does have meaning, repetition over a large number of trials leads to habituation, and as a result it is considered more neutral than using unrelated words.

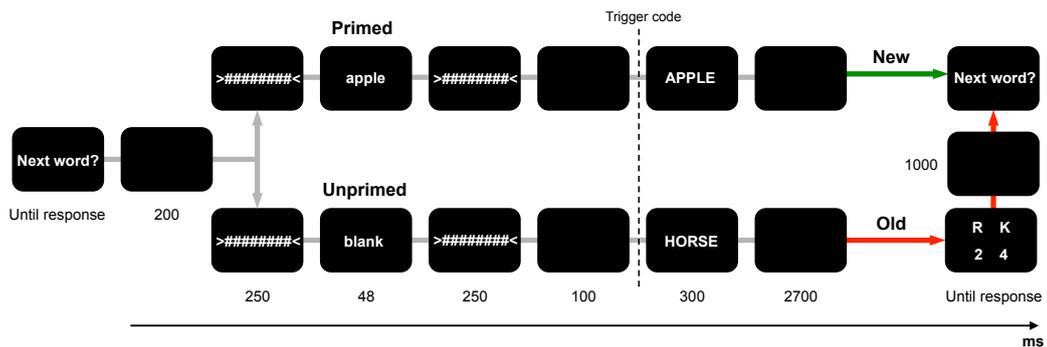


Figure 4.2: Test procedure. During the test phase participants were shown 120 words, 60 old words and 60 new words, fifty percent of old and new words were primed. A: On primed trials target presentation was preceded by a repetition of the target. B: On unprimed trials the presentation of the target word was preceded by the word blank.

Each test trial started with a screen instructing participants to press a button when they were ready to start the next trial, allowing participants some control over the speed of the test presentation, and ensuring that attention was oriented appropriately prior to display of the critical masking sequence. After a 200ms delay following the participant’s key press, a forward mask (>#####<) was presented for 250ms, followed by a matching or non-matching prime word shown for 48ms, and then a backward mask (>#####<) shown for 250ms. Presentation of the masked prime sequence was followed by a blank screen for 100ms, and then the target word was shown for 300ms, before a blank response screen was presented for a duration of 2700ms. During the blank response screen participants were required to indicate as quickly and as accurately as possible, by button press, whether the preceding target word was old or new. When a word

was classified as old, the screen then displayed details of the response options for the remember/know decision; once a response was made the screen went blank for 1000ms, and then the next trial began.

Participants were given detailed written and verbal instructions for the remember/know judgement (e.g., Gardiner et al., 1996; Rajaram, 1993). Briefly, participants were instructed to make a ‘remember’ response when recognition brought to mind some aspect of the experience of seeing the word in the study list, and to make a ‘know’ response when they were reasonably sure that the word had appeared in the study list, but did not recollect anything specific. During piloting an additional ‘guess’ response option was provided, but participants did not utilize this option during the pilot studies, so it was discontinued in the final version to reduce complexity and to allow full counterbalancing of the response options.

At the end of the experimental procedure participants were questioned to establish their awareness of the priming manipulation, before being fully debriefed. Participants were asked to report if they had noticed anything about the experiment that they had not been told about in the instructions, and were given time to think about it while the EEG cap was being removed. Responses to this questioning were classified into three broad levels of awareness (response categories that were identified based on responses collected during piloting). Participants were classified as ‘not aware’ when they were unable to report the presence of the prime during the initial questioning and also reported that they did not detect it after the manipulation was revealed. Participants were classified as ‘aware of blank’ when they were able to report its presence on some trials, but on further questioning, failed to report the presence of repetition primes. Finally, participants were classified ‘aware of flickering’ when they failed to report the manipulation,

but reported that they had noticed a flicker on the screen once the manipulation had been revealed.

The test procedure is similar to the one used by Woollams et al. (2008), but differs in three very important respects. Firstly, the current procedure employed a backwards mask between the display of prime and target words, reducing the accessibility of the prime, and increasing the SOA between prime and target pairings. Increasing the SOA provided additional time for processing of prime words, and it was assumed that it would allow better separation of processing related to prime and target words. Secondly, participants' awareness of the prime was recorded, to ensure that conscious access to prime words did not represent a significant confound in the current design. Unintended awareness is often a problem in masked priming paradigms and can make it difficult to interpret the results. For example, Woollams et al. (2008) reported the presence of an early onsetting recollection effect, but it is possible that this was merely driven by conscious access to the prime, rather than reflecting a real change in latency. Finally, the current procedure employed neutral rather than unrelated primes for comparison across the primed and unprimed conditions. Habituation of the neutral prime over a large number of repetitions should ensure that processing becomes non-semantic in nature, whilst avoiding differences in the physical appearance of masked words between conditions.

4.4 ERP recording and data processing

ERPs were employed to allow monitoring of the neural markers associated with familiarity and recollection and to look for differential effects on each process as a result of the priming manipulations. Voltage changes at the scalp were recorded

using 62 silver/silver chloride electrodes mounted in an elasticised Quick-Cap (Neuromedical Supplies: www.neuroscan.com) in accordance with an extended version of Jaspers (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). A further six electrodes were used, two positioned on the mastoids (M1, M2) to serve as a reference, two positioned on the outer canthi to the left and right of the eyes to monitor horizontal eye movements (HEOG), and two positioned above and below the left eye to monitor eye blinks (VEOG). All electrodes were referenced to an additional electrode (REF) positioned midway between the Cz and CPz electrodes. Before beginning the experiment impedances at each electrode were brought to below 2k Ω . To reduce the occurrence of EEG artifacts participants were given a break between each study-test block, and were instructed to relax and try to control body, head and eye movements. During the experiment EEG signals were amplified with a band pass filter of 0.1-40Hz and digitised at a rate of 250Hz (4ms/point). Neuroscan software was used to record the EEG data (Acquire, version 4.4/4.5), and to analyse the data offline (Edit, version 4.5).

For each participant the raw EEG data were inspected and segments were removed if they contained excessive muscle movement, or if a channel had become saturated (exceeding $\pm 495 \mu\text{V}$). The effect of eye blinks was reduced by employing the Neuroscan ocular artefact reduction procedure, using 32 blinks for each participant to remove the contribution of the average blink from all channels. The continuous EEG data were then separated into 2000ms epochs, starting 100ms before stimulus onset (from -100ms to 1900ms). Data were re-referenced

offline to linked mastoids and the individual epochs were baseline corrected and smoothed over a 5 point kernel. Note that smoothing of the ERP waveforms was performed purely for illustrative purposes in the figures. Epochs were rejected when they contained artifacts larger than $\pm 100 \mu\text{V}$, or when drift from baseline exceeded $\pm 75 \mu\text{V}$ in any of the channels. To ensure a good signal to noise ratio, a minimum limit of 16 artifact free trials was required from each participant, in each condition. Initially, ERPs were processed time-locked to the onset of the target stimulus, but inspection of the data from the first experiment evidenced the presence of pre-target differences between conditions. As a result, the data were re-processed and segmented into 2000ms epochs, starting 100ms prior to prime onset to capture this early effect (-500-1500), and this epoch was then employed across experiments for consistency.

4.5 Behavioural analyses

Behavioural measures included accuracy (discrimination and bias), response time data, and estimates of the proportion of trials supported by familiarity and recollection at test. Discrimination accuracy (Pr) was calculated separately for the primed and unprimed conditions to correct for guessing. In this case a hit was defined as the probability of making an ‘old’ response to a studied word, and a false alarm was the probability of making an ‘old’ response to a new unstudied word ($\text{Pr} = \text{pHit} - \text{pFA}$). Response bias (Br) was also computed separately for the primed and unprimed conditions ($\text{Br} = \text{pFA} / [1 - \text{Pr}]$) to look for a shift in bias as a result of the priming manipulation (Snodgrass & Corwin, 1988). Bias values greater than 0.5 demonstrate the presence of a liberal bias, and values less than 0.5 demonstrate the presence of a conservative bias. All response time data

presented in this thesis were corrected by removing trials that were outside ± 2 standard deviations of the mean for each participant within conditions, and t-test values reported for response time comparisons are all one-tailed. Estimates of recollection and familiarity were calculated using the independence RK procedure (Duarte, Raganath & Knight, 2005; Yonelinas & Jacoby, 1995), to control for underestimation of the contribution of familiarity.

$$p(\text{Recollection}) = p(R \text{ old}) - p(R \text{ new})$$

$$p(\text{Familiarity}) = p(K \text{ old})/(1 - p(R \text{ old})) - p(K \text{ new})/(1 - p(R \text{ new}))$$

Behavioural analyses were carried out using repeated measures ANOVA when more than two factors were compared, and an alpha level of 0.05 was used to assess statistical significance; full details of factors and levels will be provided in each data chapter. When it was necessary to compare data from two measures, paired samples t-tests were employed and a significance level of 0.05 was applied. All *post hoc* comparisons were carried out using paired samples t-tests and a Bonferroni-correction was applied as appropriate, depending on the number of comparisons to be performed on the data.

4.6 ERP analyses

The aim of the ERP experiments reported in this thesis was to investigate priming and memory related activity during the test phase. For priming and memory effects, grand average ERPs were formed for correct responses to old (hits) and new (correct rejections) words in the primed and unprimed conditions. ERPs

were quantified by measuring the mean amplitude over specific time windows of interest (with respect to the mean pre-stimulus baseline). For priming contrasts a latency period from 250-500ms was chosen *a priori* to be consistent with previous identifications of N400 priming effects in the literature (see Kutas & Federmeier, 2011, for a review). For memory contrasts, ERPs were initially quantified over two consecutive time windows from 300-500ms and 500-800ms, to be consistent with previous identifications of the neural correlates of familiarity and recollection (see Rugg & Curran, 2007, for a review). Where visual inspection of the data demonstrated the presence of differences outside of these latency periods for priming and memory contrasts, additional time windows were analysed as required to characterise effects for each contrast and experiment.

Selection of latency periods and sets of electrodes for analysis on the basis of visual inspection of the data is common practice in the literature, but it is important to note that this approach can be problematic. Reducing complex multi-dimensional EEG data to a single value per condition by averaging over a specific time window and set of electrodes avoids the requirement to correct for multiple comparisons. However, adopting this approach increases the chance of false positives when the choice of time window and electrode set is based only on where the effect of interest is maximal (Kilner, 2013). There are alternative methods for statistical exploration of EEG data including Principal Components Analysis (PCA) and Independent Components Analysis (ICA). In simple terms, both of these approaches use the correlational structure of a dataset to decompose the observed ERP waveform into a set of basic constituent components, extracting the features of interest based on functional relationships between components (Luck, 2005). A detailed introduction to PCA and ICA data analysis techniques lies beyond the scope of the current thesis, as these approaches were not employed to analyse the

data reported here. For the series of experiments reported in the current thesis, reliance on visual inspection for selection of time windows and electrode sets was limited to cases where the data evidenced the presence of previously unreported effects.

Electrode sets and time windows for analysis of memory effects were largely chosen based on previous identifications of familiarity, recollection and right-frontal old/new effects in the literature (see below), to control issues associated with analysis based purely upon visual inspection. Where the analysis strategy deviates from this basic approach, details are provided in the relevant chapters. Selection of time windows for analysis of priming effects was less straightforward. In addition to N400 effects that were expected to appear between 250-500ms, the data evidenced the presence of early and late onsetting priming effects across experiments that have not been reported previously. Additional time windows chosen for exploration of the early and late priming effects were chosen based on visual inspection of the data and details are provided in the relevant chapters. Across experiments priming and memory effects were analysed separately, employing different contrasts. Priming effects were initially analysed separately for hits and correct rejections to gain a measure of priming in the absence of old/new differences, before directly contrasting the magnitude and distribution of priming effects for hits and correct rejections. Memory effects were also initially analysed separately for the primed and unprimed conditions to capture old/new effects in the absence of priming related differences, before contrasting the magnitude and distribution of old/new effects for the primed and unprimed conditions. The following sections will provide an overview of the basic analysis strategy for priming and memory contrasts.

Priming analyses

For priming effects, the first level of analysis was employed to identify variations in the pattern of priming effects for hits and correct rejections across the time windows chosen for analysis, and employed ANOVA with the factors of condition (unprimed, primed), location (Fz, FCz, Cz, CPz, Pz, POz) and time window (window1, window2, window3). The sites used in this first stage of analysis are shown in Figure 4.3, and were chosen based on visual inspection of the data, which demonstrated that priming effects were consistently present over midline electrode sites across experiments. This initial stage of analysis was followed by subsidiary analysis performed separately for hits and correct rejections on the data from each time window, using ANOVA with the factors of condition (unprimed, primed) and location (Fz, FCz, Cz, CPz, Pz, POz). These initial analyses were designed to test the appropriateness of the time windows chosen for analysis of the data.

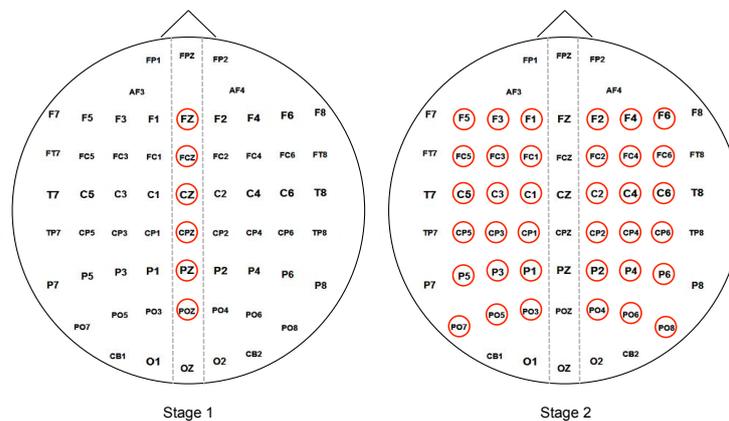


Figure 4.3: Priming analysis sites. Schematic illustration of electrode positions showing electrodes sites selected for initial stages of analysis highlighted in red. Maps appear as if looking at the head from above, dashed lines delineate the midline and the triangle represents the nose.

The second stage of analysis for each time window employed ANOVA with the factors of condition (primed, unprimed), location (frontal, fronto-central, central, centro-parietal, parietal, parieto-occipital), hemisphere (left, right) and electrode (inferior, mid, superior). The sites used in this analysis are shown in Figure 4.3, and were chosen based on visual inspection of the data, which demonstrated the presence of widespread priming effects. Locations and electrodes used for analysis were: left frontal (LF: F1, F3, F5), right frontal (RF: F2, F4, F6), left fronto-central (LFC: FC1, FC3, FC5), right fronto-central (RFC: FC2, FC4, FC6), left central (LC: C1, C3, C5), right central (RC: C2, C4, C6), left centro-parietal (LCP: CP1, CP3, CP5), right centro-parietal (RCP: CP2, CP4, CP6), left parietal (LP: P1, P3, P5), right parietal (RP: P2, P4, P6), left parieto-occipital (LPO: PO3, PO5, PO7), and right parieto-occipital (RPO: PO4, PO6, PO8). Only effects including the factor of condition were of interest for priming contrasts, as a result, main effects or interactions including the factor of condition were followed up with subsidiary ANOVAs and paired samples t-tests as required to further elucidate effects.

Memory analyses

For memory effects, the first level of analysis was employed to identify variations in the pattern of old/new effects for the primed and unprimed conditions across the time windows chosen for analysis. The location factors for this initial analysis varied across experiments to capture the locus of old/new effects across time windows. For experiments 1 and 2, this initial ANOVA included the factors of test status (old, new), location (Exp.1: Fz, FCz, Cz, CPz, Pz; Exp.2: F3, FC3, C3, CP3, P3) and time window (window1, window2, window3), to capture mid-frontal effects (Exp.1) and left-parietal effects (Exp.2) apparent in the data. For

P3, P5) and right parietal (RP: P2, P4, P6). Only effects including the factor of test status were of interest for memory contrasts, as a result main effects or interactions including the factors of test status were followed up with subsidiary ANOVAs and paired samples t-tests as required to further elucidate effects.

Magnitude analyses

For priming contrasts magnitude analysis was employed to compare the size of reliable priming effects identified in the initial analysis across hits and correct rejections. Analysis was performed on difference waveforms (primed minus unprimed), using ANOVA with the factors of test status (old, new), location (frontal, fronto-central, central, centro-parietal, parietal, parieto-occipital), hemisphere (left, right) and electrode (inferior, mid, superior). For memory contrasts magnitude analysis was performed on subtraction data (hits minus correct rejections) to compare the size of old/new effects for the primed and unprimed conditions, using ANOVA with the factors of condition (unprimed, primed), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). In addition, priming and memory data were examined to identify the maxima of effects, and then paired samples t-test were used to establish whether observed differences were statistically reliable at the identified location.

Topographic analyses

For priming and memory contrasts, topographic analysis was employed to investigate whether differences in the magnitude of effects across the scalp reflected genuine changes in topography. For these analyses subtraction waveforms were employed, based on the difference between primed and unprimed, or old and

new waveforms. The subtraction waveforms were rescaled using the max/min method prior to analysis (McCarthy & Wood, 1985). For priming contrasts, analysis comparing the distribution of the priming effects for hits and correct rejections, employed ANOVA with the factors of test status (old, new), location (frontal, fronto-central, central, centro-parietal, parietal, parieto-occipital), hemisphere (left, right) and electrode (superior, mid, inferior). For memory contrasts, analysis comparing the distribution of retrieval effects for the primed and unprimed conditions, employed ANOVA with the factors of condition (unprimed, primed), location (frontal, parietal), hemisphere (left, right) and electrode (superior, mid, inferior).

Statistical significance

As noted in chapter 2, ERP data commonly violate the assumption of sphericity required by the ANOVA model because the co-variance in the data from nearby electrodes is greater than co-variance in the data from more distant electrodes. Violating the assumption of sphericity increases the likelihood of type 1 error and the chance of incorrectly rejecting the null hypothesis. A significance level of 0.05 was used for all statistical tests; however where necessary the Greenhouse-Geisser correction for non-sphericity (Greenhouse & Geisser, 1959) was applied to the analysis of the ERP data and corrected degrees of freedom and F values are reported.

Chapter 5

ERP 1

5.1 Introduction

The relationship between priming and episodic familiarity remains unclear, despite increasing interest in this issue over the last two decades. One important reason for this lack of clarity in early work is that most of the studies carried out fall foul of a number of methodological flaws. Most notably, the operation of priming is often assumed in the absence of behavioural evidence demonstrating its contribution (e.g., Rugg et al., 1998). Secondly, it is often difficult to interpret findings due to debate over the nature of the priming and whether it should really be considered implicit (e.g., Woollams et al., 2008). Further complication is added by the overlapping nature of the neural correlates of priming and familiarity in episodic memory, making it difficult to adequately measure possible interactions between these processes. In more recent work, attempts have been made to overcome some of these issues and measure the contributions of priming and familiarity to recognition. However, in trying to ensure that perfor-

mance on explicit tests is not contaminated by implicit memory and vice versa, investigators have often sacrificed ecological validity, and prevented detection of interactions between implicit and explicit memory that presumably occur under normal circumstances.

The current study was designed to address these methodological issues and to explore interactions between priming and familiarity. As noted earlier, combining masked priming with a standard recognition test makes it possible to carry out 'interaction studies' that are designed to manipulate implicit memory, using the ERP neuro-signatures to examine the consequence of this for explicit memory. In recent years talk of implicit 'contamination' has become prominent (e.g., Voss & Paller, 2008), whereas attempts to identify how and when priming impacts standard recognition testing have been limited by the adoption of increasingly specialized tests to contrast priming and recognition. Importantly, in contrast to most of the previous research in this area, which has focused upon manipulation of stimulus properties to attempt to delineate implicit and explicit contributions to recognition, the current study aimed to directly manipulate the degree of priming via subliminal repetition of words. Manipulation of the degree of priming via repetition of words was adopted based on the logic that words represent the most common medium used in tests of recognition, and that repetition of words from study to test drives implicit 'contamination' posited to occur during recognition testing.

Extensive piloting was carried out to identify the optimal duration for masked prime words, to ensure that participants would be unaware the repetition, making the current experiment resemble a standard recognition task in all respects. This is crucial because previous research reporting fluency induced differences in memory performance using this method may have been biased by conscious access to

the prime (e.g., Lucas et al., 2012). As reported earlier, Jacoby and Whitehouse (1989) found that the pattern of behavioural results was different when contrasting subliminal and supraliminal priming during recognition testing; lengthening the duration of the prime and informing participants of its existence reduced the probability that fluency induced by repetition would be misattributed to prior exposure. While the intention in this study was not to contrast the effects of subliminal and supraliminal priming on recognition, recent research employing subliminal masked priming paradigms to investigate neural correlates of priming and recognition have potentially introduced significant confounds by failing to adequately control or measure awareness of the prime (e.g., Lucas et al., 2012; Woollams et al., 2008). As a result, interpretation of the findings is difficult, as it is plausible that participants were aware of the manipulation on a subset of primed trials, meaning that responses could be based on differing strategies across trials.

In addition to problems with prime awareness, another problem in previous research concerns the operationalization of priming within the context of episodic memory tests, and how correlates of explicit memory are identified. In a number of previous studies priming has often been indexed by comparing studied items that were not recognized (misses) with unstudied but correctly identified words (e.g., Rugg et al., 1998; Woollams et al., 2008). By contrast, recognition is normally operationalized by comparison of correctly classified old and new words collapsed across primed and unprimed conditions. Employing these different contrasts to capture neural correlates of priming and recognition again seriously limits the possibility of assessing interactions between these subsystems of memory. It is also common practice to split ERP data on the basis of subsequent RK judgements, to isolate the contribution of familiarity and recollection, but this rules out

the possibility that priming alone could be sufficient to support recognition from the outset. In essence, studies employing a two-stage RK procedure, where the initial old/new judgement is separated in time from the rating of subjective experience (e.g., Lucas et al., 2012; Woollams et al., 2008), risk that the subsequent RK classification may not be directly related to the basis of the initial old/new decision that is being measured in the ERPs, introducing another potentially significant confound.

To directly address these issues, in the current experiment priming was operationalized by comparing hits and correct rejections for both the priming and memory ERP contrasts. In addition, memory effects were analysed separately for the unprimed and primed conditions, to allow priming-related differences in the neural correlate of familiarity to emerge. While RK measures were employed to allow comparison with previous behavioural research employing fluency manipulations, the ERP data were not split on this criteria to allow the neural basis of the initial old/new judgement to be assessed in the absence of potential confounds imposed by subsequent ratings of subjective experience. The main aim of the current experiment was to explore interactions between repetition priming and neural correlates of familiarity during a standard recognition test, in the absence of potential confounds outlined above, which renders previous ERP research in this area very difficult to interpret. The bulk of ERP research to date has focused on identifying dissociations between multiple potential contributions to recognition, and as a result no detailed predictions were made about the nature of interactions between repetition priming and familiarity in advance.

5.2 Methods

Stimulus materials and experimental procedures were all identical to those specified in Chapter 4. Participants completed a practice block followed by four study/test blocks; during the study phase participants viewed a series of words and were required to decide whether or not the first and last letters were in alphabetical order. This shallow encoding task was employed to reduce the occurrence of recollection, and to encourage reliance on more automatic and familiarity-based recognition. During the test phase participants were presented with words from the study phase randomly intermixed with an equal number of unstudied words and were required to make an old/new decision followed by a remember/know judgement. At test half of the studied and unstudied trials were preceded by a brief masked repetition of the word to-be-recognized (primed) and the remaining trials were preceded by masked presentation of the word “blank” to act as a baseline (unprimed). Thirty-four undergraduate psychology students from the University of Stirling participated in the experiment; two participants were excluded due to excessive EEG artefacts, resulting in insufficient ERP trials for critical contrasts (i.e. <16 trials). The remaining thirty-two participants comprised of 19 females and 13 males with a mean age of 20 (range=18-31; SD=2.42).

5.3 Behavioural results

Confirming that prime awareness was not a confound in the current experiment, 72% of participants reported being unaware of the existence of the masked prime, 19% reported that they detected flickering on the screen, and the remaining 9% reported that they were aware of seeing the word blank appear before the onset

of the target word on a few of the trials. Initial examination of the behavioural data as a function of reported awareness confirmed no differences in the pattern of results for participants who reported being aware of flickering on the screen or aware of the word blank compared to unaware participants, and as a result the data were analysed collapsed across awareness categories. At study, participants correctly classified words in the alphabetical task on 81% of trials, suggesting that attention was being focused on the first and last letters of the words, ensuring shallow encoding as intended. More importantly, initial analysis of the test data confirmed that participants were able to discriminate between old and new words in the unprimed and primed conditions (paired t-tests comparing hits and false alarms for both conditions were significant [$p < 0.001$] in all comparisons).

Table 5.1: Memory performance. Percentage of correct responses, discrimination and bias measures for the unprimed and primed conditions (standard error of the mean). The data clearly demonstrate no difference in performance or bias across conditions.

	% Correct		Discrim. & Bias	
	Old	New	Pr	Br
Unprimed	60.11 (2.87)	78.83 (2.46)	0.39 (0.02)	0.35 (0.04)
Primed	60.70 (2.51)	76.76 (2.25)	0.37 (0.02)	0.37 (0.03)

Table 5.1 shows a summary of recognition performance for the current experiment, demonstrating that recognition and bias measures were unaffected by the priming manipulation. Mean accuracy data were analysed using ANOVA with the factors of condition (unprimed, primed) and test status (old, new). This revealed a significant main effect of test status [$F(1,31)=14.58$, $p=0.001$], reflecting higher accuracy for new words than for old words, but no main effect of condition or interaction between condition and test status. Subsidiary analysis collapsed across conditions confirmed that mean accuracy was higher for new words than

for old words at test ($t(31)=3.82$, $p=0.001$). Discrimination rates were also unaffected by the priming manipulation, and measures of response bias were equally conservative across conditions ($p>0.05$ in all comparisons). This pattern of results demonstrates that repetition priming did not impact measures of recognition performance.

Table 5.2: Response by RK. Mean proportion of responses (RK) split by test status and condition (standard error of the mean). The data demonstrate a slight but non-significant increase in the proportion of R and K false alarms in the primed condition.

		Remember	Know	New
Old	Unprimed	33.91 (2.59)	26.20 (1.40)	39.90 (2.96)
	Primed	33.88 (2.53)	26.84 (1.52)	39.30 (2.59)
New	Unprimed	5.75 (1.15)	15.44 (1.90)	78.83 (2.54)
	Primed	6.52 (1.32)	16.72 (1.68)	76.76 (2.32)

Table 5.2 shows the breakdown of responses by RK judgement for each category for old and new words in the unprimed and primed conditions. The data suggest no difference in the raw proportion of R and K responses for old words, but does suggest a slight increase in the proportion of R and K false alarms to new words in the primed compared to the unprimed condition. ANOVA including the factors of condition (unprimed, primed), test status (old, new) and response (remember, know) revealed no significant main effect or interactions including the factor of condition, indicating no difference in the raw proportion of R and K responses. Corrected estimates of familiarity and recollection were calculated as reported in Chapter 4, again analysis confirmed no differences between conditions on corrected estimates of familiarity (unprimed=0.25, primed=0.24) or recollection (unprimed=0.28, primed=0.27). As for overall recognition performance, the pattern of results clearly demonstrates that repetition priming did not influence reported levels of familiarity or recollection.

Table 5.3: Response times (ms). Mean response time data for correct responses split by test status, and the magnitude of the difference between unprimed and primed response times (standard error of the mean). The data demonstrate speeded response times for hits and correct rejections in the primed condition, with no difference in magnitude.

	Old (Hits)	New (CRs)
Unprimed	1005.02 (35.02)	984.23 (42.60)
Primed	938.86 (36.37)	915.40 (45.90)
Magnitude	66.16 (10.20)	68.83 (11.10)

Table 5.3 shows a summary of response times for hits and correct rejections in the primed and unprimed conditions, along with the magnitude of the difference between conditions. The data clearly demonstrate that the priming manipulation resulted in equivalent speeded response times for hits and correct rejections. ANOVA including the factors of condition (unprimed, primed) and test status (old, new) revealed a significant main effect of condition [$F(1,31)=75.29$, $p<0.001$], but no interaction between condition and test status, confirming that priming speeded response times to the same degree for hits and correct rejections. Importantly, the lack of difference in the magnitude of effects for hits and correct rejections suggests that priming from exposure at study did not carry over to the test phase, suggesting that the differences observed in response times were largely driven by exposure to the masked prime at test.

5.3.1 Summary

Response time data demonstrated the presence of robust priming effects that were equivalent in magnitude for hits and correct rejections, suggesting that the observed facilitation was driven by presentation of the masked prime at test. Despite this strong evidence of the operation of priming at test, measures of recognition performance and process estimates were unaffected by the manipulation.

5.4 ERP results

To examine priming and memory effects grand average ERPs were formed for hits and correct rejections in the primed and unprimed conditions. Visual inspection of the waveforms confirmed the presence of an early priming effect onsetting prior to onset of the target words. While the intention was only to examine ERPs time locked to the onset of the target word, this early negativity appeared to be driven by exposure to the masked prime and as a result the epoch was altered to include prime onset (-500-1500ms) to capture this early effect. The mean number of trials contributing to the waveforms for hits was 57 for the primed condition and 58 for the unprimed condition. The mean number of trials contributing to waveforms for correct rejections was 78 for the primed condition and 82 for the unprimed condition.

5.4.1 Priming effects

Figure 5.1 shows grand average ERPs time locked to the onset of the prime for hits and correct rejections from both the unprimed and primed conditions. Visual inspection of the waveforms indicated the presence of three priming related modulations, an early (-50-150ms) posterior negativity, followed by a widespread central positivity (250-500ms) and a later (500-1100ms) posterior negativity for primed compared to unprimed words. Based on visual inspection, three time windows were submitted for analyses of priming effects, -50-150ms, 250-500ms and 500-1100ms. To separate priming effects from memory effects the data for hits and correct rejections were analysed independently. The first level of analysis was designed to identify variations in priming effects across conditions and time windows, employing ANOVA with the factors of condition (unprimed, primed),

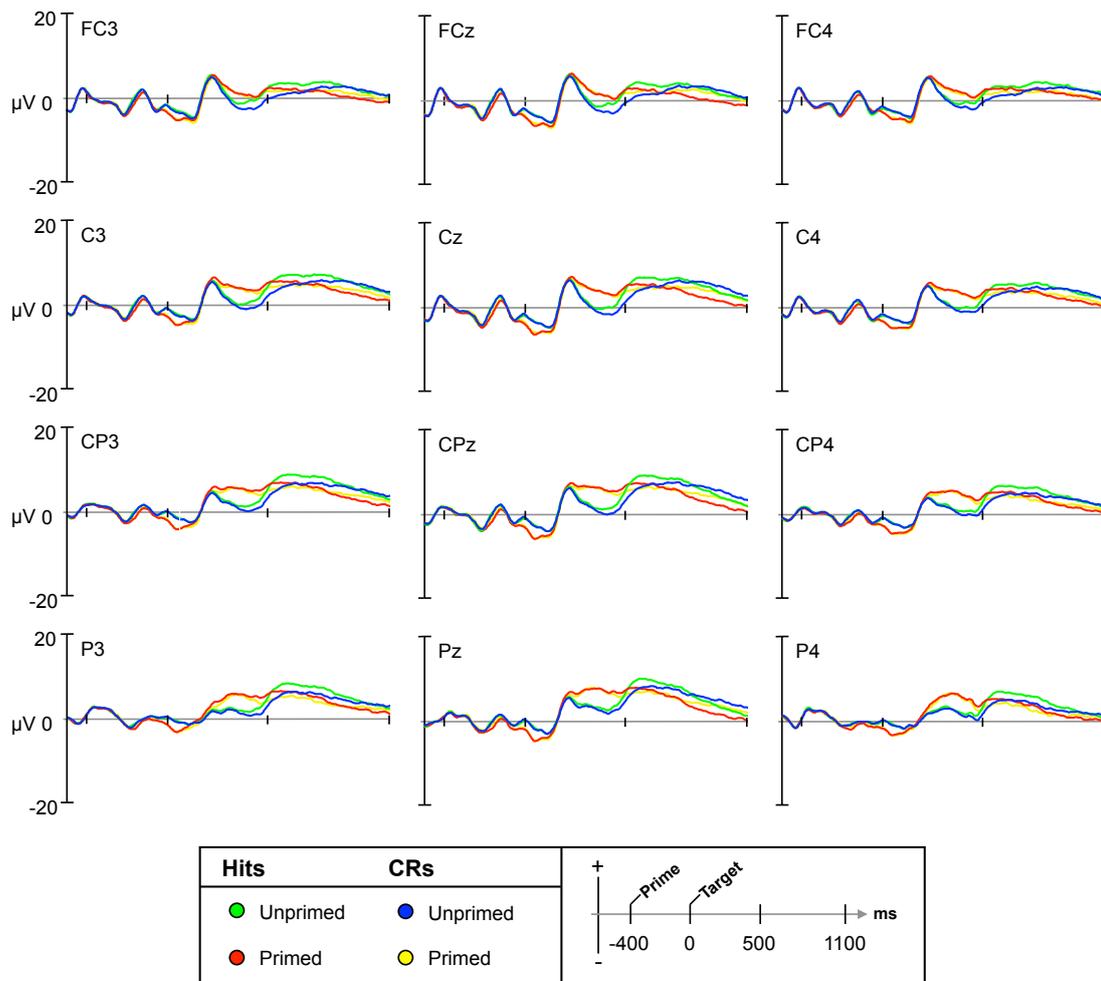


Figure 5.1: Priming effects. Grand average ERPs for hits and correct rejections in the unprimed and primed conditions. Waveforms display the presence of three priming related modulations, an early posterior negativity, followed by a widespread central positivity, and a later posterior negativity for primed compared to unprimed words.

location (Fz, FCz, Cz, CPz, Pz, POz) and time window (-50-150ms, 250-500ms, 500-1100ms). Results for hits revealed a significant interaction between condition, location and time window [$F(3.2,98.3)=23.34$, $p<0.001$]. Analysis for correct rejections produced a significant main effect of condition [$F(1,31)=4.96$, $p=0.033$], and a significant interaction between condition, location and time window [$F(2.8,86)=20.99$, $p<0.001$]. The presence of these interactions provides strong evidence of variation in the pattern of priming effects across locations and time windows for both hits and correct rejections.

Table 5.4: Priming ANOVAs by time window. Results of ANOVAs contrasting midline sites with the factors of condition and location over the three time windows chosen for analysis of priming effects.

		-50-150ms	250-500ms	500-1100ms
Hits	Cond	$F(1,31)=17.95$, $p<0.001$	$F(1,31)=28.31$, $p<0.001$	$F(1,31)=19.21$, $p<0.001$
	Cond*Loc	-	$F(1.7,51.6)=20.42$, $p<0.001$	-
CRs	Cond	$F(1,31)=44.24$, $p<0.001$	$F(1,31)=92.88$, $p<0.001$	$F(1,31)=5.97$, $p=0.020$
	Cond*Loc	$F(1.6,50.8)=6.23$, $p=0.006$	$F(1.8,56)=12.76$, $p<0.001$	$F(1.7,53.7)=13.54$, $p<0.001$

A second level of analysis was performed separately for hits and correct rejections on the data from each time window, using ANOVA with the factors of condition (unprimed, primed) and location (Fz, FCz, Cz, CPz, Pz, POz). The results of this analysis are summarised in Table 5.4 and confirm that priming effects were present in each time window for hits and correct rejections. For hits the results demonstrated a main effect of condition in all three time windows and an interaction between condition and location for the 250-500ms time window. Results for correct rejections revealed main effects and interactions between condition and location for all three time windows. These results provide evidence of priming effects for hits and correct rejections across time windows and suggest variations in the pattern of priming effects for hits and correct rejections. Subsidiary analysis

took the form of contrasts between the unprimed and primed conditions, performed separately for hits and correct rejections, using ANOVA with the factors of condition (unprimed, primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). The results for each time window are reported separately in the following sections.

5.4.1.1 Time window -50 to 150ms

From 50ms prior to the onset of target words waveforms for primed hits and correct rejections were more negative going than for unprimed hits and correct rejections across central and posterior locations (see Figure 5.2 for the data from CPz). Initial analysis for hits revealed a significant main effect of condition [$F(1,31)=15.80$, $p<0.001$] and an interaction between condition and electrode [$F(1.1,34.2)=14.18$, $p<0.001$]. As can be seen in the topographic map in Figure 5.2 these results reflect a negativity for primed hits compared to unprimed hits across locations at superior electrode sites. This result was supported by subsidiary analysis on the data collapsed across locations and hemispheres, which confirmed that effects were larger over superior sites than at medial ($t(31)=3.43$, $p=0.002$) or inferior sites ($t(31)=3.77$, $p=0.001$). Consistent with the posterior maxima evident in Figure 5.2, further examination of the data confirmed that the effect was maximal for hits at electrode CPz ($t(31)=4.34$, $p<0.001$).

Initial analysis for correct rejections revealed a significant main effect of condition [$F(1,31)=43.67$, $p<0.001$], along with interactions between condition and location [$F(1.4,42.3)=4.16$, $p=0.036$], and condition and electrode [$F(1.1,34.9)=16.70$, $p<0.001$]. As can be seen in Figure 5.2 these results reflect the presence of a negativity for primed correct rejections compared to unprimed correct rejections

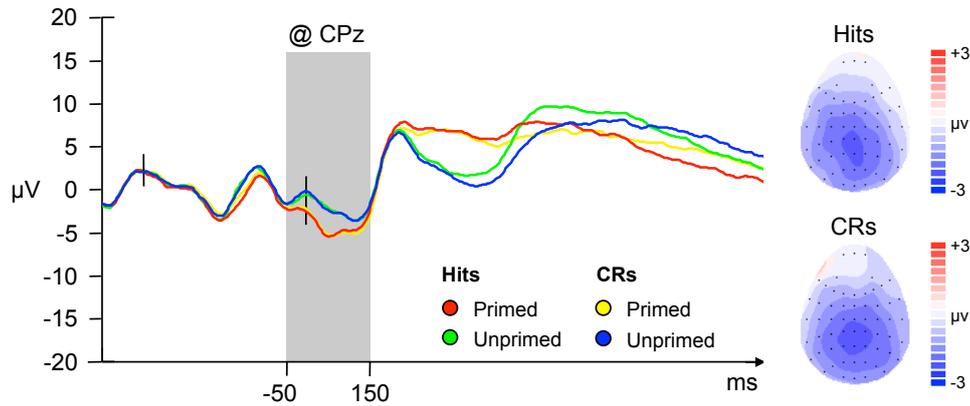


Figure 5.2: Priming @ CPz (-50-150ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode CPz, where effects were maximal. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Primed hits and correct rejections were more negative going than for unprimed hits and correct rejections across central and posterior locations.

at superior electrode sites over posterior locations. Subsidiary analysis focused on midline sites, contrasting the data at anterior (F, FC, C) and posterior (CP, P, PO) locations, confirmed that effects were significantly larger over posterior locations ($t(31)=2.23$, $p=0.034$). Further analysis on the data collapsed across posterior locations (CP, P, PO) and hemispheres, confirmed that effects were larger over superior sites than at medial ($t(31)=3.07$, $p=0.004$) or inferior sites ($t(31)=4.27$, $p<0.001$). Consistent with these results and the posterior maxima evident in Figure 5.2, further examination of the data confirmed that the effect for correct rejections was maximal at CPz ($t(31)=8.03$, $p<0.001$).

The next level of analysis was employed to compare the magnitude of priming effects for hits and correct rejections and was performed on difference waveforms, using ANOVA with the factors of test status (old, new), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Analysis revealed a significant interaction between test status, location and hemisphere [$F(2.1,63.6)=3.28$, $p=0.043$], indicating that the effect for hits is larger than the effect for correct rejections over the left hemisphere at frontal locations. Sub-

subsidiary analysis revealed a significant interaction between test status, hemisphere and electrode at frontal sites [$F(1,31)=5.16$, $p=0.013$], an interaction between test status and hemisphere at fronto-central sites [$F(1,31)=4.82$, $p=0.036$], and an interaction between test status, hemisphere and electrode at parieto-occipital sites [$F(1.5,45.4)=3.87$, $p=0.04$]. These results confirm the presence of a widely distributed effect maximal at centro-parietal locations for hits and correct rejections, which appears slightly larger for hits towards left frontal sites and for correct rejections over parieto-occipital sites in the right hemisphere.

The foregoing results suggest slight distributional differences between hits and correct rejections on the outer edges of the priming effects. To investigate whether these differences reflected genuine changes in topography, follow up analysis was performed on difference waveforms (primed-unprimed) for hits and correct rejections, on rescaled data. ANOVA was performed with the factors of test status (old, new), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (superior, mid, inferior). Analysis failed to identify a significant main effect of test status or any interactions including the factors of test status ($p>0.05$), confirming that the distribution of effects for hits and correct rejections did not differ, and suggesting that priming effects in both cases were driven by the same underlying neural generators.

In summary, during the -50-150ms time window primed hits and correct rejections were more negative going than unprimed hits and correct rejections, and these effects were maximal towards midline sites at centro-parietal locations. Crucially, magnitude analysis demonstrated only minor differences in amplitude on the outer edges of effects for hits and correct rejections, and topographic analysis confirmed the absence of differences in distribution, suggesting that this early effect was driven largely by exposure to the masked prime at test.

5.4.1.2 Time window 250 to 500ms

From 250ms after target onset waveforms for primed hits and correct rejections were more positive going than for unprimed hits and correct rejections across central and posterior locations (see Figure 5.3 for data from CPz). Initial analysis for hits revealed a significant main effect of condition [$F(1,31)=33.40$, $p<0.001$], along with significant interactions between condition, location and hemisphere [$F(1.5,46.6)=3.89$, $p=0.038$], condition, location and electrode [$F(3.2,99)=6.08$, $p=0.001$], and condition, hemisphere and electrode [$F(1.1,34.5)=6.56$, $p=0.013$]. Analysis for correct rejections produced a main effect of condition [$F(1,31)=82.59$, $p<0.001$], and a significant interaction between condition location and electrode [$F(3.9,120.2)=5.26$, $p=0.001$].

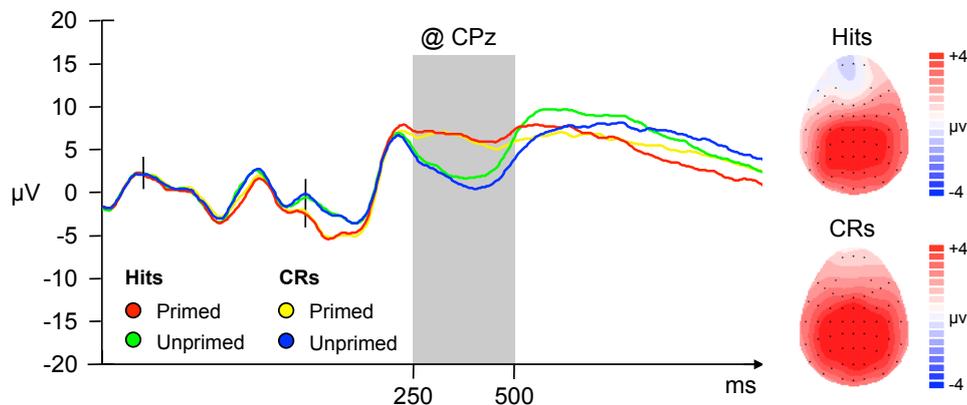


Figure 5.3: Priming @ CPz (250-500ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode CPz, where effects were maximal. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Primed hits and correct rejections were more positive going than unprimed hits and correct rejections across central and posterior locations

Table 5.5 shows the results of subsidiary analysis for hits and correct rejections at each location. Results for correct rejections revealed significant main effects and interactions between condition and electrode across locations, reflecting the presence of a widespread positivity for primed correct rejections toward superior

Table 5.5: Priming by location (250-500ms). Results of subsidiary analysis at separate locations for his and correct rejections.

Hits (250-500ms)	F	FC	C	CP	P	PO
Cond		$F(1,31)=12.55, p=0.001$	$F(1,31)=33.20, p<0.001$	$F(1,31)=48.43, p<0.001$	$F(1,31)=57.32, p<0.001$	$F(1,31)=57.74, p<0.001$
Cond*Hem	$F(1,31)=5.37, p=0.027$	$F(1,31)=4.98, p=0.033$				
Cond*Elec		$F(1.1,35.9)=7.87, p=0.006$	$F(1.1,33.9)=13.55, p=0.001$	$F(1.1,33.2)=21.33, p<0.001$	$F(1.1,34.6)=16.56, p<0.001$	$F(1.1,33.5)=11.84, p=0.001$
Cond*Hem*Elec		$F(1.4,42.7)=5.27, p=0.017$	$F(1.3,39.2)=9.71, p=0.002$			$F(1.6,48.8)=4.59, p=0.022$
CRs (250-500ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=26.62, p<0.001$	$F(1,31)=52.35, p<0.001$	$F(1,31)=84.90, p<0.001$	$F(1,31)=95.53, p<0.001$	$F(1,31)=92.57, p<0.001$	$F(1,31)=72.06, p<0.001$
Cond*Hem						
Cond*Elec	$F(1.3,40.4)=9.65, p=0.002$	$F(1.2,38.5)=20.80, p<0.001$	$F(1.3,39.9)=47.53, p<0.001$	$F(1.1,34.5)=58.48, p<0.001$	$F(1.1,35)=69.20, p<0.001$	$F(1.2,38.1)=45.87, p<0.001$
Cond*Hem*Elec						

electrode sites. Further examination of the data for correct rejections collapsed across locations and hemispheres confirmed that effects were larger at superior sites than at medial ($t(31)=7.43$, $p<0.001$) or inferior sites ($t(31)=7.54$, $p<0.001$). For hits analysis revealed main effects and interactions between condition and electrode extending from fronto-central to parietal-occipital locations, along with interactions including the factor of hemisphere at frontal, fronto-central, central and parieto-occipital locations. As can be seen in Figure 5.3, these interactions including the factor of hemisphere reflect that the effect for hits was slightly skewed over the right hemisphere at the locations identified. To allow comparison with effects for correct rejections, subsidiary analysis was performed on the data for hits collapsed across locations and hemispheres, to characterise interactions including the factor of electrode. Results confirmed that effects for hits were also larger at superior sites than at medial ($t(31)=2.82$, $p=0.008$) or inferior sites ($t(31)=3.78$, $p=0.001$). Further examination of the data demonstrated that the effects were maximal at electrode CPz for both hits ($t(31)=6.71$, $p<0.001$) and correct rejections ($t(31)=9.95$, $p<0.001$).

Magnitude analysis contrasting effects for hits and correct rejections revealed an interaction between test status, location and hemisphere [$F(1.8,55.8)=5.49$, $p=0.008$]. Subsidiary analysis at separate locations revealed a significant main effect of test status [$F(1,31)=6.94$, $p=0.013$], along with significant interactions between test status and hemisphere [$F(1,31)=15.95$, $p<0.001$], and test status and electrode [$F(1.5,46.9)=13.62$, $p<0.001$] at frontal locations. As can be seen in Figure 5.3 these results reflect greater differences for correct rejections than for hits over medial ($t(31)=2.53$, $p=0.017$) and inferior ($t(31)=2.58$, $p=0.015$) sites in the left hemisphere at frontal locations. These results suggest the presence of differences in the distribution of effects for hits and correct rejections,

with additional activation present at left-frontal locations for correct rejections. To investigate whether these differences reflected genuine changes in topography, follow up analysis was performed on difference waveforms (primed-unprimed) for hits and correct rejections, on rescaled data. Analysis revealed significant interactions between between test status and electrode [$F(1.1,34.7)=13.82$, $p<0.001$], and test status, location and hemisphere [$F(1.8,55)=4.42$, $p=0.020$], confirming the operation of additional sets of neural generators at left-frontal locations for correct rejections.

In summary, during the 250-500ms time window primed hits and correct rejections were more positive going than unprimed hits and correct rejections, and these effects were both maximal towards midline sites at centro-parietal locations, but differed in magnitude and distribution, with additional activity at left-frontal locations for correct rejections. Taken together the findings demonstrate similar posterior effects for hits and correct rejections, but for correct rejections this posterior effect was also accompanied by left-frontal activation, suggesting that matching information from the subliminal prime produces additional processing at left-frontal locations when words have not been studied previously.

5.4.1.3 Time window 500 to 1100ms

From 500ms after target onset waveforms for primed hits and correct rejections were more negative going than for unprimed hits and correct rejections at posterior locations, with the largest difference between conditions for hits (see Figure 5.4 for the data from CP1). Initial analysis for hits revealed a main effect of condition [$F(1,31)=19.65$, $p<0.001$], and a significant interaction between condition, hemisphere and electrode [$F(1.1,33.8)=4.62$, $p=0.036$]. As can be seen

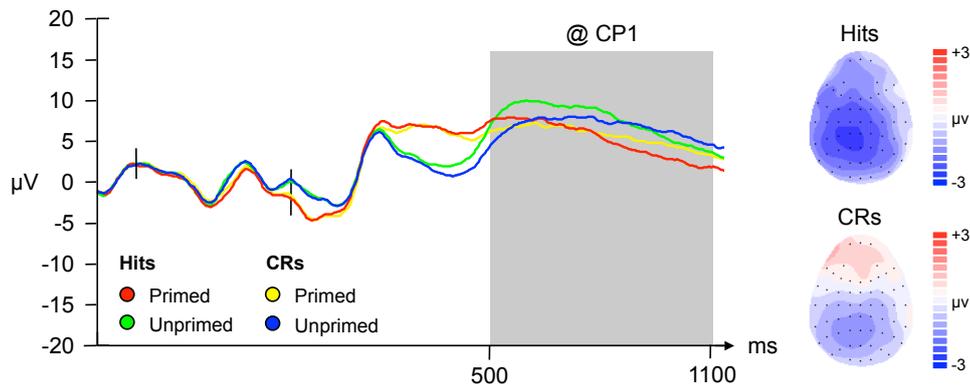


Figure 5.4: Priming @ CP1 (500-1100ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode CP1, where effects for hits were maximal. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Primed hits and correct rejections were more negative going than unprimed hits and correct rejections at posterior locations in the left hemisphere, with the largest difference between conditions for hits.

in Figure 5.4 these results reflect the presence of a negativity for primed compared to unprimed hits across locations, a difference that is stronger in the left hemisphere and over superior electrode sites. Subsidiary analysis collapsed across locations and electrodes demonstrated greater negativity over the left hemisphere ($t(31)=2.07$, $p=0.047$) and focused comparison of electrode sites in the left hemisphere revealed that effects for hits were larger at medial sites than at inferior sites ($t(31)=2.62$, $p=0.014$), with no significant difference apparent between medial and superior sites. Further examination of the data demonstrated that the effect for hits was maximal at electrode CP1 ($t(31)=4.77$, $p<0.001$).

Analysis for correct rejections produced a significant main effect of condition [$F(1,31)=5.92$, $p=0.021$], and a significant interaction between condition, location, hemisphere and electrode [$F(4.9,150.7)=2.37$, $p=0.044$]. Table 5.6 shows results of subsidiary analysis at separate locations for correct rejections. Results revealed significant main effects and interactions between condition and electrode extending from central to parieto-occipital locations, with interactions including

Table 5.6: Priming for CRs by location (500-1100ms). Results of subsidiary analysis at separate locations for correct rejections.

CRs (500-1100ms)	F	FC	C	CP	P	PO
Cond			$F(1,31)=5.76, p=0.023$	$F(1,31)=10.49, p=0.003$	$F(1,31)=17.19, p<0.001$	$F(1,31)=16.63, p<0.001$
Cond*Hem						$F(1,31)=4.55, p=0.041$
Cond*Elec			$F(1.3,39.7)=3.81, p=0.048$	$F(1.2,36.6)=7.55, p=0.007$	$F(1.1,35.5)=10.82, p=0.002$	$F(1.2,38)=11.84, p=0.001$
Cond*Hem*Elec				$F(1.3,40.2)=4.91, p=0.024$		

the factor of hemisphere at centro-parietal and parieto-occipital locations. Follow up analysis failed to demonstrate significant differences between hemispheres at centro-parietal or parieto-occipital locations ($p > 0.05$ in all comparisons). Further analysis on the data collapsed from central to parieto-occipital locations and across hemispheres revealed that effects were stronger at superior sites than at medial ($t(31) = 2.92$, $p = 0.006$) or inferior sites ($t(31) = 3.35$, $p = 0.002$). As can be seen in Figure 5.4 these findings reflect the presence of a slight negativity for primed correct rejections extending from central to parieto-occipital locations, with the largest difference between conditions over superior electrode sites. Further examination of the data demonstrated that the priming effect for correct rejections was maximal at electrode P1 ($t(31) = 4.34$, $p < 0.001$).

Magnitude analysis contrasting effects for hits and correct rejections revealed a significant main effect of test status [$F(1,31) = 6.12$, $p = 0.019$], and a significant interaction between test status, location and hemisphere [$F(2.2,67.2) = 5.81$, $p = 0.004$]. Subsidiary analysis at separate locations revealed main effects of condition extending from frontal to parietal locations ($p < 0.001$ in all comparisons), along with a significant interaction between test status, hemisphere and electrode [$F(1.8,57.2) = 7.82$, $p = 0.001$] at frontal sites, and an interaction between test status and hemisphere [$F(1,31) = 4.48$, $p = 0.043$] at fronto-central sites. As can be seen in Figure 5.4 these results confirm greater priming for hits than for correct rejections across locations and suggest a slightly more anterior distribution for hits than for correct rejections over the left hemisphere. Topographic analysis contrasting hits and correct rejections revealed a significant interaction between test status location and hemisphere [$F(2.1,66.4) = 5.73$, $p = 0.004$], confirming a difference in distribution, with a slightly more anterior focus for hits.

In summary, during the 500-1100ms time window primed hits and correct rejections were more negative going than for unprimed hits and correct rejections at central and posterior locations, with the largest difference between conditions for hits. The magnitude and topography of these effects differed, with a larger magnitude and a more anterior focus for hits than for correct rejections. Taken together these results demonstrate that this late post-retrieval priming effect was modulated by study exposure, being larger and more widespread for studied than for unstudied words.

5.4.2 Summary

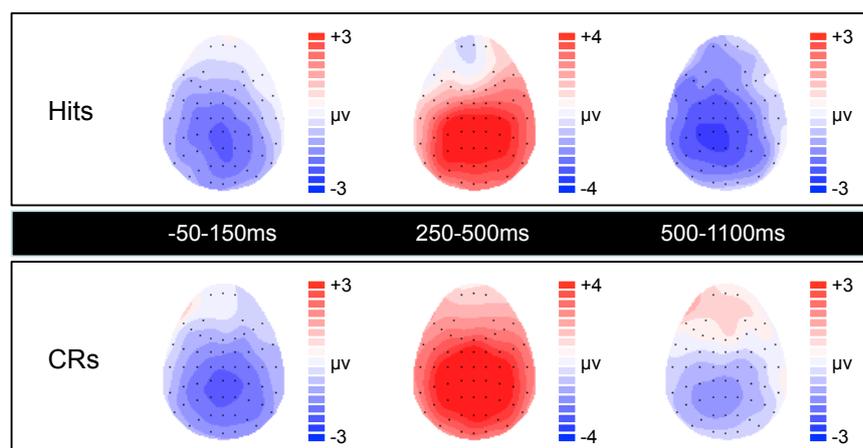


Figure 5.5: Priming topographic summary. Topographic maps summarise differences between the unprimed and primed conditions for hits and correct rejections over time.

Analysis of the data confirmed the presence of three priming related modulations, an early (-50-150ms) posterior negativity, followed by a widespread central positivity (250-500ms), and a later (500-1100ms) posterior negativity for primed compared to unprimed words. The early negativity, evident between -50-150ms, was maximal towards superior sites at centro-parietal locations for hits and correct rejections and did not differ substantially in magnitude or distribution. Be-

tween 250-500ms, primed hits and correct rejections were more positive going than unprimed hits and correct rejections, and these effects were maximal towards midline sites at centro-parietal locations, but effects for hits and correct rejections did differ in magnitude and distribution, with additional activity at left-frontal locations for unstudied compared to studied words. The late post-retrieval negativity, evident between 500-1100ms, was maximal at superior sites over central and posterior locations and appeared to be reliably modulated by exposure to words at study, being larger in overall magnitude and recruiting additional left-frontal regions for processing of studied compared to unstudied words.

5.4.3 Memory effects

Figure 5.6 shows grand average ERPs time locked to the onset of the prime for hits and correct rejections in the unprimed condition, and Figure 5.7 shows grand average ERPs for the primed condition. Visual inspection of the grand average waveforms shows that ERPs elicited in the unprimed condition were more positive going for hits than for correct rejections between 300-500ms and 500-800ms, with the greatest differences at mid-frontal and left centro-parietal locations. By contrast old/new differences were not evident in the primed waveforms during the 300-500ms time window and there was only a slight positivity over left-parietal locations for primed hits compared to primed correct rejections between 500-800ms. From around 800ms after target onset the waveforms for hits were more negative going than waveforms for correct rejections in both conditions at midline sites.

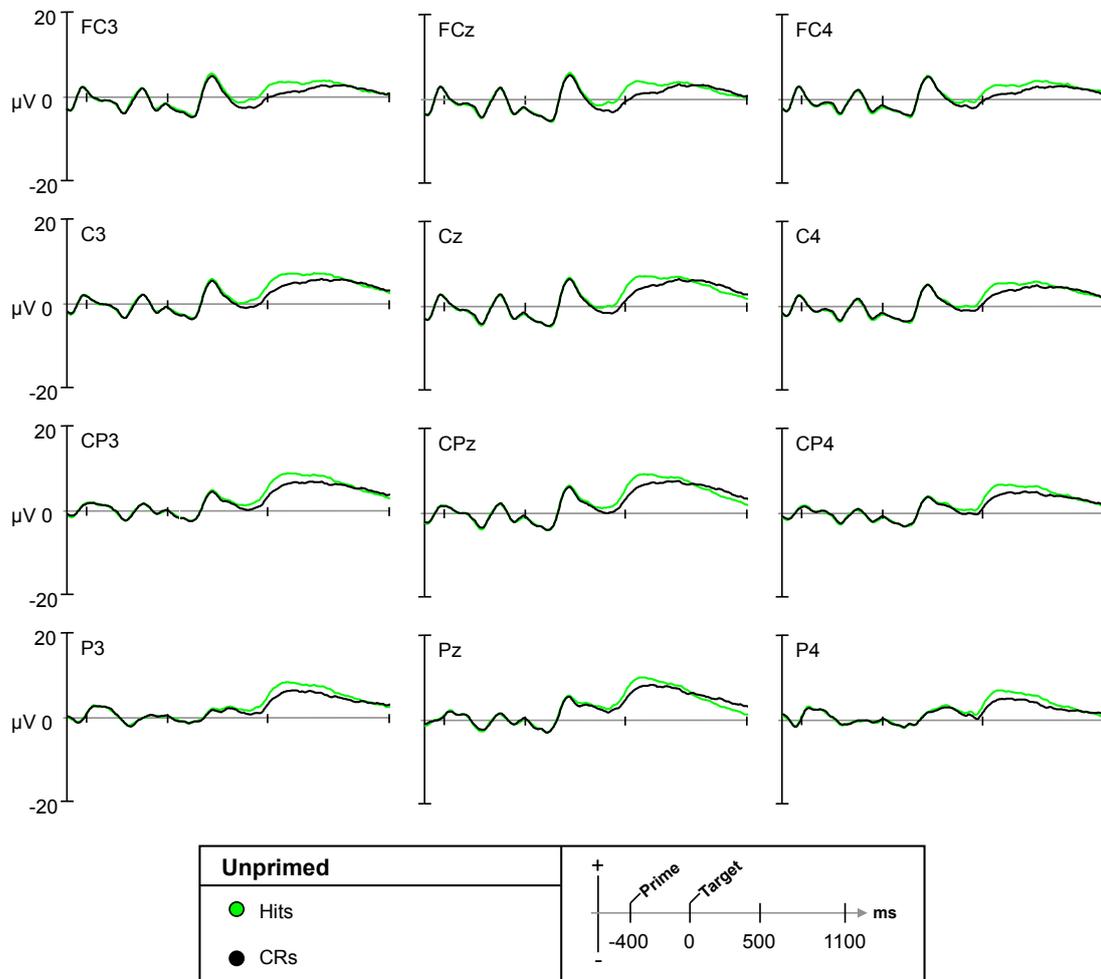


Figure 5.6: Memory ERPs for unprimed words. Grand average ERPs for hits and correct rejections in the unprimed condition. Waveforms were more positive going for hits than for correct rejections at mid-frontal and left centro-parietal locations between 300-500ms and 500-800ms. From 800ms onwards waveforms for hits were more negative going than for correct rejections at midline sites.

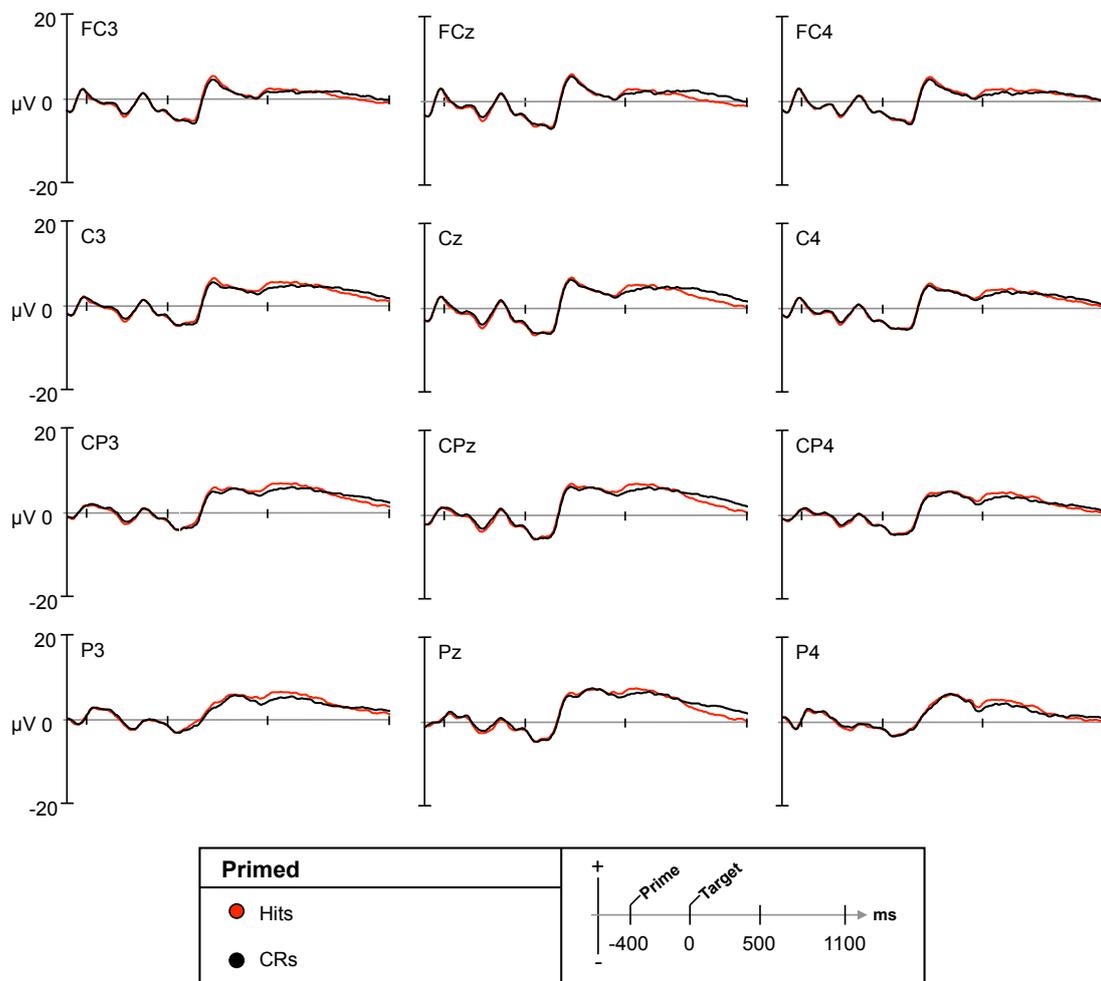


Figure 5.7: Memory ERPs for primed words. Grand average ERPs for hits and correct rejections in the primed condition. In contrast to the unprimed condition, no mid-frontal memory effects are evident between 300-500ms for the primed condition. From 500-800ms waveforms show a very small positivity for hits at left parietal locations and from 800ms onwards waveforms for hits were more negative going than for correct rejections at midline sites.

For memory contrasts the data were analysed over 300-500ms, 500-800ms and 800-1100ms time windows, chosen to capture the neural correlates of familiarity, recollection and late right-frontal old/new effects reported in the literature. The first level of analysis was designed to identify variations in old/new effects across conditions and time windows, employing ANOVA with the factors of condition (unprimed, primed), test status (old, new), location (Fz, FCz, Cz, CPz, Pz) and time window (300-500ms, 500-800ms, 800-1100ms). Results produced significant interactions between test status and time window [$F(1.6,48.4)=15.31$, $p<0.001$], and test status, condition and location [$F(1.6,48.7)=6.69$, $p=0.005$]. The presence of these significant interactions provides evidence of variation in the pattern of old/new effects between conditions and across time windows.

Table 5.7: Memory ANOVAs by time window. Results of ANOVAs contrasting midline sites with the factors of condition, test status and location over the three time windows chosen for analysis of old/new effects.

	300-500ms	500-800ms	800-1100ms
Test status	$F(1,31)=14.70$, $p=0.001$	$F(1,31)=6.80$, $p=0.014$	$F(1,31)=4.22$, $p=0.048$
Test status*Cond	-	$F(1,31)=10.02$, $p=0.003$	-
Test status*Cond*Loc	$F(1.8,55.9)=8.24$, $p=0.001$	$F(1.5,47.2)=3.47$, $p=0.051$	-

To further elucidate the pattern of memory related activity, a second level of analysis was performed separately on the data from each time window, using ANOVA with the factors of condition (unprimed, primed), test status (old, new) and location (Fz, FCz, Cz, CPz, Pz, POz). The results of this analysis are summarised in Table 5.7 and demonstrate that old/new effects varied across time windows and interacted with the factors of condition and location in the first two time windows. Subsidiary analyses employed to investigate old/new effects were performed separately for each condition on the average activity over three electrodes sites for four regions of interest: left-frontal (LF: F1, F3, F5), right-frontal (RF:

F2, F4, F6), left-parietal (LP: P1, P3, P5) and right-parietal (RP: P2, P4, P6), using ANOVA with the factors of test status (old, new), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior); the results for each time window are reported separately in the following sections.

5.4.3.1 Time window 300 to 500ms

Between 300 and 500ms unprimed hits were more positive going than unprimed correct rejections at mid-frontal locations, but no differences between hits and correct rejections were evident for the primed condition (see Figure 5.8 for the data from FCz). Importantly, analysis of the primed condition confirmed the absence of old/new effects, demonstrating no main effect or interactions including the factor of test status ($p > 0.05$ in all comparisons). By contrast, initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,31)=20.53$, $p < 0.001$], and a significant interaction between test status, location and electrode [$F(1.2,37.3)=4.00$, $p=0.046$]. Subsidiary analysis at parietal locations produced a significant main effect of test status [$F(1,31)=10.23$, $p=0.003$], but no significant interactions including the factor of test status, reflecting a very slight positivity across sites at parietal locations. Analysis at frontal locations revealed a significant main effect of test status [$F(1,31)=18.08$, $p < 0.001$] and a significant interaction between test status and electrode [$F(1.2,38)=9.87$, $p=0.002$].

These findings suggest the presence of a positivity for unprimed hits that is maximal towards superior sites at frontal locations, further analysis on the data from frontal sites collapsed across hemispheres demonstrated that the old/new difference was larger at superior ($t(31)=3.31$, $p=0.002$) and medial sites ($t(31)=3.21$,

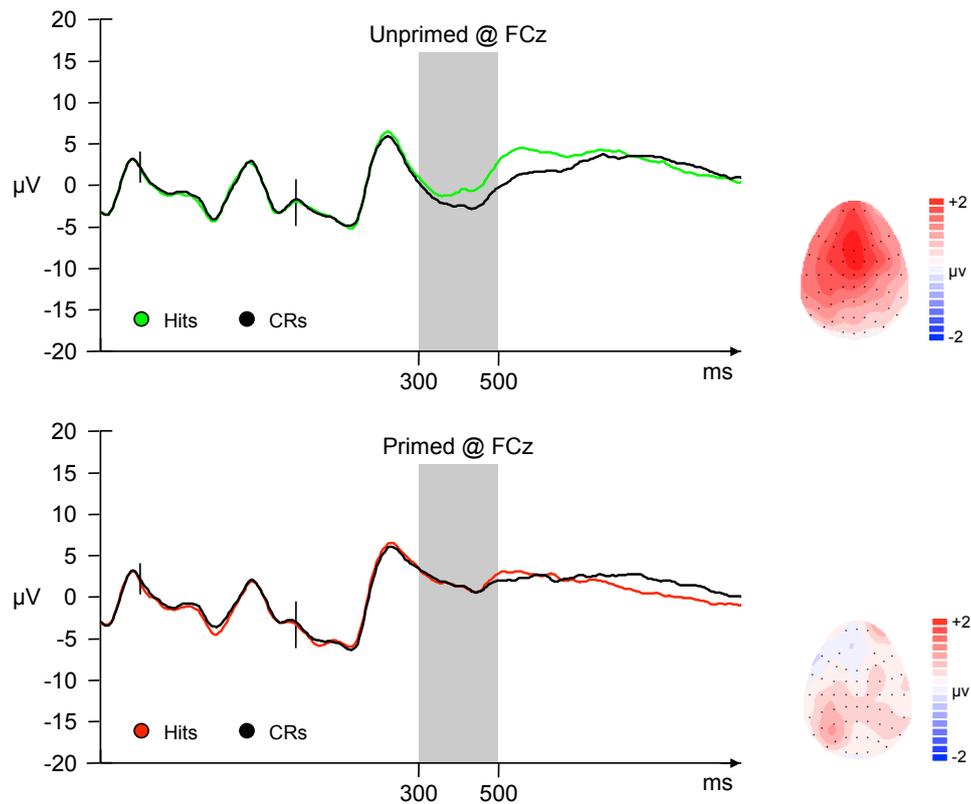


Figure 5.8: Memory @ FCz (300-500ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode FCz. Topographic maps show the difference between the hits and correct rejections for both conditions. Mid-frontal old/new effects were only evident in the unprimed condition during the 300-500ms time window.

$p=0.003$) than at inferior sites, confirming the presence of mid-frontal old/new effects for the unprimed condition. Further examination of the data demonstrated that the old/new effect for unprimed words was maximal at electrode FCz ($t(31)=5.10$, $p<0.001$). As can be seen in the topographic map in Figure 5.8, the distribution of the old/new effect reported for the unprimed condition closely resembles FN400 effects previously reported in the literature. Magnitude and topographic analysis contrasting the primed and unprimed conditions were not performed for the current time window due to the absence of significant old/new effects in the primed condition.

In summary, analysis for the unprimed condition demonstrated the presence of a mid-frontal old/new effect, consistent with the distribution of FN400 effects previously reported in the literature. By contrast, analysis for the primed condition demonstrated the absence of mid-frontal old new effects; a finding that is particularly surprising given recent links between the FN400 and conceptual priming in the literature.

5.4.3.2 Time window 500 to 800ms

Between 500 and 800ms unprimed hits and correct rejections differed over frontal and central locations, with a focus over the left hemisphere at centro-parietal locations (see Figure 5.9 for data from CP3). For the primed condition hits were slightly more positive going than for correct rejections at parietal locations in both hemispheres. Initial analysis for the primed condition revealed a marginally significant main effect of test status [$F(1,31)=3.97$, $p=0.056$] and a significant interaction between test status and electrode [$F(1.3,40.4)=4.87$, $p=0.025$]. Subsidiary analysis focused on parietal sites, where differences between hits and correct rejections appeared to be maximal, revealed a significant main effect of test status [$F(1,31)=7.23$, $p=0.011$] and a significant interaction between test status and electrode [$F(1.3,39.2)=4.40$, $p=0.032$]. As can be seen in Figure 5.9 these results reflect the presence of a slight positivity for primed hits over medial sites in both hemispheres. Further analysis on the data from parietal locations collapsed across hemispheres confirmed this result, demonstrating larger effects at medial sites than at superior sites ($t(31)=4.31$, $p<0.001$).

Initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,31)=18.94$, $p<0.001$], but no significant interactions including the

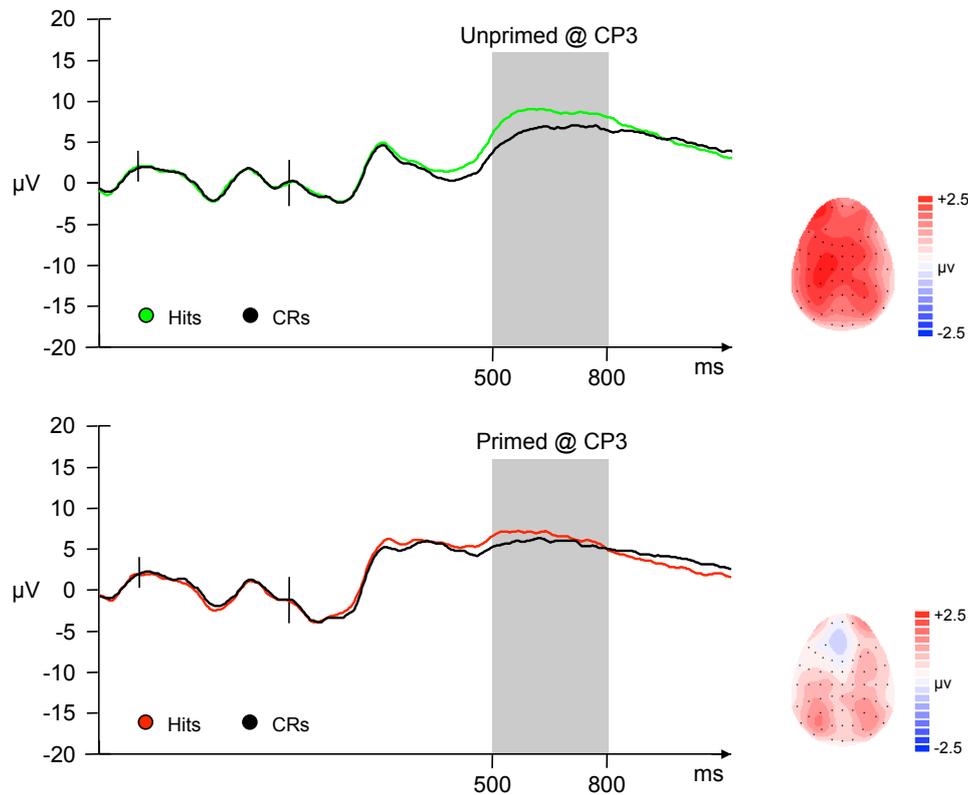


Figure 5.9: Memory @ CP3 (500-800ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode CP3. Topographic maps show the difference between the hits and correct rejections in both conditions. Unprimed hits and correct rejections differed across locations, with an apparent focus over the left hemisphere at centro-parietal locations. Primed hits were slightly more positive going than correct rejections over parietal sites.

factor of test status, reflecting more positive going activity for hits across frontal and parietal locations. Further examination of the data demonstrated that the old/new difference for the unprimed condition was maximal at electrode CP3 ($t(31)=4.07$, $p<0.01$). As can be seen in Figure 5.9, the distribution of effects for the unprimed condition suggests a continuation of mid-frontal activity from the 300-500ms time window, combined with a shift towards centro-parietal locations in the left hemisphere. Analysis focused on centro-parietal locations revealed a main effect of test status [$F(31)=16.16$, $p<0.001$], but failed to demonstrate an interaction between test status and hemisphere, suggesting that this effect does

not exhibit a significant shift towards left-parietal locations and merely reflects continuation of mid-frontal differences from the previous time window.

To investigate whether old/new effects evident for the unprimed condition between 300-500ms and 500-800ms differed in topography, analysis was performed on rescaled data, using ANOVA with the factors of time window (300-500ms, 500-800ms), location (frontal, parietal), hemisphere (left, right), electrode (inferior, mid, superior). Results revealed no significant main effects or interactions including the factor of time window ($p > 0.05$), demonstrating that the later effect was not topographically dissociable from the FN400 effect present during the 300-500ms time window.

In summary, analysis for the primed condition demonstrated a very slight positivity for hits over medial sites at parietal locations in both hemispheres. Despite the appearance of a slight shift towards a more left-sided distribution for the unprimed condition, analysis of the data confirmed continuation of FN400 old/new effects from the previous time window, clearly demonstrating that this later effect was not topographically dissociable from the earlier FN400.

5.4.3.3 Time window 800 to 1100ms

During the post-retrieval period, waveforms in both conditions were more negative going for hits than for correct rejections at midline sites, where effects appeared larger and more distributed for primed words (see Figure 5.10 for data from Pz). Initial analysis for the unprimed condition revealed a significant interaction between test status, location and electrode [$F(1.2,37.4)=5.25$, $p=0.022$]. Subsidiary analysis at frontal locations revealed no main effects or interactions, but analysis at parietal locations did reveal an interaction between test status

and electrode [$F(1.1,35.6)=17.65$, $p<0.001$]. As can be seen in Figure 5.10 these results reflect the presence of a negativity for unprimed hits at posterior locations over superior sites. Subsidiary analysis on the data from parietal locations collapsed across hemispheres confirmed this result, demonstrating larger effects over superior sites than at medial ($t(31)=4.56$, $p<0.001$) or inferior sites ($t(31)=4.30$, $p<0.001$).

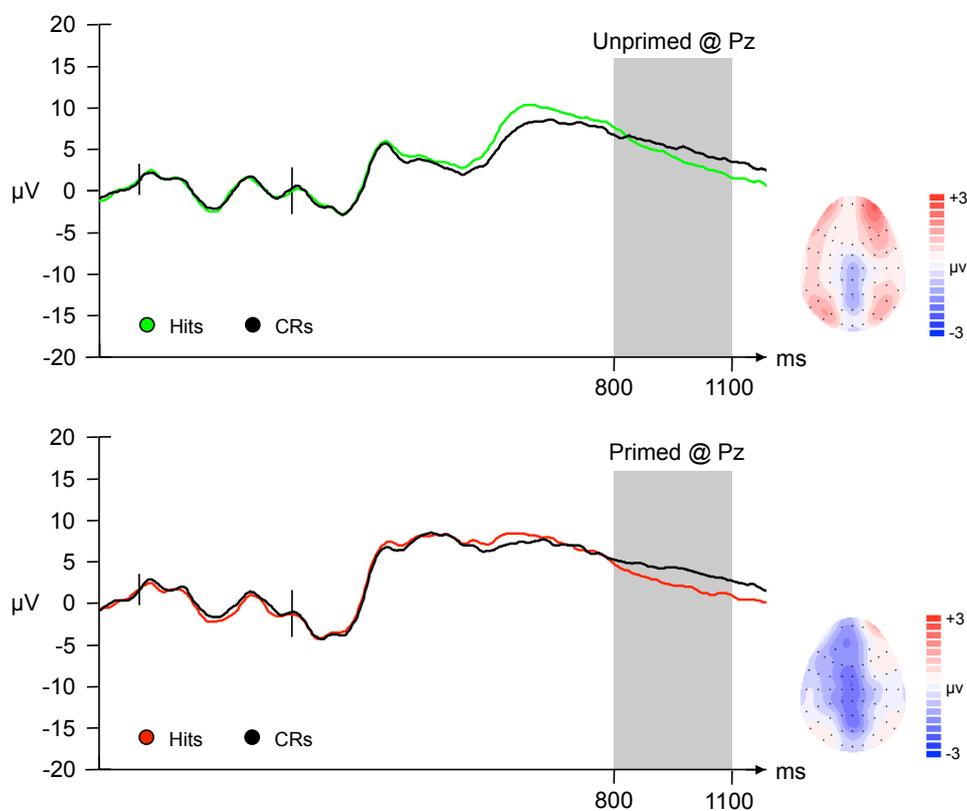


Figure 5.10: Memory @ Pz (800-1100ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode Pz. Topographic maps show the difference between the hits and correct rejections in both conditions. Waveforms in both conditions were more negative going for hits than for correct rejections at midline sites, where the effect appeared larger and more distributed for primed words.

Initial analysis for the primed condition revealed significant interactions between test status, location and hemisphere [$F(1,31)=4.73$, $p=0.037$], test status, location and electrode [$F(1.4,44.7)=4.36$, $p=0.029$], and test status, hemisphere

and electrode [$F(1.5,46.4)=4.28$, $p=0.029$]. Subsidiary analysis at frontal locations demonstrated a significant interaction between test status, hemisphere and electrode [$F(1.3,40.7)=4.49$, $p=0.031$] and analysis at parietal locations revealed a significant interaction between test status and electrode [$F(1.2,36.5)=32.70$, $p<0.001$]. As can be seen in Figure 5.10 these results confirm the presence of a negativity for hits extending from frontal to parietal locations at superior electrode sites, with a slight skew over the left hemisphere at frontal sites. Further analysis on the data from parietal locations collapsed across hemispheres confirmed the presence of larger effects over superior sites than at medial ($t(31)=6.94$, $p<0.001$) or inferior sites ($t(31)=5.87$, $p<0.001$). Further analysis on the data from frontal sites confirmed the presence of larger effects over the left hemisphere across electrode sites (inferior: $t(31)=2.90$, $p=0.007$, medial: $t(31)=3.96$, $p<0.001$, superior: $t(31)=2.68$, $p=0.012$), with the largest difference between hemispheres evident for medial sites.

The foregoing pattern of results suggests slight differences between conditions in the magnitude and distribution of these late old/new effects, with greater negativity overall, and more widespread activity over left-frontal sites for primed words. Magnitude analysis contrasting effects for the unprimed and primed conditions revealed a marginally significant main effect of condition [$F(31)=4.18$, $p=0.049$], reflecting slightly greater negativity across locations for the primed condition. In summary, analysis for the unprimed and primed conditions demonstrated the presence of a negativity for hits over superior electrode sites, that was slightly greater in magnitude for the primed condition, suggesting that this late memory effect was modulated by priming.

5.4.4 Summary

Between 300-500ms data for the unprimed condition demonstrated the presence of mid-frontal old/new effects, that were consistent with the distribution of FN400 old/new effects previously reported in the literature. Surprisingly, given recent links between priming induced fluency and familiarity, mid-frontal old new effects were not evident in the data for the primed condition. During the 500-800ms time window the data demonstrated the continuation of mid-frontal old/new differences for the unprimed condition, while data for the primed condition demonstrated very small old/new differences over medial sites at parietal locations in both hemispheres. Between 800-1100ms the data demonstrated the presence of a negativity for hits over superior electrode sites in both conditions that was modulated by the priming manipulation, being slightly larger in overall magnitude for primed words.

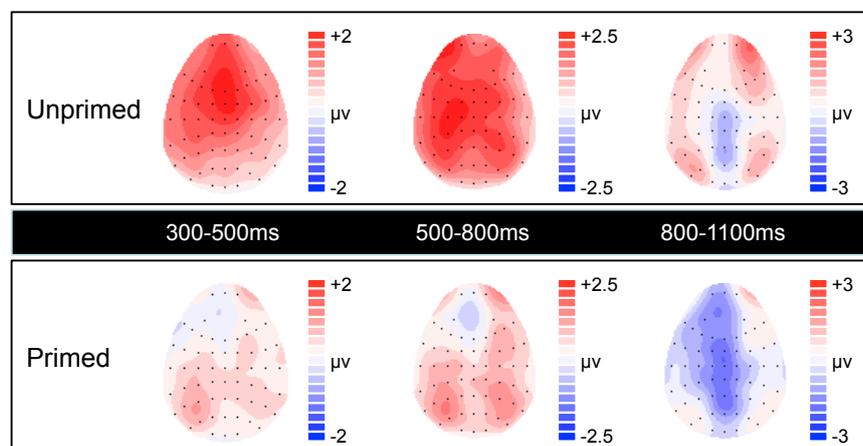


Figure 5.11: Memory topographic summary. Topographic maps summarise differences between hits and correct rejections for the unprimed and primed conditions over time.

5.5 Discussion

The aim of the current experiment was to explore interactions between repetition priming and neural correlates of familiarity, based on previous behavioural research demonstrating that fluency induced by priming should selectively impact familiarity. To encourage reliance on familiarity based recognition, a shallow encoding task was employed and responses at test were speeded, reasoning that this would enhance reliance on rapid and automatic processing. Response time data demonstrated the presence of robust priming effects that were equivalent in magnitude for hits and correct rejections. Despite this strong evidence of the operation of priming at test, measures of accuracy, discrimination, bias, and process estimates of familiarity and recollection were unaffected by the priming manipulation. These findings are in direct contrast to previous research, demonstrating that priming selectively impacts familiarity and is normally associated with an increase in the hit rate accompanied by an increase in the proportion of false alarms (e.g., see Rajaram, 1993, Exp.3). Based on the work of Jacoby and Whitehouse (1989), the current findings may appear to suggest that participants were indeed aware of the prime words, but ratings of prime awareness in the current study do not support this conclusion.

Recent work has suggested that prime duration can also exert an influence on recognition performance, demonstrating that durations of less than 100ms produce positive priming effects, while longer durations produce negative priming effects (Huber, Clark, Curran & Winkielman, 2008). On the basis of this evidence, it is possible that the 48ms prime duration employed in the current experiment is responsible for failure to detect increases in false alarm rates. However, the prime duration used here closely matches those used in previous studies that do

report such changes in performance (e.g., Rajaram, 1993; Woollams et al., 2008), making this explanation unlikely. One potentially critical difference between the current study and previous research is the nature of the unprimed baseline. Unprimed targets are commonly preceded by an unrelated word to act as a baseline, while the current study employed repetition of the word “blank” to act as a more neutral baseline. Recent research has demonstrated that lexical priming for unassociated and dissimilar words can occur rapidly and uncontrollably (Estes & Jones, 2009), suggesting that the use of unrelated words may represent a significant confound. As such, it is plausible that the use of unrelated words in previous research may have actually influenced performance on unprimed trials, making it appear as if there was a change in performance on primed trials. Alternatively, forced reliance on more automatic responding may have inhibited conscious fluency attributions in the current study, which in turn eliminated differences in performance across conditions. While it is difficult to discriminate between these alternative explanations of the current findings at this stage, this issue will be re-addressed after discussion of the ERP results.

Contrasting ERPs for primed and unprimed words revealed the presence of three priming related modulations; an early (-50-150ms) centro-parietal negativity, followed by a centro-parietal positivity (250-500ms), and a later (500-1100ms) negativity at centro-parietal locations. Previous research on the time course of visual word recognition has identified a number of early onsetting components that are modulated by immediate masked priming, including a posterior P150 component, an anterior N250 component, and a posterior P325 component (Holcomb & Grainger, 2006). However, the early effect found here 50ms prior to target onset (350ms post-prime) does not map directly onto any of these early visual components, which have all been found to be more positive going for primed than

for unprimed words. The early negativity reported here did not differ substantially in magnitude or distribution for hits and correct rejections, suggesting that exposure to words at study did not influence this effect. Waveforms diverge just prior to target onset suggesting that this early effect may reflect some form of anticipation of the upcoming target, being more negative going when the prime was predictive of the target, but its exact functional significance remains unclear at this stage. The centro-parietal positivity present between 250-500ms, replicates the findings of Woollams et al. (2008) and Lucas et al. (2012), reflecting a modulation of the N400 component.

Attenuation of the N400 is commonly found in priming experiments and is generally thought to reflect facilitated processing of stimulus meaning (see Kutas & Federmeier, 2011, for a recent review). While some studies have suggested that semantically related primes require conscious processing to produce N400 effects and do not appear under masked conditions (Brown & Hagoort, 1993), others have found that N400 semantic priming occurs under masked and unmasked conditions (e.g., Deacon, Hewitt, Yang & Nagata, 2000). However, repetition priming has been found to reliably attenuate N400 effects in masked and unmasked priming paradigms (e.g., Holcomb, Reder, Misra & Grainger, 2005; Misra & Holcomb, 2003; Schnyer, Allen & Foster, 1997). In addition to N400 effects, a late negativity for primed versus unprimed items was also observed between 500-1100ms over posterior locations, and appeared to be reliably modulated by exposure to words at study, being larger in overall magnitude and recruiting additional left-frontal regions for processing of studied compared to unstudied words. It is not common in priming experiments to investigate effects occurring later than the N400, but one paper has reported post-retrieval effects for conceptual fluency.

Wolk et al. (2004) identified a frontally focused positivity for unstudied compared to studied words between 800-1600ms for items preceded by predictive sentence frames. The authors interpreted this result as reflecting the assessment and attribution of enhanced fluency. However, late effects in the current study onset earlier, had a posterior distribution and were more negative going for primed words. Despite differences between these studies, it is plausible that the late effect observed here may also reflect processing related to whether fluency should be attributed to prior exposure. The larger magnitude of this late effect for hits than for correct rejections provides tentative support for this view, as a higher degree of fluency would be expected for studied than for unstudied words.

Memory research has identified a late posterior negativity (LPN) onsetting from around 600ms that exhibits a similar distribution to the one reported in the current study, and this late component has often been found in item recognition tasks where response conflict creates a need for enhanced action monitoring (Johansson & Mecklinger, 2003). This exact functional significance of this effect remains unclear, for example, it has been related to processes operating on the products of retrieval (Mecklinger, 1998), and has also been described as a strategic search process for retrieving source information (Senkfor & Van Petten, 1998). More importantly, it has been related to monitoring retrieval to avoid classifying similar lures as old (Curran, 2000), which fits well with the idea that items that are associated with a greater degree of fluency (i.e., studied and primed) will elicit a larger LPN, as was found in the current study.

For memory effects, contrasting ERPs for the primed and unprimed conditions revealed an intriguing pattern of results. Data for the unprimed condition demonstrated the presence of mid-frontal old/new effects that were consistent with the distribution of FN400 old/new effects previously reported in the literature, and

continued into the 500-800ms time window. Surprisingly, given recent links between priming induced fluency and familiarity, mid-frontal old/new effects were not evident in the data for the primed condition. One potential criticism of the current data is that old/new differences were present in the primed condition but were not measurable due to overlap with the N400 effect during the same time window. However, this explanation of the current data is highly unlikely, given that previous research employing a design analogous to the one used has clearly demonstrated the presence of priming and familiarity effects during the same time period (e.g., Lucas et al., 2012; Woollams et al., 2008). In addition, it could be argued that failure to find FN400 effects in the primed condition was due to a lack of power, but as trial numbers were matched across conditions and FN400 effects were present in the unprimed condition, it is also highly unlikely that this can account for the difference in findings across conditions. In short, the current data demonstrates a genuine absence of the FN400 following priming, suggesting that repetition priming can support recognition in the absence of explicit memory signals.

The current results are only partially consistent with prior research demonstrating the absence of mid-frontal old/new effects, because unlike earlier work significant left-parietal old/new effects were not clearly evident in the data for the primed condition, and the stimuli employed here were meaningful (e.g., Voss et al., 2010b; Yovel & Paller, 2004). The current findings strongly suggest that it is not merely the degree of meaningfulness that determines the presence or absence of FN400 effects, but that its presence or absence directly relates to the mode of retrieval. In a previous ERP study, Badgaiyan and Posner (1997) employed a word-stem completion task and varied the retrieval instructions. Implicit instructions required participants to complete stems with the first word that came to mind, and

explicit instructions required participants to complete stems with words shown during the study phase. The authors found activity reductions for primed words in the right posterior cortex under implicit and explicit instructions, but only found additional activity at frontal sites under explicit instructions, when priming was not a sufficient basis for making a response. While the current study did not directly manipulate retrieval instructions, speeding the old/new decision and employing a two stage RK procedure, where subjective reports were only required after the old/new decision had been made, may have reduced requirement for an explicit memory search, driving the observed absence of FN400 effects in the primed condition.

The absence of explicit old/new effects in the primed condition combined with matched behavioural performance across conditions demonstrates that priming is sufficient to support accurate recognition, consistent with previous findings (Voss et al., 2008), but goes further in demonstrating that priming can also support recognition for meaningful stimuli. N400 priming effects found in the current study differed in magnitude and distribution on the outer edges of effects, with additional activity at left-frontal locations for unstudied compared to studied words. A number of functional imaging studies have implicated reductions in the Left Inferior Prefrontal Cortex (LIPC) with the retrieval of lexical/semantic knowledge (e.g., Fiez, 1997; Poldrack et al., 1999). As such, the appearance of additional left-frontal activity for correct rejections could actually be driven by an underlying reduction in the LIPC for studied words, cancelling out positivity at left-frontal sites for hits as a result of prior exposure to words at study. While this claim is tentative, interpreting the difference in N400 effects found here in this way provides evidence for changes in effects as a result of study exposure, and suggests that implicit recognition may be based on fluency signals from enhanced

lexical access driven by repetition. However, this account is not straightforward as it would also imply that performance should be poorer for unstudied words that were primed at test, as these too would be processed more fluently, leading to misattribution.

Between 800-1100ms the data demonstrated the presence of a negativity for hits that was larger for the primed than for the unprimed condition. This late on-setting difference between hits and correct rejections also resembled the LPN reported earlier for the priming contrast. Previous research has demonstrated that the LPN is larger when source information is necessary for accurate discrimination (Cycowicz, Friedman & Snodgrass, 2001). On this view, the late negativity reported in the current experiment may act as a control mechanism for lexical fluency by reconstructing information from the study episode prior to response execution (Johansson & Mecklinger, 2003). Recognition performance driven by facilitated access to abstract lexical representations may predict an increase in false alarm rates following priming, but it is plausible that if multiple repetitions lead to a high degree of fluency, as is the case for studied words that are also primed, that this fluency initiates a search for a corresponding episodic trace. The greater negativity for primed hits found in the current study is consistent with this interpretation, and on this view, facilitated access to lexical representations does not necessitate changes in behavioural performance when recognition is not reliant upon explicit familiarity.

5.5.1 Summary

Overall, the findings are consistent with the existence of neural circuits supporting priming that are independent of circuits associated with familiarity, and that

priming signals are sufficient to drive accurate recognition in the absence of the FN400. Crucially, in contradiction to recent findings in the literature, the current study strongly suggests that the FN400 is not directly related to conceptual priming. In line with the findings reported here, a recent study by De Chastelaine, Friedman, Cykowicz and Horton (2009) demonstrated that FN400 effects were not related to familiarity or conceptual priming, suggesting instead that the FN400 may reflect a control process that is required to support retrieval only when memory traces are weak. Moreover, it has been demonstrated that priming can enhance the formation of episodic memory traces (Gagnepain, Lebreton, Desgranges & Eustache, 2008), suggesting that priming in the current experiment negated the need for explicit control of retrieval by producing a stronger memory trace. While the details of the exact mechanisms driving recognition in the absence of awareness remain unclear at this stage, the current study clearly demonstrates that under certain circumstances feelings of familiarity may become redundant and unnecessary.

Chapter 6

ERP 2

6.1 Introduction

ERP research to date has largely focused on the relationship between priming and episodic familiarity as indexed by the FN400, based on a wealth of behavioural evidence suggesting that fluency induced by priming selectively impacts familiarity. However, recent evidence suggests that measures used to identify the contribution of familiarity and recollection behaviourally, particularly the standard remember know procedure, may prevent detection of interactions between priming and recollection (e.g., Higham & Vokey, 2004). Basically, the problem posed is that dual-process models and the binary RK decisions based on them, presuppose that R responses can only be reported for studied words, due to reliance of retrieval of context to characterize recollection, excluding the possibility that the phenomenological experience of recollection could be illusory and influenced by fluency. Higham and Vokey (2004) investigated illusory recognition, employing an independent scales methodology, where participants were asked to rate each item

for familiarity and recollection on a 4-point scale, to address issues associated with binary RK decisions, and demonstrated an increase in illusory R responses for old/new targets preceded by repetition primes. These findings suggest that repetition induced fluency can also impact recollection and have been supported by more recent studies employing this independent ratings method.

Kurilla and Westerman (2008) demonstrated that under standard RK conditions fluency induced by masked repetition primes selectively increases the proportion of know responses, but under independent RK conditions they found increases in the proportion of both R and K responses for repetition and conceptual primes. Brown and Bodner (2011) took this approach further and found parallel effects of priming and levels of processing on both processes, demonstrating increases in the proportion of recollection and familiarity for both manipulations. Taken together, the findings from these behavioural studies suggest that under certain circumstances recollection is influenced by priming, but this independent ratings method has not been widely adopted in the literature, making it difficult to assess whether it is the independent or standard RK ratings that in fact lead to artifactual conclusions in this case. Importantly for the purposes of the current investigation, reports of fluency increasing the proportion of recollection are not limited to investigations employing independent ratings and have also been found on occasion by studies employing more standard RK procedures.

Taylor and Henson (2012) employed a masked priming paradigm with a binary RK decision to examine the effects of repetition and conceptual priming on subjective reports of familiarity and recollection. Results demonstrated an increase in the proportion of remember responses for studied words that were preceded by conceptual primes, but not for words preceded by repetition primes, which were associated with the standard increase in K responses for studied and unstudied

words. This behavioural finding was replicated in a follow-up fMRI study using the same design, which additionally demonstrated that conceptual primes modulated activity in parietal regions previously associated with recollection (Taylor, Buratto & Henson, 2013). The finding that only conceptual priming increased the proportion of R responses is odd given that the evidence reported earlier demonstrates increases in R responses for repetition and conceptual primes, and in light of the fact that the authors failed to replicate the result when conceptual blocks were not intermixed with repetition blocks. It is likely that differences in results across these experiments can be accounted for by factors other than the specific nature of the prime itself, such as differences in prime duration or visibility between experiments. Nonetheless, the fMRI findings of Taylor and colleagues go some way towards moving beyond difficulties with the details of RK procedures, relating conceptual priming to brain regions previously associated with recollection.

The studies reviewed so far have all employed priming during the recognition test phase, but recollection has also been related to priming in another fMRI study examining the impact of priming at encoding on subsequent memory. Gagnepain et al. (2011) contrasted primed and unprimed auditory words presented along with distracting sounds and found that priming at encoding increased the occurrence of subsequent recollection. In addition, the authors demonstrated that repetition priming reduced activity in MTL regions previously associated with recollection. The authors suggest that priming facilitates better encoding of contextual details, resulting in the observed increase in recollection, because it reduces the level of attentional resources tied up in processing of the item information. While these findings deal with encoding rather than retrieval, they highlight the key point that priming serves to facilitate processing by reducing

level of cognitive resources recruited to process previously encountered items, leading to faster and more efficient processing.

As noted in the introduction, dual-process models posit that familiarity is a fast and automatic process, while recollection is a slow and effortful process that places larger demands on cognitive resources (Yonelinas, 2002). Further evidence supporting the idea of potential interactions between priming and recollection comes from studies demonstrating that under certain circumstances recollection can operate faster than familiarity, undermining the assumptions of dual-process models. Gardiner, Ramponi and Richardson-Klavehn (1999) employed a response deadline procedure to contrast R and K responses and found that for the shorter deadline, designed to force reliance on more automatic responding, conceptual processing produced a greater proportion of R than K responses, suggesting that remembering can also be fast and automatic in nature. Recollection has also been demonstrated to be available earlier than familiarity in reaction time studies employing RK measures (Dewhurst & Conway, 1994; Henson, Rugg, Shallice, Josephs & Dolan, 1999). However, early reports of faster reaction times for R responses were claimed to be driven by the nature of RK instructions rather than differences in underlying processing, because participants only make a K responses once both processes are complete and they have failed to recollect (Yonelinas, 2002).

In a more recent study, Dewhurst, Holmes, Brandt and Dean (2006) set out to address issues concerning the specifics of the RK procedure by contrasting results from one-step and two-step RK measures, reasoning that the two-step procedure could lead to R responses in the RK decision when the initial old/new decision was in fact made on the basis of familiarity, giving the appearance of faster responses on the old/new decision for items that are reported to be recollected.

The authors demonstrated faster reaction times for R responses irrespective of the RK procedure employed and suggest that experiences of remembering are rapid and automatic in nature, while the experiences of knowing are more likely to involve decision processes that require conscious control. While these studies make no reference to priming specifically, faster R responses have also been observed following masked repetition priming of recognition test cues (Woollams et al., 2008), suggesting that the degree of priming from prior exposure may at least partially contribute to this earlier onsetting, more automatically driven, form of recollection.

It is difficult to assess, based on the evidence reported above, the precise nature of interactions between priming and recollection, but the findings clearly support the conclusion that they do in fact occur. The current study sought to investigate interactions between priming and recollection further, by employing ERPs to look for changes in the left-parietal effect, which indexes recollection, as a function of masked priming following a deep encoding task. The evidence reported above suggests two independent predictions of how priming may influence brain activity in areas associated with recollection. Firstly, based on the work of Gagnepain and colleagues, interactions between priming and recollection may be expected to reduce the magnitude of left-parietal old/new effects, indexing a reduction in the amount of cognitive resources engaged in retrieving a recently encountered item. Secondly, based on studies demonstrating fast R responses, repetition priming may produce observable changes in the timing of left-parietal old/new effects associated with recollection, speeding their onset.

6.2 Methods

Stimulus materials and experimental procedures were identical to those specified in Chapter 4, but differed in the encoding task employed. To encourage recollection participants performed a deep encoding task at study and were either instructed to read each word out loud, or to fit each one into a short sentence as it appeared on the screen. The alternative encoding tasks were employed to allow examination of recollection as a function of the depth of meaning employed at encoding, reasoning that this difference may produce differential engagement of the neural correlates of priming and recollection. However, differences in priming and recollection as a function of encoding task were not evident in the ERP data and as a result all data are reported collapsed across encoding task. Thirty-four undergraduate psychology students from the University of Stirling participated in the experiment, two participants were excluded due to excessive EEG artefacts, resulting in insufficient ERP trials for critical contrasts (<16 trials). The remaining thirty-two participants comprised of 17 females and 15 males with a mean age of 21 (range=18-34; SD=3.09).

6.3 Behavioural results

In total 85% of participants reported being unaware of the existence of the masked prime, 6% reported that they detected flickering on the screen but were unable to detect any of the words, and the remaining 9% reported that they were aware of seeing the word blank appear before the onset of the target on a few trials, but none of the participants reported being aware of the repetition of the target words. Initial examination of the behavioural data as a function of reported awareness

confirmed no differences in the pattern of results for participants who reported being aware of flickering on the screen or aware of the word blank compared to unaware participants, and as a result the data were analysed collapsed across awareness categories.

Table 6.1: Memory performance. Percentage of correct responses, discrimination and bias measures for the unprimed and primed conditions (standard error of the mean). The data clearly demonstrate no difference in performance measures or bias across conditions.

	Correct %		Discrim. & Bias	
	Old	New	Pr	Br
Unprimed	75.11 (3.33)	93.05 (1.29)	0.68 (0.04)	0.25 (0.04)
Primed	75.69 (3.14)	92.44 (1.30)	0.68 (0.04)	0.27 (0.04)

Table 6.1 shows a summary of recognition performance for the current experiment, and demonstrates that measures of recognition and bias were unaffected by the priming manipulation. Crucially, initial analysis confirmed that participants were able to discriminate between old and new words in both conditions (paired t-tests comparing hits and false alarms for both conditions were significant [$p < 0.001$] in all comparisons). Mean accuracy data were analysed using ANOVA with the factors of condition (unprimed, primed) and test status (old, new). This revealed a significant main effect of test status [$F(1,31)=28.60$, $p < 0.001$], but no main effect of condition or interaction between condition and test status, reflecting higher accuracy for new words. Subsidiary analysis collapsed across conditions confirmed that mean accuracy was higher for new words than for old words at test ($t(31)=5.35$, $p < 0.001$). Discrimination rates were also unaffected by the priming manipulation, and measures of response bias were equally conservative across conditions ($p > 0.05$ in all comparisons). Overall, this pattern of results suggests that priming did not impact recognition performance.

Table 6.2: Response by RK. Mean percentage of all response types split by test status and condition (standard error of the mean). The data demonstrate a slight increase in the proportion of K hits in the primed condition.

		Remember	Know	New
Old	Unprimed	56.64 (4.17)	18.48 (2.70)	24.89 (3.33)
	Primed	56.06 (4.10)	19.62 (2.84)	24.29 (3.14)
New	Unprimed	1.62 (0.48)	5.33 (1.15)	93.05 (1.29)
	Primed	1.68 (0.58)	5.88 (1.15)	92.44 (1.31)

Table 6.2 shows the breakdown of responses by RK judgement in each category for old and new words in the unprimed and primed conditions. The data suggests a slight increase in the proportion of K responses to old words in the primed compared to the unprimed condition. ANOVA contrasting old responses revealed no significant main effect or interactions including the factor of condition, indicating no difference in the raw proportion of R and K responses. Corrected estimates of familiarity and recollection were calculated as reported in Chapter 4, and analysis again demonstrated no differences in the engagement of familiarity (unprimed=0.40, primed=0.40) or recollection (unprimed=0.55, primed=0.54) across conditions. As for overall recognition performance, the pattern of results clearly demonstrates that repetition priming did not impact reported levels of familiarity and recollection.

Table 6.3 shows a summary of response times for hits and correct rejections in the primed and unprimed conditions, along with the magnitude of the priming difference between conditions. The data clearly demonstrate that the priming manipulation speeded response times for hits and correct rejections. ANOVA revealed a significant main effect of condition [$F(1,31)=71.52$, $p<0.001$], and a significant interaction between condition and test status [$F(1,31)=20.46$, $p<0.001$]. Follow up t-tests confirmed that response times were significantly faster for hits

Table 6.3: Response times (ms). Mean response time data for correct responses split by test status and the magnitude of the difference between unprimed and primed response times split by test status (standard error). The data demonstrate speeded response times for hits and correct rejections in the primed condition, with a larger effect for hits than for correct rejections.

	Old (Hits)	New (CRs)
Unprimed	959.65 (26.78)	947.25 (31.39)
Primed	844.05 (32.72)	877.24 (33.45)
Difference	115.60 (12.41)	70.01 (11.73)

($t(31)=9.31$, $p<0.001$) and for correct rejections ($t(31)=5.97$, $p<0.001$) in the primed compared to the unprimed condition. The data and the reported interaction between condition and test status suggest an increase in the magnitude of priming effects for hits compared to correct rejections (45.59ms). Subsidiary analysis performed on the difference in response times between the unprimed and primed conditions confirmed that the magnitude of priming was larger for hits than for correct rejections ($t(31)=4.52$, $p<0.001$). Importantly, this difference in magnitude between hits and correct rejections indicates a greater degree of facilitation as a result of exposure to words at study.

While it is unlikely, given the low proportion of K responses in the current experiment, it is possible that facilitation effects for hits reported above could have been driven by faster K and not R responses in the primed condition. Examination of response time data for correct responses in the initial old/new decision that were subsequently rated as remembered suggested faster response times for the primed (mean=855.79ms, S.E=33.23ms) compared to the unprimed (mean=969.64ms, S.E=28.86ms) condition. Analysis confirmed that response times for words subsequently reported to be remembered were significantly faster for primed words than for unprimed words ($t(31)=8.24$, $p<0.001$), suggesting that priming speeded

the onset of recollection. The magnitude of the difference between correct R responses to unprimed and primed words (113.85ms, S.E=13.83) did not differ substantially from the magnitude reported for hits collapsed across correct R and K responses.

6.3.1 Summary

In summary, response time data demonstrated the presence of robust priming effects for hits and correct rejections, which were larger in magnitude for hits, providing clear evidence of priming carried over from exposure to words at study. In addition, the data provided evidence of faster remember responses in the primed condition, suggesting that priming speeded the onset of recollection. Despite clear evidence of priming on response times, measures of recognition performance and estimates of familiarity and recollection were unaffected by the priming manipulation.

6.4 ERP results

To examine priming and memory effects grand average ERPs were formed for hits and correct rejections in the primed and unprimed conditions. The prime inclusive epoch (-500-1500ms) was used in all analyses to maintain consistency across experiments. The mean number of trials contributing to the waveforms for hits was 78 for the primed condition, and 78 for the unprimed condition. The mean number of trials contributing to waveforms for correct rejections was 94 for the primed condition and 93 for the unprimed condition.

6.4.1 Priming effects

Figure 6.1 shows grand average ERPs time locked to the onset of the prime for hits and correct rejections from both the unprimed and primed conditions at a representative sample of electrodes. Visual inspection of the waveforms again indicated the presence of three priming related modulations, an early (-50-150ms) posterior negativity, followed by a widespread central positivity (250-500ms) and a later (500-1100ms) posterior negativity for primed compared to unprimed words. The central positivity evident between 250-500ms and the later posterior negativity evident between 500-1100ms both appear larger for hits than for correct rejections, suggesting that these effects were modulated by priming carried over from encoding. Time windows submitted for analyses of priming effects were identical to those employed in the first experiment (-50-150ms, 250-500ms, 500-1100ms) and the data for hits and correct rejections were again analysed separately.

The first level of analysis on the data to identify variations in priming effects across conditions and time windows employed ANOVA with the factors of condition (unprimed, primed), location (Fz, FCz, Cz, CPz, Pz, POz) and time window (-50-150ms, 250-500ms, 500-1100ms). Results for hits revealed a significant main effect of condition [$F(1,31)=5.43$, $p=0.026$], and a significant interactions between condition, location and time window [$F(3,92.8)=41.41$, $p<0.001$]. Analysis for correct rejections produced no main effect of condition, but did produce a significant interaction between condition, location and time window [$F(2.6,80.3)=44.47$, $p<0.001$]. The presence of these interactions provides strong evidence of variation in the pattern of priming effects across locations and time windows for both hits and correct rejections.

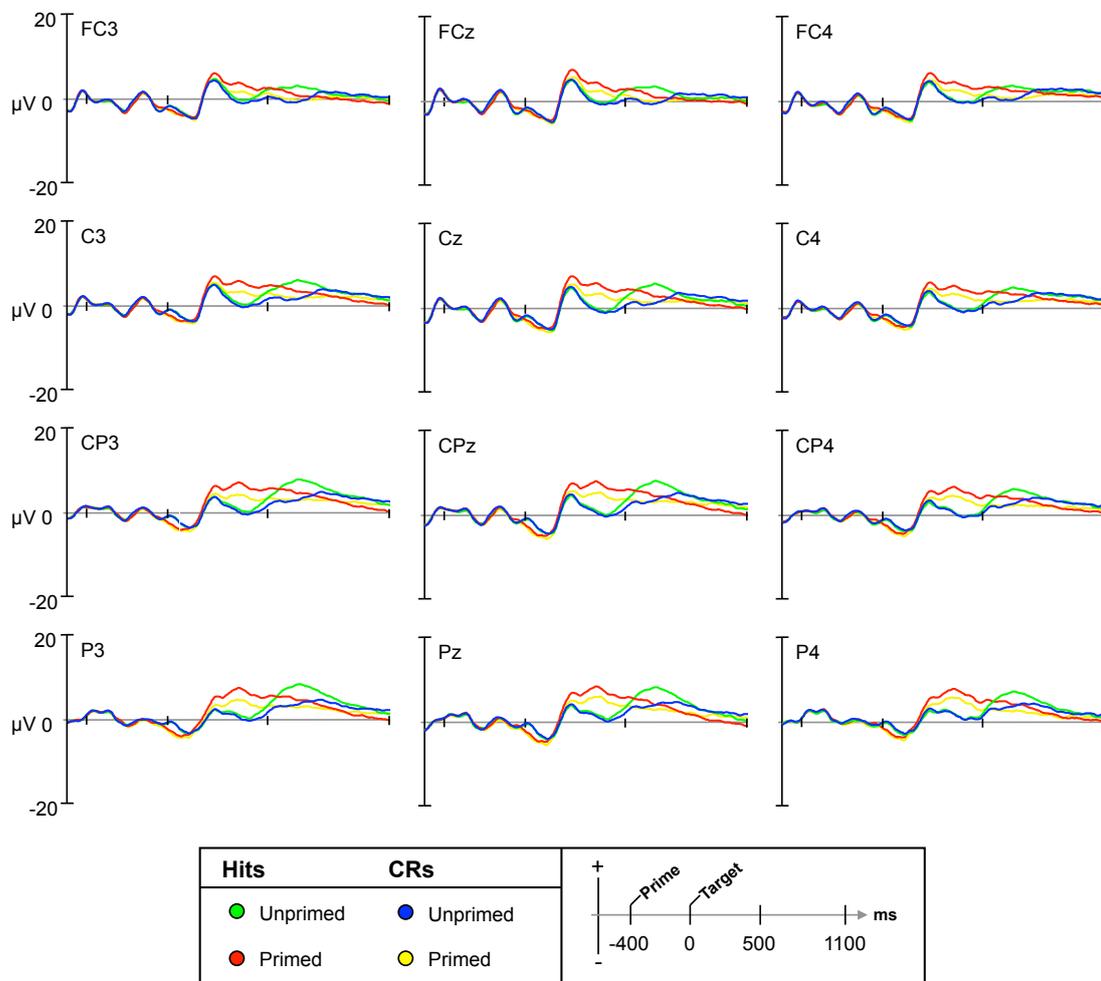


Figure 6.1: Priming effects. Grand average ERPs for hits and correct rejections in the unprimed and primed conditions. Waveforms display the presence of three priming related modulations, an early posterior negativity, followed by a widespread central positivity and a later posterior negativity for primed compared to unprimed words. Both of the later effects appear to be modulated by priming carried over from encoding, with larger effects for hits than for correct rejections.

Follow up analysis was performed separately for hits and correct rejections on the data from each time window, using ANOVA with the factors of condition (unprimed, primed) and location (Fz, FCz, Cz, CPz, Pz, POz); the results of this analysis are summarised in table 6.4. For hits the results demonstrated interactions between condition and location in all three time windows, along with main effects of condition in the later two time windows. Results for correct rejections demonstrated significant interactions between condition and location for all three time window, with main effects evident only for the first two time windows. These results provide evidence of variation in the pattern of priming effects by location within each time window, suggesting that the time windows chosen were suitable for examination of priming effects for hits and correct rejections.

Table 6.4: Priming ANOVAs by time window. Results of ANOVAs contrasting midline sites with the factors of condition and location over the three time windows chosen for analysis of priming effects.

		-50-150ms	250-500ms	500-1100ms
Hits	Cond	-	$F(1,31)=33.27, p<0.001$	$F(1,31)=17.10, p<0.001$
	Cond*Loc	$F(1.7,51.8)=9.89, p<0.001$	$F(1.7,53.3)=30.18, p<0.001$	$F(1.7,51.5)=14.45, p<0.001$
CRs	Cond	$F(1,31)=13.23, p=0.001$	$F(1,31)=48.98, p<0.001$	-
	Cond*Loc	$F(1.4,43.5)=18.30, p<0.001$	$F(1.8,55.7)=32.91, p<0.001$	$F(1.5,46.1)=4.15, p=0.032$

Subsidiary analysis took the form of contrasts between unprimed and primed conditions, performed separately for hits and correct rejections, using ANOVA with the factors of condition (unprimed, primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). The results for each time window are reported separately in the following sections.

6.4.1.1 Time window -50 to 150ms

From 50ms prior to the onset of target words, waveforms for primed hits and correct rejections were more negative going than waveforms for unprimed hits and correct rejections at posterior locations (see Figure 6.2 for the data from POz). For hits, this posterior negativity was also accompanied by a frontal positivity over the right hemisphere. Initial analysis for hits revealed a significant interaction between condition, location, hemisphere and electrode [$F(3.8,119.3)=3.38$, $p=0.013$]. As can be seen in the topographic map shown in Figure 6.2 this interaction suggests the presence of a negativity for primed hits compared to unprimed hits towards posterior locations in the left hemisphere, accompanied by a positivity over right frontal locations.

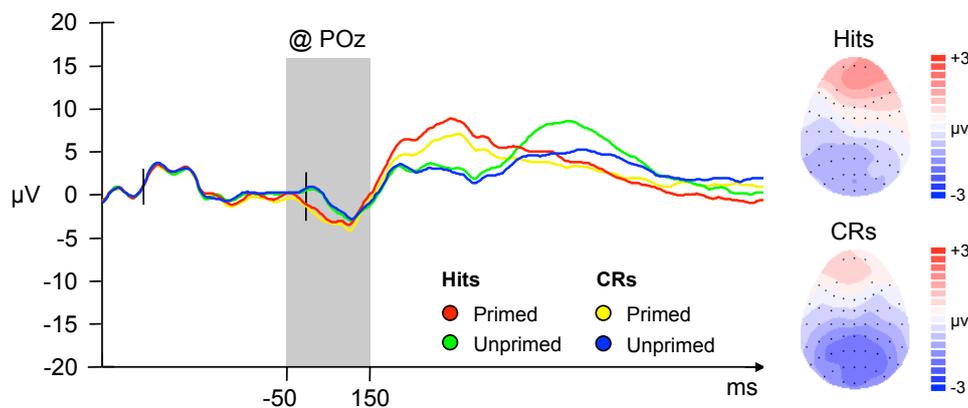


Figure 6.2: Priming @ POz (-50-150ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode POz. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Primed hits and correct rejections were more negative going than unprimed hits and correct rejections at posterior locations, accompanied by right-frontal positivity for hits.

Results of subsidiary analysis at separate locations are summarised in Table 6.5, and demonstrate interactions between condition, hemisphere and electrode at frontal and fronto-central locations, along with main effects of condition at parietal and parieto-occipital locations. Focused analysis confirmed that differences

between conditions at right-frontal locations were larger over inferior electrode sites ($t(31)=2.58$, $p=0.015$) than at medial sites. The presence of main effects at parietal and parieto-occipital locations demonstrates the presence of an evenly distributed negativity for primed words across posterior locations. Further examination of the data demonstrated that overall, differences between conditions for hits were maximal at PO3 ($t(31)=2.66$, $p=0.012$).

Initial analysis for correct rejections revealed a significant main effect of condition [$F(1,31)=14.88$, $p=0.001$], along with significant interactions between condition and location [$F(1.4,42.7)=17.04$, $p<0.001$] and condition and electrode [$F(1.1,33.8)=5.51$, $p=0.022$]. As can be seen in the topographic map in Figure 6.2, these interactions reflect the presence of a negativity at posterior locations, maximal towards superior electrode sites. Results of subsidiary analysis at separate locations are shown in table 6.5, analysis revealed significant interactions between condition and electrode extending from central to parieto-occipital locations. Focused analysis, collapsed across locations demonstrating significant interactions and hemispheres, revealed that differences between conditions were significantly larger over medial ($t(31)=3.71$, $p=0.001$) and superior sites ($t(31)=3.17$, $p=0.004$) than at inferior sites, confirming the presence of a negativity for primed correct rejections at posterior locations focused over the midline. Further examination of the data demonstrated that the difference between conditions was maximal at POz ($t(31)=5.81$, $p<0.001$).

Magnitude analysis was performed to compare the amplitude of priming effects for hits and correct rejections, and employed ANOVA with the factors of test status (old, new), Location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior), The results revealed no significant main effect or interactions including the factor of test status. These findings indicate that

Table 6.5: Priming by location (-50-150ms). Results of subsidiary analysis at separate locations for hits and correct rejections.

Hits (-50-150ms)	F	FC	C	CP	P	PO
Cond					$F(1,31)=5.48, p=0.026$	$F(1,31)=6.34, p=0.017$
Cond*Hem	$F(1,31)=4.77, p=0.037$	$F(1,31)=4.64, p=0.039$				
Cond*Elec						
Cond*Hem*Elec	$F(1.4,44)=7.74, p=0.004$	$F(1.3,41.6)=5.68, p=0.014$				
CRs (-50-150ms)	F	FC	C	CP	P	PO
Cond			$F(1,31)=11.15, p=0.002$	$F(1,31)=21.24, p<0.001$	$F(1,31)=27.93, p<0.001$	$F(1,31)=32.49, p<0.001$
Cond*Hem						
Cond*Elec			$F(1.2,36.7)=5.26, p=0.023$	$F(1.2,38.1)=7.00, p=0.008$	$F(1.1,34.5)=9.07, p=0.004$	$F(1.1,34.9)=9.63, p=0.003$
Cond*Hem*Elec						

priming effects for hits and correct rejections were comparable in size and distribution, and suggest that right-frontal effects evident in the data for hits could not be differentiated. Focused analysis on the magnitude of the priming difference for hits and correct rejections at right-frontal site F6 demonstrated larger differences between condition for hits ($t(31)=2.24$, $p=0.032$), providing tentative evidence supporting the presence of additional right-frontal activation for hits.

In summary, during the -50 to 150ms time window primed hits and correct rejections were more negative going than unprimed hits and correct rejections, and these effects were maximal over parieto-occipital locations. In addition, waveforms for hits were slightly more positive going for primed words than for unprimed words at inferior right-frontal locations. Crucially, magnitude analysis confirmed the absence of differences in amplitude, suggesting that this early priming effect was driven largely by exposure to the masked prime at test.

6.4.1.2 Time window 250 to 500ms

Between 250-500ms time waveforms for primed hits and correct rejections were more positive going than waveforms for unprimed hits and correct rejections over central and posterior locations, where the effect appears larger for hits than for correct rejections (see Figure 6.3 for the data from CPz). Initial analysis for hits revealed a significant main effect of condition [$F(1,31)=36.17$, $p<0.001$], and a significant interaction between condition, location, hemisphere and electrode [$F(3.7,113.5)=3.37$, $p=0.015$]. As can be seen in the topographic maps in Figure 6.3, these interactions suggest that the positivity for primed words is maximal towards superior electrodes over central and posterior locations, with a slight skew towards the right hemisphere at more anterior locations. Ini-

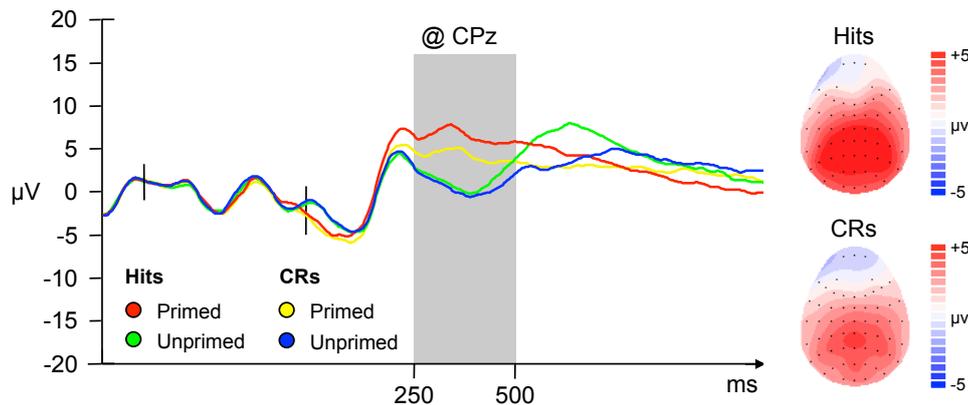


Figure 6.3: Priming @ CPz (250-500ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode CPz. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Primed hits and correct rejections were more positive going than unprimed hits and correct rejections across central and posterior locations, where the effect appears larger for hits than for correct rejections.

tial analysis for correct rejections revealed a significant main effect of condition [$F(1,31)=51.33$, $p<0.001$], and significant interactions between condition and location [$F(1.6,50.1)=44.32$, $p<0.001$], and condition, hemisphere and electrode [$F(1.3,41.1)=7.63$, $p=0.005$]. As can be seen in the topographic maps in Figure 6.3 these interactions suggest that the positivity for primed words is maximal towards superior electrodes over central and posterior locations, again displaying a slight skew over the right hemisphere towards more anterior locations.

Table 6.6 shows the results of subsidiary analysis at separate locations for hits and correct rejections. For hits analysis revealed interactions including the factor of hemisphere extending from frontal to centro-parietal locations, along with interactions between condition and electrode across locations. Focused analysis on the data collapsed from frontal to centro-parietal locations and across electrodes confirmed the presence of stronger effects over the right hemisphere ($t(31)=3.36$, $p=0.002$). Further investigation revealed that priming effects for hits were maximal towards superior locations for the left hemisphere (mid: $t(31)=4.04$, $p<0.001$,

Table 6.6: Priming by location (250-500ms). Results of subsidiary analysis at separate locations for hits and correct rejections.

Hits (250-500ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=8.04, p=0.008$	$F(1,31)=17.37, p<0.001$	$F(1,31)=32.35, p<0.001$	$F(1,31)=47.67, p<0.001$	$F(1,31)=54.72, p<0.001$	$F(1,31)=59.79, p<0.001$
Cond*Hem	$F(1,31)=9.08, p=0.005$	$F(1,31)=13.45, p=0.001$	$F(1,31)=9.76, p=0.004$			
Cond*Elec	$F(1.4,44)=4.51, p=0.027$	$F(1.1,34.5)=17.00, p<0.001$	$F(1.2,35.7)=25.61, p<0.001$	$F(1,32.2)=26.57, p<0.001$	$F(1.1,33.3)=14.39, p<0.001$	$F(1.1,34.6)=23.61, p<0.001$
Cond*Hem*Elec	$F(1.2,37.5)=4.23, p=0.040$	$F(1.5,45.3)=6.44, p=0.007$	$F(1.5,47.7)=7.27, p=0.004$	$F(1.2,37.6)=8.89, p=0.003$		
CRs (250-500ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=6.13, p=0.019$	$F(1,31)=24.48, p<0.001$	$F(1,31)=48.83, p<0.001$	$F(1,31)=72.24, p<0.001$	$F(1,31)=79.06, p<0.001$	$F(1,31)=75.38, p<0.001$
Cond*Hem						
Cond*Elec	$F(1.3,40.9)=7.95, p=0.004$	$F(1.1,32.8)=11.06, p=0.002$	$F(1.1,33.7)=12.86, p=0.001$	$F(1.1,33.6)=24.40, p<0.001$	$F(1.1,33.1)=25.74, p<0.001$	$F(1.1,33.5)=46.47, p<0.001$
Cond*Hem*Elec	$F(1.4,42.1)=7.78, p=0.004$	$F(1.7,51.8)=7.12, p=0.003$	$F(1.3,40.54)=5.84, p=0.014$			

inferior: $t(31)=5.47$, $p<0.001$), priming effects for the right hemisphere did not differ across superior and mid electrode sites ($t(31)=1.40$, $p=0.171$), but effects were larger at both sites than effects at inferior sites (superior: $t(31)=3.16$, $p=0.004$, mid: $t(31)=4.14$, $p<0.001$). This pattern of results demonstrates the presence of a widespread positivity for primed hits focused over midline sites, with a slight skew over the right hemisphere at frontal and central locations.

Analysis for correct rejections also demonstrated interactions between condition and electrode across locations, and interactions including the factor of hemisphere extended from frontal to central locations. Focused analysis on the data collapsed from frontal to central locations and across electrodes failed to demonstrate a significant difference between hemispheres ($t(31)=1.83$, $p=0.077$). Further analysis contrasting electrode sites revealed larger effects towards superior sites in the left hemisphere (mid: $t(31)=3.27$, $p=0.003$, inferior: $t(31)=4.24$, $p<0.001$), and no difference between superior and mid electrode sites in the right hemisphere ($t(31)=1.04$, $p=0.302$), reflecting a slight skew over the right hemisphere at more anterior locations.

Overall, the pattern of results demonstrates the presence of a widespread positivity for primed hits and correct rejections focused over midline sites, but with a slight skew over the right hemisphere at the locations identified, and suggest that effects observed for hits and correct rejections had a similar focus. Further examination of the data demonstrated that priming effects for hits ($t(31)=6.81$, $p<0.001$) and correct rejections ($t(31)=8.12$, $p<0.001$) were both maximal at electrode CPz. Magnitude analysis, performed to compare priming effects identified for hits and correct rejections, employing ANOVA with the factors of test status (old, new), Location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior), revealed a significant main effect of test status

[$F(1,31)=6.29$, $p=0.018$], but no interactions including the factor of test status. Results confirm that the magnitude of priming was larger for hits than for correct rejections across locations and suggests that effects for hits and correct rejections differed only in amplitude and not in distribution, providing evidence that this positive effect was modulated by additional priming carried over from encoding for hits.

In summary, during the 250 to 500ms time window primed hits and correct rejections were more positive going than unprimed hits and correct rejections. This effect was maximal at superior centro-parietal locations for hits and correct rejections and exhibited a slight skew over the right hemisphere towards frontal and central locations. Importantly, the magnitude of this effect was larger for hits than for correct rejections, providing clear evidence of priming carried over from the encoding phase.

6.4.1.3 Time window 500 to 1100ms

From 500ms after target onset, waveforms for primed hits and correct rejections were more negative going than for unprimed hits and correct rejections at posterior locations, with the largest difference between conditions for hits (see Figure 6.4 for the data from POz). Initial analysis for hits revealed a significant main effect of condition [$F(1,31)=17.31$, $p<0.001$], along with a significant interaction between condition, location and electrode [$F(3,94.1)=5.65$, $p=0.001$], and a marginally significant interaction between condition, hemisphere and electrode [$F(1.3,39.2)=3.59$, $p=0.056$]. Initial analysis for correct rejections produced a significant main effect of condition [$F(1,31)=5.27$, $p=0.029$], but no significant interactions including the factor of condition. Exploration of the data revealed that

main effects of condition were present at centro-parietal [$F(1,31)=5.18, p=0.030$], parietal [$F(1,31)=8.03, p=0.008$] and parieto-occipital [$F(1,31)=44.20, p<0.001$] locations for correct rejections. Further examination of the data confirmed that the effect for correct rejections was maximal at POz [$t(31)=3.11, p=0.004$].

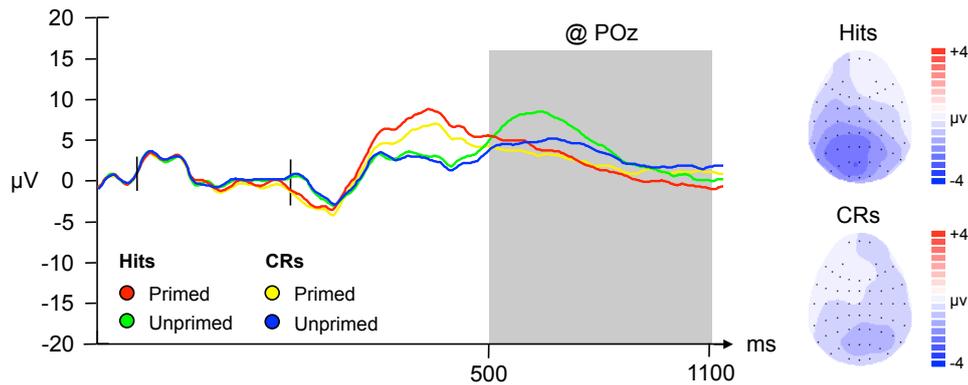


Figure 6.4: Priming @ POz (500-1100ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode POz. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Primed hits and correct rejections were more negative going than unprimed hits and correct rejections at posterior locations, with the largest difference between conditions for hits.

Table 6.7 shows results of subsidiary analysis at separate locations for hits. Results revealed main effects and interactions including the factor of hemisphere extending from fronto-central to parieto-occipital locations and interactions including the factors of hemisphere and electrode at centro-parietal and parietal locations. As can be seen in Figure 6.4 these results confirm the presence of a negativity for primed compared to unprimed hits at posterior locations that is larger over the left hemisphere and towards superior electrode sites. Further examination of the data demonstrated that the effect for hits was maximal at POz ($t(31)=7.05, p<0.001$). The foregoing results and inspection of the data suggests potential differences in the magnitude and distribution of this late priming effect for hits and correct rejections.

Table 6.7: Priming for hits by location (500-1100ms). Results of subsidiary analysis at separate locations for hits.

Hits (500-1100ms)	F	FC	C	CP	P	PO
Cond		$F(1,31)=4.70, p=0.038$	$F(1,31)=10.99, p=0.002$	$F(1,31)=25.55, p<0.001$	$F(1,31)=40.73, p<0.001$	$F(1,31)=44.21, p<0.001$
Cond*Hem		$F(1,31)=4.99, p=0.033$	$F(1,31)=9.62, p=0.004$	$F(1,31)=13.39, p=0.001$	$F(1,31)=10.93, p=0.002$	$F(1,31)=6.69, p=0.015$
Cond*Elec				$F(1.1,34.5)=6.54, p=0.013$	$F(1.1,34.2)=11.31, p=0.001$	$F(1.2,36.4)=27.73, p<0.001$
Cond*Hem*Elec				$F(1.1,35.3)=5.11, p=0.026$	$F(1.4,44.3)=7.04, p=0.005$	

Contrasting the magnitude of effects revealed a significant interaction between test status, hemisphere and electrode [$F(1.2,37.1)=5.13$, $p=0.024$]. Follow up analysis at separate locations confirmed the presence of interactions between test status, hemisphere and electrode at central [$F(1.4,42.2)=3.94$, $p=0.042$], centroparietal [$F(1.2,38.4)=4.63$, $p=0.030$], and parietal [$F(1.3,40.9)=6.83$, $p=0.008$] locations, reflecting larger effects towards superior electrode sites in the left hemisphere for hits and towards superior sites in the right hemisphere for correct rejections. Topographic analysis on the rescaled data produced a significant interaction between test status and hemisphere [$F(1,31)=5.39$, $p=0.027$], confirming that the priming effects for hits and correct rejections differed in distribution and suggesting that the effects were driven by at least partially non-overlapping sets of neural generators.

In summary, during the 500-1100ms time window primed hits and correct rejections were more negative going than unprimed hits and correct rejections, and these effects were maximal at parieto-occipital locations. These late priming effects differed in magnitude and distribution, with larger effects focused over superior sites in the left hemisphere for hits, in contrast to smaller effects with a focus over superior sites in the right hemisphere for correct rejections.

6.4.2 Summary

Analysis of the data confirmed the presence of three priming related modulations, an early (-50-150ms) negativity, followed by a widespread positivity (250-500ms) and a later (500-1100ms) negativity for primed compared to unprimed words (see Figure 6.5). Between -50-150ms primed hits and correct rejections were more negative going than unprimed hits and correct rejections at posterior locations.

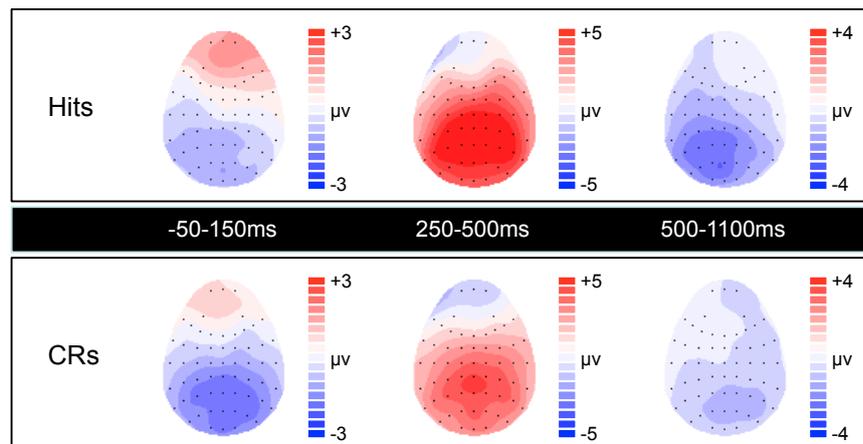


Figure 6.5: Priming topographic summary. Topographic maps summarise differences between the unprimed and primed conditions for hits and correct rejections over time.

In addition, waveforms for hits were more positive going for primed than for unprimed words at inferior right-frontal sites. During the 250-500ms time window primed hits and correct rejections were more positive going than unprimed hits and correct rejections. This effect was maximal at superior centro-parietal locations for hits and correct rejections and exhibited a slight skew over the right hemisphere towards over frontal and central locations. Importantly, the magnitude of this effect was larger for hits than for correct rejections, providing clear evidence of priming carried over from the encoding phase. Between 500-1100ms primed hits and correct rejections were more negative going than unprimed hits and correct rejections at posterior locations, where effects differed in magnitude and distribution, with larger effects focused over superior sites in the left hemisphere for hits, in contrast to smaller effects with a focus over superior sites in the right hemisphere for correct rejections.

6.4.3 Memory effects

Figure 6.6 shows grand average ERPs time locked to the onset of the prime for hits and correct rejections in the unprimed condition, and Figure 6.7 shows grand average ERPs for the primed condition. Visual inspection of the grand average waveforms shows that ERPs elicited in the unprimed condition were more positive going for hits than for correct rejections between 500 and 800ms, with the greatest differences at left-parietal locations. By contrast, for the primed condition old/new differences with a left-parietal distribution were evident earlier between 300 and 500ms. Critically, familiarity related mid-frontal old/new differences were not evident in either condition during the 300 to 500ms time window. In contrast to the first experiment, neither condition exhibited a clear negativity for hits compared to correct rejections between 800 and 1100ms, with only a slight negativity at midline sites towards the end of the epoch evident in the primed condition. Based on visual inspection and to maintain consistency with the previous experiment, the time windows chosen for analysis of memory effects were 300-500ms, 500-800ms and 800-1100ms.

The first level of analysis was designed to identify variations in the patterns of old/new effects across conditions and time windows. Due to the left sided distribution of memory effects in the current experiment, the data was submitted to ANOVA with the factors of condition (unprimed, primed), test status (old, new), location (F3, FC3, C3, CP3, P3, PO5) and time window (300-500ms, 500-800ms, 800-1100ms). Results identified an interaction between condition, test status, location and time window [$F(3,93.8)=6.75, p<0.001$], indicating variation in the pattern of old/new effects between conditions and across time windows. To further elucidate the pattern of memory related activity, a second level of analysis

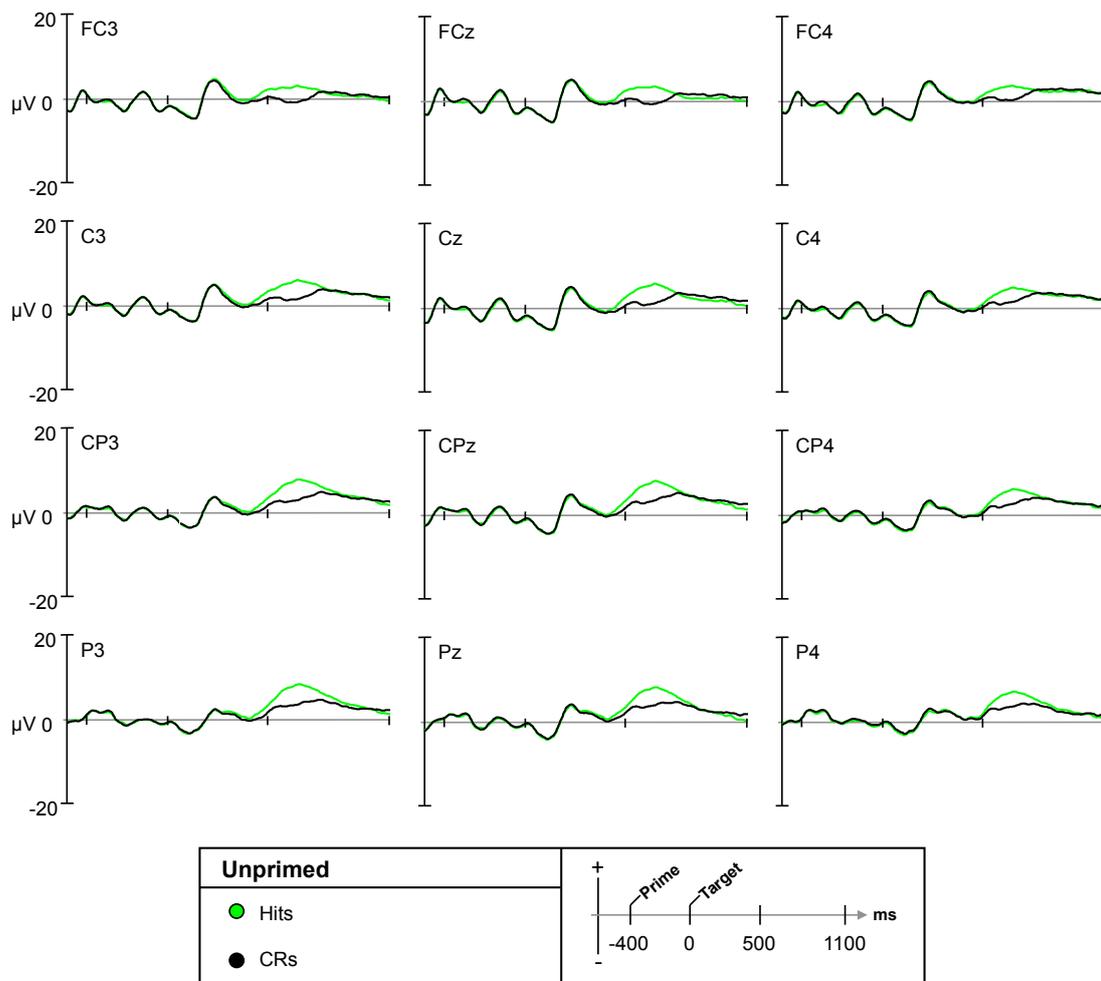


Figure 6.6: Memory effects for unprimed words. Grand average ERPs for hits and correct rejections in the unprimed condition. Waveforms were more positive going for hits than for correct rejections at left-parietal locations between 500-800ms, consistent with previous identifications of recollection.

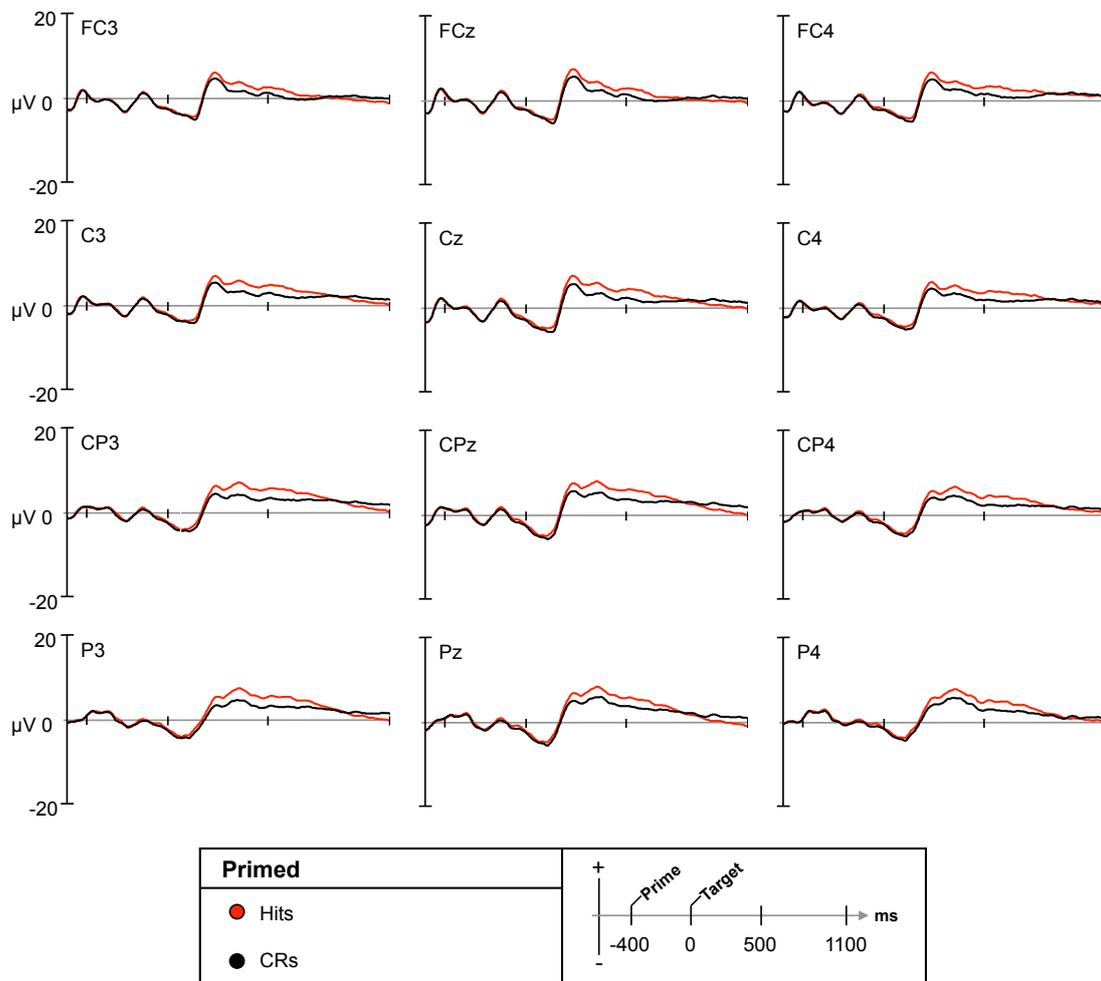


Figure 6.7: Memory effects for primed words. Grand average ERPs for hits and correct rejections in the primed condition. Waveforms were more positive going for hits than for correct rejections at left-parietal locations between 300-500ms, during the time window normally associated with familiarity, and continued into the 500-800ms time window. Towards the end of the epoch, waveforms for hits were slightly more negative going than waveforms for correct rejections at posterior midline sites.

was performed separately on the data from each time window, using ANOVA with the factors of condition (unprimed, primed), test status (old, new) and location (F3, FC3, C3, CP3, P3, PO5). The results of this analysis are summarised in Table 6.8 and demonstrate that old/new effects varied across time windows but only interacted with the factor of condition during the 300-500ms and 500-800ms, as a result only these windows were submitted to further analysis.

Table 6.8: Memory ANOVAs by time window. Results of ANOVAs contrasting midline sites with the factors of condition, test status and location over the three time windows chosen for analysis of old/new effects.

	300-500ms	500-800ms	800-1100ms
Test status	$F(1,31)=32.86, p<0.001$	$F(1,31)=22.74, p<0.001$	-
Test status*Loc	-	-	$F(1.7,52.7)=5.16, p=0.012$
Test Status*Cond	$F(1,31)=4.98, p=0.033$	$F(1,31)=9.64, p=0.004$	-
Test status*Cond*Loc	$F(1.8,58.19)=3.64, p=0.035$	-	-

Subsidiary analyses employed to investigate old/new effects were performed on the average activity over three electrodes sites for four regions of interest: left-frontal (LF: F1, F3, F5), right-frontal (RF: F2, F4, F6), left-parietal (LP: P1, P3, P5) and right-parietal (RP: P2, P4, P6). The analysis took the form of contrasts between hits and correct rejections performed separately for each condition, using ANOVA with the factors of test status (old, new), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior); the results for each time window are reported separately in the following sections.

6.4.3.1 Time window 300 to 500ms

Between 300-500ms waveforms in the primed condition were more positive going for hits than for correct rejections at left-parietal locations. Unprimed waveforms

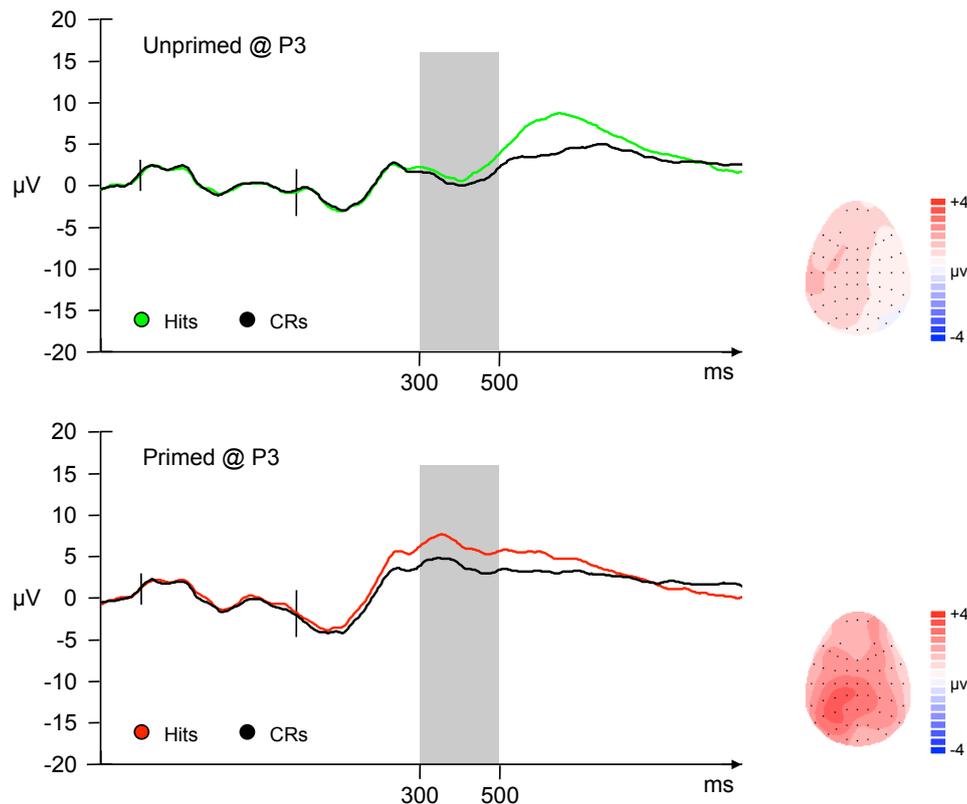


Figure 6.8: Memory @ P3 (300-500ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode P3. Topographic maps show the difference between the hits and correct rejections for both conditions. Primed waveforms were more positive going for hits than for correct rejections at left parietal locations. Unprimed waveforms show a very slight positivity for hits compared to correct rejections across locations in the the left hemisphere.

show a very slight positivity for hits compared to correct rejections across locations in the the left hemisphere (see Figure 6.8 for the data from P3). Initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,31)=5.33$, $p=0.028$], and a significant interaction between test status, hemisphere and electrode [$F(1.2, 35.7)=4.27$, $p=0.041$]. As can be seen in Figure 6.8, these results reflect the presence of a slight positivity for hits compared to correct rejections across locations in the left hemisphere that appears larger towards inferior electrode sites. This result was confirmed with additional analysis, collapsed across locations in the left hemisphere, to directly compare the effects

across electrode sites (inferior vs. medial: $t(31)=4.46$, $p<0.001$). Consistent with this interpretation of the data, further examination confirmed that old/new differences for the unprimed condition were maximal at electrode CP5 ($t(31)=4.73$, $p<0.001$).

Initial analysis for the primed condition revealed a significant main effect of test status [$F(1,31)=19.23$, $p<0.001$], and a significant interaction between test status, location and hemisphere [$F(1,31)=6.18$, $p=0.019$]. As can be seen in Figure 6.8 these results reflect the presence of a positivity for hits compared to correct rejections over posterior locations in the left hemisphere. Subsidiary analysis at frontal locations revealed a significant main effect of test status [$F(1,31)=10.94$, $p=0.002$], but no significant interactions including the factor of test status, reflecting slightly more positive going effects for hits than for correct across frontal sites. Analysis at parietal locations revealed a significant main effect of test status [$F(1,31)=24.89$, $p<0.001$], and a significant interaction between test status and hemisphere [$F(1,31)=8.03$, $p=0.008$], reflecting the presence of an old/new difference over the left hemisphere at parietal locations. This result was confirmed by analysis performed on subtraction data, contrasting effects for each hemisphere at parietal locations, collapsed across electrode sites ($t(31)=2.83$, $p=0.008$). Consistent with this view of the data, further examination revealed that old/new differences for the primed condition were maximal at electrode CP3 ($t(31)=4.81$, $p<0.001$).

Magnitude analysis was performed on subtraction data to compare the amplitude of old/new effects for the primed and unprimed conditions, using ANOVA with the factors of condition (unprimed, primed), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). The results revealed a significant main effect of condition [$F(1,31)=4.99$, $p=0.033$], but no interactions

including the factor of condition, indicating much weaker effects for the unprimed compared to the primed condition across locations. In summary, analysis for the unprimed condition confirmed the presence of a slight positivity for hits across locations in the left hemisphere that was maximal over inferior centro-parietal sites. Analysis for the primed condition confirmed the presence of a stronger old/new difference focused over parietal locations in the left hemisphere, consistent with the distribution of effects that have previously been associated with recollection.

6.4.3.2 Time window 500 to 800ms

Between 500 and 800ms waveforms in the unprimed condition became more positive going for hits than for correct rejections at left-parietal locations. For the primed condition waveforms continued to be more positive going for hits than for correct rejections into the the 500-800ms time window at left-parietal locations (see Figure 6.9 for the data from P3). Initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,31)=34.19$, $p<0.001$], along with interactions between test status and location [$F(1,31)=7.63$, $p=0.010$], test status and hemisphere [$F(1,31)=5.57$, $p=0.025$], and a marginally significant interaction between test status, hemisphere and electrode [$F(1.5,46.5)=3.49$, $p=0.051$]. As can be seen in Figure 6.9 these results confirm the presence of a widespread old/new difference with a focus over left-parietal locations.

Subsidiary analysis at frontal locations revealed a significant main effect of test status [$F(1,31)=21.87$, $p<0.001$], and a significant interaction between test status and electrode [$F(1.3,39.4)=5.05$, $p=0.023$], reflecting more positive going activity for hits than for correct rejections over medial sites at frontal locations

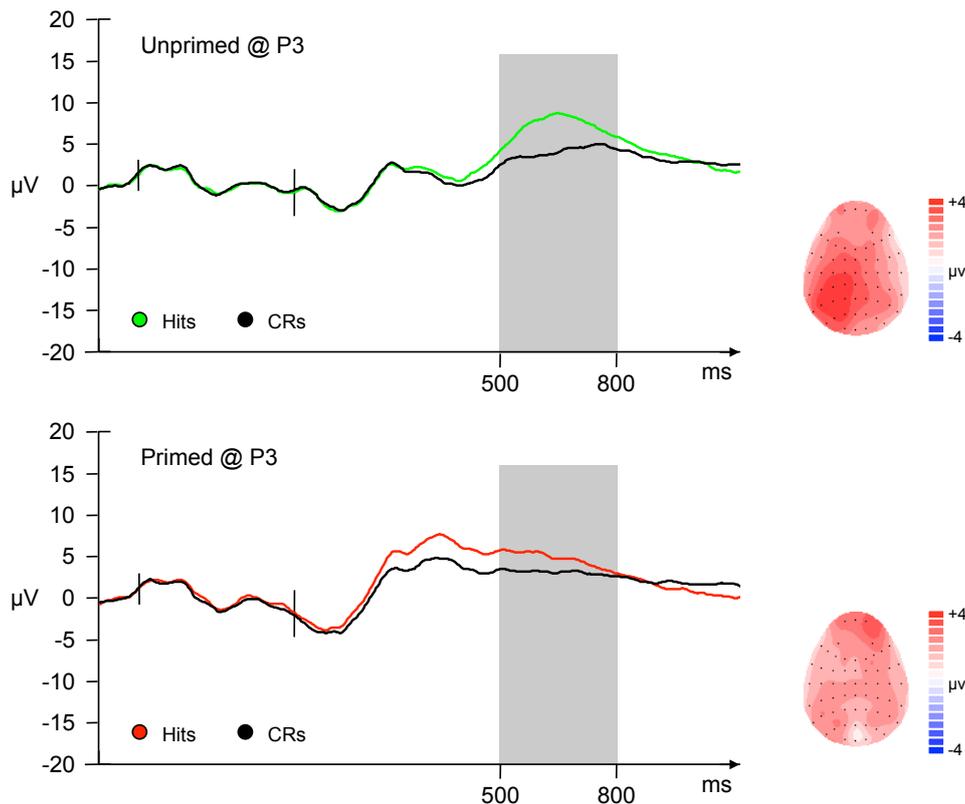


Figure 6.9: Memory @ P3 (500-800ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode P3. Topographic maps show the difference between the hits and correct rejections for both conditions. Unprimed waveforms were more positive going for hits than for correct rejections at left-parietal locations. For the primed condition waveforms continued to be more positive going for hits than for correct rejections into the the 500 to 800ms time window at left-parietal locations.

(inferior: $t(31)=2.88$, $p=0.07$, superior: $t(31)=2.34$, $p=0.026$). Analysis at parietal locations produced a significant main effect of test status [$F(1,31)=39.91$, $p<0.001$], and a significant interaction between test status, hemisphere and electrode [$F(1.4,42.8)=7.03$, $p=0.006$], reflecting the presence of an old/new difference in the left hemisphere, with a maxima over medial electrode sites. Consistent with this pattern of results, further examination of the data confirmed that the old/new difference for the unprimed condition was maximal at electrode P3 ($t(31)=7.07$, $p<0.001$).

Initial analysis for the primed condition revealed a significant main effect of test status [$F(1,31)=11.21$, $p=0.002$] and a significant interaction between test status, location and hemisphere [$F(1,31)=4.31$, $p=0.046$]. As can be seen in Figure 6.9, this pattern of results suggests a slight continuation of old/new differences with a left-parietal distribution into the 500 to 800ms time window. Subsidiary analysis at frontal locations revealed a significant main effect of test status [$F(1,31)=9.18$, $p=0.005$], reflecting more positive going activity for hits than for correct rejections across frontal locations. Analysis at parietal locations produced a significant main effect of test status [$F(1,31)=9.86$, $p=0.004$] and a significant interaction between test status and electrode [$F(1.3,40.4)=7.63$, $p=0.005$], reflecting more positive going activity for hits than for correct rejections at parietal locations with focus over mid and inferior electrodes. Follow up analysis contrasting electrode sites collapsed across hemispheres demonstrated larger effects over mid ($t(31)=3.99$, $p<0.001$) and inferior ($t(31)=2.91$, $p=0.007$) electrodes sites than at superior sites. Despite the presence of additional activity over the right hemisphere at parietal locations, the data is consistent with the presence of continued activation over left-parietal sites from the earlier time window, and further examination of the data confirmed that old/new differences for the primed condition were maximal at electrode P5 ($t(31)=3.44$, $p=0.002$).

Magnitude analysis was performed on subtraction data using activity averaged over three electrode sites (LP: P5, P3, P1) to compare the amplitude of old/new effects at left-parietal locations for the primed and unprimed conditions. Results revealed significantly larger old/new differences for the unprimed than for the primed condition ($t(31)=3.66$, $p=0.001$), suggesting that the 500-800ms time window captures the reduction to offset of old/new effects at left-parietal sites for the primed condition. In summary, the data demonstrate the onset of left-

parietal old/new effects for the unprimed condition, and continuation of old/new effects with a left-parietal distribution from the earlier time window for the primed condition.

6.4.3.3 Left-parietal old/new effects

The next level of analysis sought to detect differences in magnitude or distribution of left-parietal old/new effects across the 300 to 500ms and 500 to 800ms time windows for the primed and unprimed conditions.

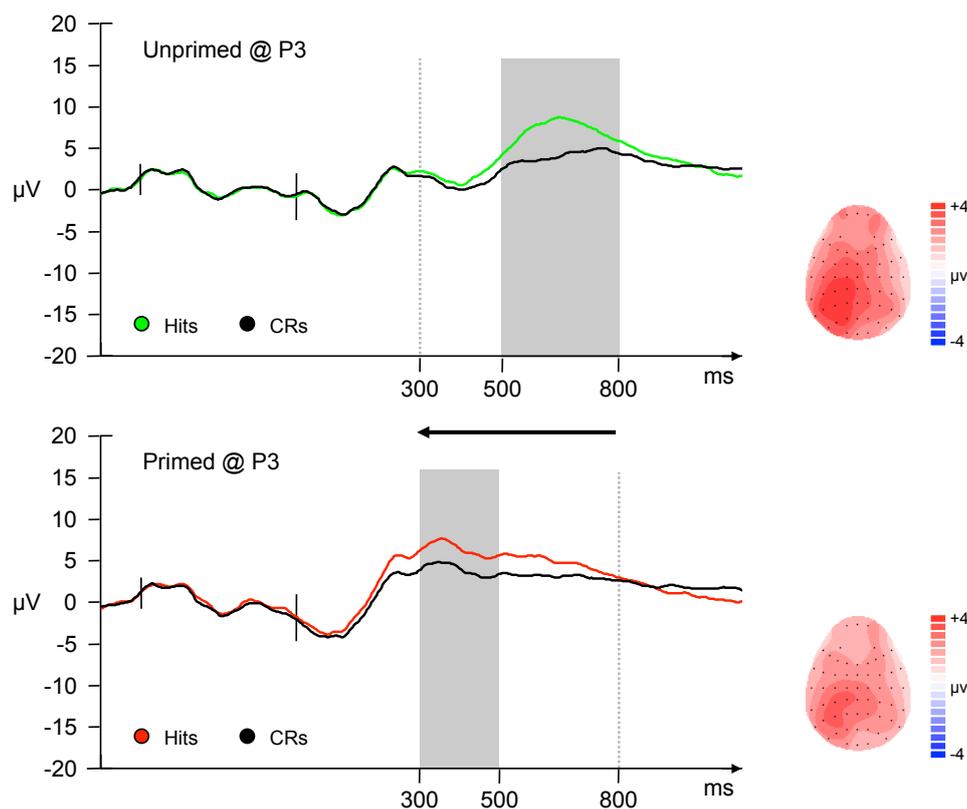


Figure 6.10: Memory @ P3 (300-500ms & 500-800ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode P3. Topographic maps show the difference between the hits and correct rejections for both conditions. Waveforms demonstrate early onset of left-parietal old/new effects for the primed compared to the unprimed condition.

Magnitude analysis contrasting left-parietal effects evident between 300-500ms for the primed condition and between 500 and 800ms for the unprimed condition revealed no main effect or interactions including the factor of condition, suggesting that left-parietal effects evident in the data did not differ in size or distribution across conditions or time windows. These findings support the conclusion that the same effect is present in both conditions and that left-parietal effects onset earlier in the primed condition (see Figure 6.10 for the data from P3). The next level of analysis was designed to quantify this difference in the onset time of left-parietal effects across conditions.

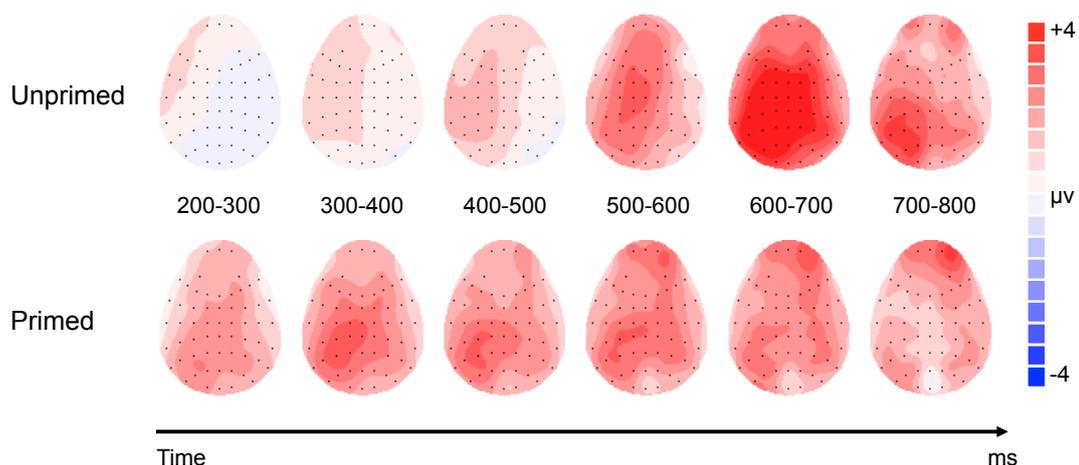


Figure 6.11: Topographic maps 200-800ms. Topographic maps showing the difference between the hits and correct rejections for both conditions between 200-800ms after target onset, split into the 100ms time bins that were used for comparison of the onset time of left-parietal old/new effects across conditions.

To establish the difference in onset times, the data from parietal electrode sites were first split into six consecutive time bins (200-300ms, 300-400ms, 400-500ms, 500-600ms, 600-700ms, 700-800ms). Figure 6.11 shows topographic maps of effects for the primed and unprimed conditions over time and inspection of the data suggests that left-parietal effects for the primed condition are evident as early as

200ms after target onset, with effects for the unprimed condition onsetting later around 500ms after target onset. The data were submitted to ANOVA with the factors of test status (old, new), hemisphere (left, right) and electrode (inferior, mid, superior), performed separately for the unprimed and primed conditions and for each time bin. Onset times of left-parietal effects were identified by the earliest bin demonstrating a main effect of test status and an interaction between test status and hemisphere for the unprimed and primed conditions.

The results are summarised in Table 6.9, and suggest a clear difference between conditions in the onset-time of left-parietal effects, with differences for the primed condition onsetting from around 200ms after target onset, and differences for the unprimed condition not becoming significant at left-parietal locations until between 400-500ms after target onset. To confirm this result, follow up t-tests were performed contrasting activity for hits and correct rejections at electrode P3, for each condition and time bin from 200-800ms. Onset time in this case was defined as the first window of three consecutive windows demonstrating the presence of significant differences between hits and correct rejections. Results were consistent with the previous level of analysis, demonstrating a significant difference between hits and correct rejections for the primed condition onsetting from 200ms after target onset ($t(31)=4.91$, $p<0.001$), with differences for the unprimed condition not onsetting until later from 400ms after target onset ($t(31)=4.38$, $p<0.001$).

As noted earlier in Chapter 2, the onset time of differences in average waveforms represent the earliest onset time from all contributing waveforms, and may not always be representative. To investigate the possible impact of a difference across participants in the latency of left-parietal effects for the primed condition, the ERP data were split into two equal groups based on the median average response

Table 6.9: Timing of LP effects by condition. Results of subsidiary analysis at parietal locations investigating the onset time of old/new effects shown separately for the unprimed and primed conditions.

Unprimed	200-300ms	300-400ms	400-500ms	500-600ms	600-700ms	700-800ms
Test status			$F(1,31)=6.29, p=0.018$	$F(1,31)=42.46, p<0.001$	$F(1,31)=55.90, p<0.001$	$F(1,31)=8.67, p=0.006$
Test*Hem	$F(1,31)=4.23, p=0.048$	$F(1,31)=5.61, p=0.024$	$F(1,31)=13.56, p=0.001$	$F(1,31)=10.55, p=0.003$	$F(1,31)=18.14, p<0.001$	$F(1,31)=6.71, p=0.014$
Test*Elec			$F(1.1,34.7)=4.35, p=0.041$	$F(1.2,35.8)=7.45, p=0.007$		
Test*Hem*Elec			$F(1.1,35.2)=8.70, p=0.004$	$F(1.3,38.9)=4.50, p=0.032$	$F(1.5,46.5)=10.59, p=0.001$	
Primed	200-300ms	300-400ms	400-500ms	500-600ms	600-700ms	700-800ms
Test status	$F(1,31)=21.72, p<0.001$	$F(1,31)=30.03, p<0.001$	$F(1,31)=18.25, p<0.001$	$F(1,31)=16.51, p<0.001$	$F(1,31)=9.19, p=0.005$	
Test*Hem	$F(1,31)=5.76, p=0.023$	$F(1,31)=10.57, p=0.003$	$F(1,31)=4.78, p=0.036$			
Test*Elec					$F(1.3,40.9)=7.05, p=0.007$	$F(1.3,40)=20.11, p<0.001$
Test*Hem*Elec		$F(1,4,43.5)=5.26, p=0.017$				

time for primed hits, reasoning that contrasting participants with fast and slow response times may also reveal differences in the onset time of left-parietal effects. The median response time for primed hits was 806.16ms, and splitting the data produced a fast response group (mean=689.72ms, S.E=20.49ms, range=557.50-799.47ms) and a slower response group (mean=998.39ms, S.E=28.79ms, range=843.19-1265.71ms) that differed significantly ($t(30)=8.74$, $p<0.001$). As above, t-tests were employed to contrast activity for hits and correct rejections at electrode P3 for both groups. Results revealed no difference in the onset time of left-parietal effects between groups, with significant differences between hits and correct rejections evident between 200-300ms for the fast ($t(15)=3.95$, $p=0.001$) and slow groups ($t(15)=2.97$, $p=0.010$).

In summary, analysis revealed the presence of left-parietal old/new effects in both conditions, that did not differ in magnitude or distribution, but did differ in onset time. Left-parietal effects for the primed condition onset around 200ms after target onset, continuing into the time window normally associated with the FN400. By contrast, effects for the unprimed did not become evident until around 400ms after target onset, consistent with previous reports of the time window for recollection.

6.4.4 Summary

In summary, the preceding analyses clearly demonstrated that left-parietal effects, linked in the literature to recollection, were modulated by repetition induced fluency. ERPs revealed statistically significant old/new effects with a left-parietal distribution in both conditions, but the conditions differed in the onset time of these effects. Unprimed ERPs were consistent with previous identifications of rec-

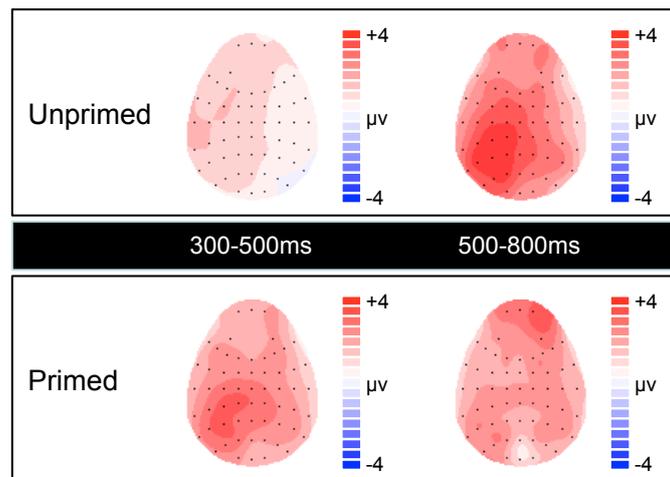


Figure 6.12: Memory topographic summary. Topographic maps summarise differences between hits and correct rejections for the unprimed and primed conditions over time.

ollection (500-800ms), but in primed ERPs the left-parietal old/new effect was evident earlier during the 300-500ms time window, which is normally associated with the onset of familiarity as indexed by the FN400. Further analysis demonstrated that left-parietal effects for the primed condition onset around 200ms after target onset, with effects for the unprimed not evident until around 400ms after target onset. Overall, this pattern of results strongly suggests that repetition induced fluency speeds the onset of recollection signals.

6.5 Discussion

The main aim of the current experiment was to query the relationship between repetition induced fluency and neural correlates of recollection. Two independent predictions were made concerning how fluency could impact signals of recollection based on the evidence reported earlier. Firstly, that interactions between priming and recollection may reduce the magnitude of old/new effects, indexing a reduction in the amount of cognitive resources engaged in retrieving a recently

encountered item. Secondly, that repetition priming may produce observable changes in the timing of left-parietal old/new effects associated with recollection, speeding their onset. The current data confirmed the latter prediction, demonstrating earlier onsetting left-parietal old/new effects for the primed condition, consistent with the findings of Woollams et al. (2008). Response time measures evidenced the presence of fluency, demonstrating faster reaction times for primed hits and correct rejections. In addition, an increase in the magnitude of facilitation for hits provided evidence of priming carried over from exposure during the encoding phase. Despite this clear demonstration of fluency all other behavioural measures were again unaffected by the priming manipulation.

Three priming related modulations were again evident in the ERP data, an early (-50-150ms) posterior negativity, followed by a widespread centro-parietal positivity (250-500ms), and a later (500-1100ms) posterior negativity for primed compared to unprimed words. Overall, the priming effects found in the current experiment largely replicated those reported in the first experiment, but differed in one important respect. The N400 effect evident between 250-500ms at centro-parietal locations was larger in magnitude for hits than for correct rejections, mapping onto the response time data, and providing evidence of additional priming from study exposure. Analysis of the memory data clearly demonstrated that left-parietal effects, linked in the literature to recollection, were modulated by repetition induced fluency. ERPs revealed statistically significant old/new effects with a left-parietal distribution in both conditions, but the conditions differed in the onset time of these effects. Unprimed ERPs were consistent with previous identifications of recollection (500-800ms), but in primed ERPs the left-parietal old/new effect was evident earlier during the 300-500ms time window, which is normally associated with the onset of familiarity as indexed by the FN400. Fur-

ther analysis demonstrated that left-parietal effects for the primed condition onset around 200ms after target onset, with effects for the unprimed not evident until around 400ms post target onset.

As noted earlier, this pattern of results is consistent with those reported by Woollams et al. (2008), but differs in the exact onset latency of effects for the primed condition. The current experiment ensured that presentation of prime words was subliminal, and the onset time of parietal old/new effects was not found to be proportionate to the prime-target SOA, as was the case in the earlier study by Woollams and colleagues. As a result, the current findings provide stronger evidence of a genuine change in the onset latency of recollection following priming. Vilberg, Moosavi and Rugg (2006) also reported an early onsetting left-parietal effect similar to the one found here, during a source memory task employing a modified RK procedure, where participants were required to indicate whether visual objects were fully or partially recollected. Crucially, the authors found that full recollection of contextual information was associated with earlier onsetting left-parietal effects between 200-500ms after stimulus onset. Interpreting the current findings in light of this evidence suggests that priming in this case may have served to reinstate the study context, which led to faster and more complete retrieval of contextual information associated with the study episode.

De Chastelaine et al. (2009) also found that parietal old/new effects decreased in latency over multiple study-test repetitions, moving into the time window for the FN400 (decreasing from 400ms to 300ms), and were associated with a matched increase in discrimination and reduction in reaction times across test repetitions. Crucially, the authors found that decreases in the onset time of parietal effects were selectively associated with R responses, demonstrating that this reflected a change in recollection. Both of these studies suggest that early onsetting parietal

old/new effects are associated with superior recollection, but the current data did not demonstrate differences in discrimination as a result of the earlier onset of old/new differences in the primed condition, so it is difficult to interpret the findings on this basis. Alternatively, this early onsetting form of recollection, while not topographically dissociable from the standard old/new effect associated with recollection between 500-800ms, may index a more automatic non-strategic form of recollection that is divorced from subjective experience.

Moscovitch (2008) proposes that recollection should be conceived of as a two-stage process. The first stage is considered to be rapid automatic retrieval process which occurs when a retrieval cue interacts with stored information, but its products are not accessible to consciousness although it can influence performance. The second stage is more closely aligned with dual-process accounts of recollection, being slower and accessible to consciousness. This view is supported by studies demonstrating hippocampal contributions during implicit memory tests in the absence of explicit retrieval (e.g., Daselaar, Fleck, Prince & Cabeza 2006; Hannula & Ranganath, 2009; Schacter, Dobbins & Schnyer, 2004). It is plausible that the presence of the repetition primes in the current study acted as a proximal retrieval cue, engaging the first stage of recollection in the primed condition, while the unprimed condition relied on conscious recollection to bridge the temporal gap between study and test. On this view, the early onsetting parietal old/new effect observed in the primed condition reflects an implicit form of recollection, and the later effect observed in the unprimed condition reflects the strategic search associated with the subjective feeling of recollection.

These views and the current data are difficult to reconcile with dual-process models that assume that recollection is always slow and effortful, indexing a strategic conscious memory search. However, the current findings are consistent

with behavioural research questioning this key assumption of dual-process models, which demonstrate faster reaction times for R than for K judgements and suggest that experiences of remembering are sometimes rapid and automatic in nature (Dewhurst & Conway, 1994; Dewhurst et al., 2006; Henson et al., 1999). As noted in the introduction, it has been argued that these behavioural findings are driven by the nature of RK instructions rather than differences in underlying processing, because participants only make a K responses once both processes are complete and they have failed to recollect (Yonelinas, 2002). The current findings refute this criticism evidencing a clear change in the timing of underlying neural processing related to recollection, and demonstrating that the degree of priming influences the speed of recollection during recognition tests.

6.5.1 Summary

The current findings clearly demonstrate the presence of an interaction between repetition priming and neural correlates of recollection, and challenge a key assumption of dual-process models of recognition, namely that recollection is slow and effortful. Moreover, the findings prove that priming from exposure at encoding can carry over to the test phase during standard recognition tests, modulating the same N400 component as masked priming during the 250-500ms time window. In addition to the response time data, which showed greater facilitation for studied words, this modulation confirms that evidence of neural priming would have been present at test in the absence of masked primes. Importantly, the memory data demonstrated that priming influenced the neural correlates of recollection, with left-parietal effects for the primed condition onsetting 200ms after target onset and effects for the unprimed not evident until 400ms after target onset.

While early onsetting recollection effects have been reported previously in the literature, the exact nature of the early onsetting recollection effect reported here remains an open question. It could reflect a more automatic form of recollection, divorced from subjective experience, or it could index more complete retrieval of contextual information. Nonetheless, the current study contributes additional insights to a slowly growing literature demonstrating that priming and recollection do in fact interact.

Chapter 7

ERP 3

7.1 Introduction

The first two experiments reported in this thesis were specifically designed to manipulate the degree of priming within the confines of a standard recognition task by including masked repetition at test. Across both of these experiments the degree of repetition was held constant, while varying the encoding task to re-create conditions that are commonly used in tests of recognition. The remaining experiments reported in this thesis represent a departure from this initial strategy, and focus on manipulating the degree of masked priming more directly. Specifically, the remaining experiments were designed to investigate mechanisms driving the absence of FN400 old/new effects reported in the first data chapter, in an attempt to identify some of the factors that determine whether retrieval will be implicit or explicit. In addition, we sought to investigate N400 effects observed in the first experiment, in an attempt to delineate lexical and post-lexical interpretations of the observed outcome. To achieve these goals, the study reported in the current

chapter manipulated the Stimulus Onset Asynchrony (SOA) between prime and target pairings to vary the degree of priming.

The choice of prime-target SOA in ERP research is partially driven by the pragmatics of measuring overlapping neural signals related to presentation of prime and target items in close proximity (Holcomb & Grainger, 2006). As far as we are aware, this approach of directly manipulating the SOA between prime and target pairings during recognition testing is novel with respect to the ERP literature, despite the fact that across studies the prime-target SOA tends to be highly variable. For example, Woollams et al. (2008) employed a prime-target SOA of 43ms, while Lucas et al. (2012) employed an SOA of 600ms. The findings of these studies differed appreciably with respect to the N400 signals observed; in the former N400 signals onset 150ms post target and continued into the 300-500ms time window, while in the latter N400 signals were much shorter lived, appearing only between 300-400ms. It is plausible that the exact nature of priming eliciting N400 like effects may have differed across these experiments. Previous research has demonstrated that while increasing the SOA between prime-target pairings consistently increases response priming (Van den Bussche, Van den Noortgate & Reynvoet, 2009), most lexical and sub-lexical masked priming effects are eliminated by 500ms after prime onset (Ferrand, 1996), and it has been suggested that all that remains beyond 500ms is residual semantic activity (Holcomb & Grainger, 2006).

On this basis, the effect characterized as an N400 by Woollams et al. (2008) could be largely lexical in nature, while the effect reported by Lucas et al. (2012) may entirely reflect post-lexical semantic processing. The first two experiments reported in this thesis employed a prime-target SOA of 398ms, and the timing of N400 effects observed in both experiments was highly consistent with the la-

tency of previous reports of N400 effects in the literature, appearing during the 250-500ms time window (Kutas & Federmeier, 2011). However, given that the prime-target SOA was less than 500ms, and that the N400 observed in the first experiment did not appear to be modulated over centro-parietal locations for studied compared to unstudied words, it could be argued that effects in the first experiment were driven by lexical rather than post-lexical fluency. Therefore, to gain a better understanding of the mechanisms driving implicit recognition in the first experiment, it is essential to establish the level and nature of priming contributing to this outcome. The current experiment employed the standard SOA from the previous experiments, and contrasted this with a longer SOA of 698ms to differentiate between these accounts of the N400. In addition, we reasoned that increasing the SOA between prime-target pairings should elicit a greater degree of fluency by allowing extra time for semantic information to be processed, and that this higher degree of fluency may promote reliance on familiarity.

7.2 Methods

Stimulus materials and procedures were identical to those reported in chapter 4 with an added manipulation of SOA between prime and target words. In all other experiments reported in this thesis the SOA between prime and target was 398ms, the current experiment employed this standard SOA on 50% of trials and the remaining trials employed an SOA of 698ms. The SOA of 698ms was chosen to reduce the contribution of sub-lexical and lexical effects resulting from presentation of the masked prime. To implement the longer SOA, the duration of the backwards mask was increased by 300ms, and to maintain consistency in the appearance of the masking procedure the duration of the forwards mask

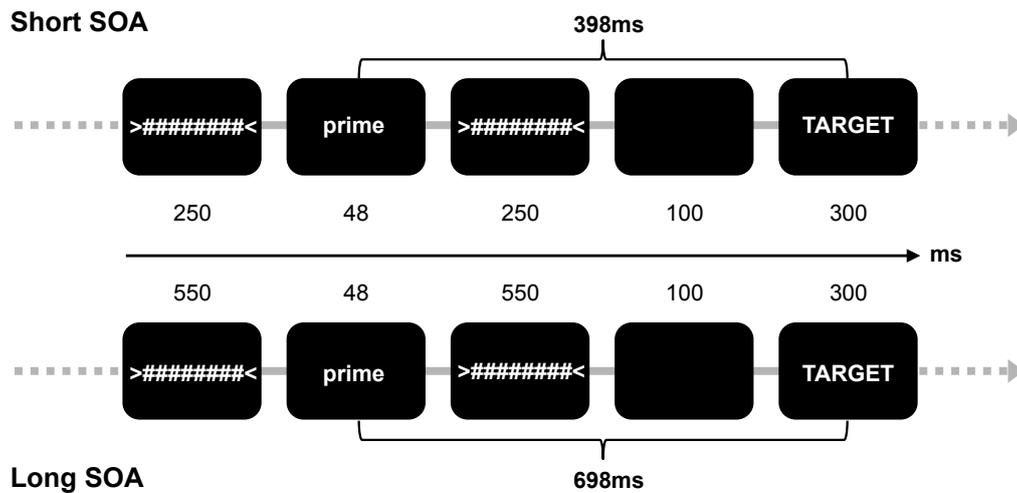


Figure 7.1: Test procedure. During the test phase participants were shown 120 words, 60 old words and 60 new words, fifty percent of old and new words were primed. A: On primed trials target presentation was preceded by a repetition of the target. B: On unprimed trials the presentation of the target word was preceded by the word blank.

was also increased (see Figure 7.1). The number of words in each test list was maintained at 120. Across the entire experiment participant viewed 240 trials in each condition (unprimed, primed), 120 trials with the 398ms SOA and 120 with the 698ms SOA (60 old, 60 new) randomly intermixed. Thirty-eight undergraduate psychology students from the University of Stirling participated in the experiment. Six participants were excluded due to excessive EEG artefacts, resulting in insufficient ERP trials for critical contrasts (<16 trials). The remaining thirty-two participants comprised of 21 females and 11 males with a mean age of 20 (range=18-26; SD=2.25).

7.3 Behavioural results

In total 69% of participants reported being unaware of the existence of the masked prime, 9% reported that they detected flickering on the screen but were unable

to detect any of the words, and the remaining 22% reported that they were aware of seeing the word blank appear before the onset of the target on a few trials, but none of the participants reported being aware of the repetition of the target words. Initial examination of the behavioural data as a function of reported awareness confirmed no differences in the pattern of results for participants who reported being aware of flickering on the screen or aware of the word blank compared to unaware participants, and as a result the data were analysed collapsed across awareness categories. Table 7.1 shows a summary of memory performance measures for the current experiment. The data demonstrate a reduction in mean accuracy for new words in the primed condition, accompanied by an overall reduction in discrimination for primed words. Response bias was conservative across conditions, but the data suggest a trend towards a more liberal bias for primed words.

Table 7.1: Memory performance. Percentage of correct responses, discrimination and bias measures for the unprimed and primed conditions split by SOA (standard error of the mean). The data demonstrate a slight reduction in mean accuracy for new words, and a slight reduction in discrimination accompanied a slight increase in response bias for the primed compared to the unprimed condition at both SOAs.

		Correct %		Discrimination	
		Old	New	Pr	Br
398ms	Unprimed	54.82 (2.07)	81.67 (1.98)	0.36 (0.02)	0.28 (0.03)
	Primed	55.55 (2.49)	78.49 (2.33)	0.34 (0.03)	0.32 (0.03)
698ms	Unprimed	55.56 (2.37)	80.34 (1.86)	0.36 (0.02)	0.31 (0.03)
	Primed	55.70 (2.01)	75.77 (2.13)	0.31 (0.02)	0.35 (0.03)

Crucially, analysis confirmed that participants were able to discriminate between old and new words in both conditions (paired t-tests comparing hits and false alarms for both conditions and at each SOA were significant [$p < 0.001$] in all comparisons). Mean accuracy data were submitted to analysis using ANOVA

with the factors of condition (unprimed, primed), test status (old, new), and SOA (398ms, 698ms). Results revealed main effects of condition [$F(1,31)=5.95$, $p=0.021$], and test status [$F(1,31)=50.36$, $p<0.01$], and a marginally significant interaction between condition and test status [$F(1,31)=3.77$, $p=0.061$]. Subsidiary analysis performed on the data collapsed across SOA confirmed that mean accuracy was lower for new words in the primed compared to the unprimed condition ($t(31)=3.73$, $p=0.001$).

For the discrimination data, ANOVA revealed a significant main effect of condition [$F(1,31)=6.02$, $p=0.02$], but no interaction between condition and SOA. Follow up analysis collapsed across SOA confirmed a significant reduction in discrimination for primed words ($t(31)=2.45$, $p=0.02$). Analysis of response bias also revealed a main effect of condition [$F(1,31)=6.65$, $p=0.015$], but no interaction between condition and SOA. Subsidiary analysis collapsed across SOA identified a more liberal response bias for primed than for unprimed words ($t(31)=2.57$, $p=0.015$). Overall the pattern of results demonstrates lower performance rates for primed new words irrespective of SOA and that this reduction was driven by an increase in false alarm rates to new words, supported by the reported increase in response bias for primed words.

Table 7.2: Response by RK. Mean percentage of RK responses split by condition, test status and SOA (standard error of the mean). The data demonstrate a slight increase in the proportion of R and K false alarms in the primed condition for both SOAs.

		398ms		698ms	
		R	K	R	K
Old	Unprimed	29.31 (2.32)	25.50 (1.64)	29.97 (2.47)	25.59 (2.02)
	Primed	29.53 (2.41)	26.02 (1.95)	28.90 (2.33)	26.79 (1.90)
New	Unprimed	5.94 (1.36)	12.39 (1.59)	5.21 (1.26)	14.45 (1.62)
	Primed	6.54 (1.39)	14.97 (1.94)	7.35 (1.52)	16.88 (1.87)

Table 7.2 shows the breakdown of responses by RK judgement for each category of old and new words in the unprimed and primed conditions split by SOA, and suggests that priming slightly increased the raw proportion of R and K false alarms. ANOVA contrasting RK responses, including the factors of condition (unprimed, primed), test status (Hits, FAs), response type (R, K) and SOA (398ms, 698ms), produced an interaction between condition and test status [$F(1,31)=5.96$, $p=0.021$]. Subsidiary analysis on false alarms collapsed across SOA revealed main effects of condition [$F(1,31)=13.63$, $p=0.001$], and response [$F(1,31)=15.43$, $p<0.001$]. Follow up t-tests confirmed that the main effect of condition indicated an increase in the proportion of R ($t(31)=2.84$, $p=0.008$) and K false alarms ($t(31)=2.49$, $p=0.019$) for the primed compared to the unprimed condition, and that the main effect of response reflected a higher proportion of K than R false alarms ($t(31)=3.93$, $p<0.001$). Estimates of familiarity and recollection were calculated and submitted to ANOVA including the factors of condition (unprimed, primed), SOA (398ms, 698ms) and retrieval process (familiarity, recollection). Analysis demonstrated that differences apparent in the raw proportions of RK responses did not survive correction for independence.

Table 7.3 shows the response time data for hits and correct rejections in the unprimed and primed conditions split by SOA, and the magnitude of the difference between the unprimed and primed conditions at each SOA. The data demonstrates speeded response times for primed words compared to unprimed words for hits and correct rejections, with larger effects for the 698ms SOA. Mean response time data were analysed using ANOVA including the factors of condition (unprimed, primed), test status (old, new), and SOA (398ms, 698ms), which revealed significant main effects of condition [$F(1,31)=138.37$, $p<0.001$], test status [$F(1,31)=4.68$, $p=0.038$] and SOA [$F(1,31)=93.25$, $p<0.001$], along with signifi-

Table 7.3: Response times (ms). Mean response time data for correct responses split by SOA and test status, and the magnitude of the difference between unprimed and primed response times split by SOA and test status (standard error of the mean). The data demonstrate that response times were faster for hits and correct rejections in the primed condition at both SOAs, with much larger effects for hits and correct rejections at the 698ms SOA, and slightly larger effects for hits compared to correct rejections at both SOAs.

	398ms		698ms	
	Old (Hits)	New (CRs)	Old (Hits)	New (CRs)
Unprimed	933.53 (31.62)	864.40 (26.05)	894.37 (34.53)	848.20 (26.88)
Primed	833.97 (38.34)	788.52 (33.29)	681.47 (40.60)	666.17 (36.68)
Magnitude	99.56 (17.14)	75.78 (13.13)	212.90 (15.75)	182.03 (17.65)

cant interactions between condition and test status [$F(1,31)=4.23$, $p=0.48$], and condition and SOA [$F(1,31)=95.57$, $p<0.001$]. This result clearly indicates that priming effects were present on response times and suggests that differences in the size of these effects exist as a function of test status and SOA. Despite the data suggesting a trend towards larger priming effects for hits than for correct rejections (398ms: 23.78ms, 698ms: 30.87ms), subsidiary analysis performed on the magnitude of the difference between unprimed and primed response times revealed that these differences were not significant for either SOA ($p>0.05$). Contrasting the magnitude of the difference for hits and correct rejections across SOA confirmed the presence of larger priming effects for hits ($t(31)=6.25$, $p<0.001$) and for correct rejections ($t(31)=7.60$, $p<0.001$) at the 698ms SOA.

7.3.1 Summary

In summary, the accuracy data demonstrated a slight increase in false alarm rates and a slightly more liberal bias for the primed condition, resulting in poorer discrimination for primed words irrespective of SOA. The Remember/Know data

demonstrated a slight increase in the raw proportion of R and K false alarms for the primed condition across SOAs, but analysis on corrected estimates of familiarity and recollection failed to reveal differences between the unprimed and primed conditions as a function of SOA. Response time data demonstrated faster responses for primed words across SOAs, with larger effects overall for the 698ms SOA.

7.4 ERP results

Grand average ERPs were formed for hits and correct rejections in the unprimed and primed conditions. Visual inspection confirmed the presence of early priming effects onsetting prior to the onset of the target words for both SOAs. Due to the manipulation of SOA, it was necessary to employ two different epochs to capture the onset of the prime. For the 398ms SOA the epoch ran from -500-1500ms, and for the 698ms SOA the epoch ran from -800-1200ms. For the -500-1500ms epoch the mean number of trials contributing to waveforms for hits was 29 in both conditions and the mean number of trials contributing to waveforms for correct rejections was 44 for the unprimed condition and 42 for the primed conditions. For the -800-1200ms epoch 30 trials contributed to waveforms for hits in both conditions and waveforms for correct rejections comprised of 43 trials in the unprimed condition and 40 trials in the primed condition. Due to different epochs and timing, priming and memory effects for each SOA were analysed separately and the analysis proceeded in the same manner as in the previous chapters. Magnitude and topographic comparisons performed on the data from matching time windows across SOAs are reported at the end of each section.

7.4.1 Priming 398ms SOA

Figure 7.2 shows grand average waveforms for hits and correct rejections in the unprimed and primed conditions. Visual inspection of the waveforms confirmed the presence of three priming related modulations. An early negativity (-50-150ms) at central locations for primed compared to unprimed correct rejections, followed by a widespread central positivity (250-500ms), and then later posterior negativity (500-1100ms) towards the end of the epoch for primed words compared to unprimed words. In short, the data for the standard SOA exhibits priming effects similar to those reported for the previous experiments. The first level of analysis on the data was designed to identify variations in priming effects across conditions and time windows, employing ANOVA with the factors of condition (unprimed, primed), location (Fz, FCz, Cz, CPz, Pz, POz) and time window (-50-150ms, 250-500ms, 500-1100ms). Results for hits revealed a significant main effect of condition [$F(1,31)=7.76$, $p=0.009$] and a significant interaction between condition, location and time window [$F(2.7,82.4)=18.18$, $p<0.001$]. Analysis for correct rejections also revealed a significant main effect of condition [$F(1,31)=11.02$, $p=0.002$] and an interaction between condition, location and time window [$F(2.7,82.5)=23.86$, $p<0.001$]. The presence of these interactions provides strong evidence of variation in the pattern of priming effects across locations and time windows for both hits and correct rejections.

Follow up analysis was performed separately for hits and correct rejections on the data from each time window, using ANOVA with the factors of condition (unprimed, primed) and location (Fz, FCz, Cz, CPz, Pz, POz); the results of this analysis are summarised in Table 7.4. For hits the results demonstrated no main effect or interaction in the first time window, but did reveal main effects

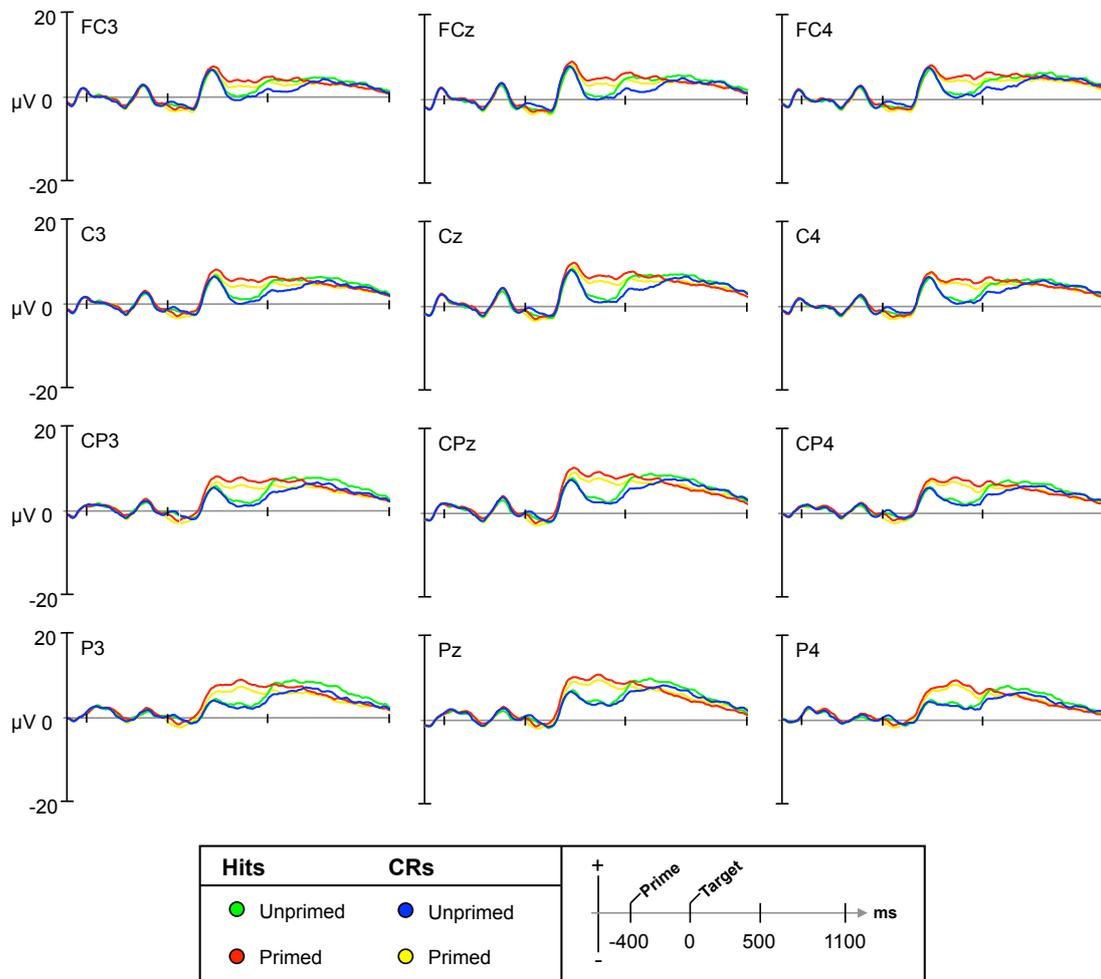


Figure 7.2: Priming effects 398ms SOA Grand average ERPs for hits and correct rejections in the unprimed and primed conditions with the 398ms prime-target SOA. Waveforms display the presence of three priming related modulations, an early central negativity for primed correct rejections, followed by a widespread central positivity and a later posterior negativity for primed compared to unprimed words.

and interactions with the factor of location in the later two windows. Results for correct rejections revealed a main of condition in the first and second time window and interactions between condition and location in the second and third time windows. This pattern of results is consistent with the presence of priming effects that vary by location for hits and correct rejections in the later windows and suggests differences in the pattern of effects for hits and correct rejections in the first and last time windows.

Table 7.4: Priming ANOVAs by time window. Results of ANOVAs contrasting midline sites with the factors of condition and location over the three time windows chosen for analysis of priming effects.

		-50-150ms	250-500ms	500-1100ms
Hits	Cond	-	$F(1,31)=43.44, p<0.001$	$F(1,31)=4.87, p=0.035$
	Cond*Loc	-	$F(1.6,48.4)=17.02, p<0.001$	$F(1.6,48.6)=6.20, p=0.007$
CRs	Cond	$F(1,31)=6.39, p=0.017$	$F(1,31)=64.21, p<0.001$	
	Cond*Loc	-	$F(1.6,49.8)=19.21, p<0.001$	$F(2,63.7)=8.68, p<0.001$

Subsidiary analysis took the form of contrasts between the unprimed and primed conditions, performed separately for hits and correct rejections, using ANOVA with the factors of condition (unprimed, primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior) and the results for each time window are reported separately in the following sections.

7.4.1.1 Time window -50 to 150ms

From 50ms prior to the onset of target words, waveforms for primed correct rejections were more negative going than for unprimed correct rejections across frontal and central locations, but waveforms for hits did not demonstrate this early central negativity (see Figure 7.3 for the data from Cz). Initial analysis

for hits revealed no main effect or interactions including the factor of condition, confirming that no priming effects were evident for hits during the -50-150ms time window. Analysis for correct rejections revealed a significant main effect of condition [$F(1,31)=8,79$, $p=0.006$], but no significant interactions including the factor of condition.

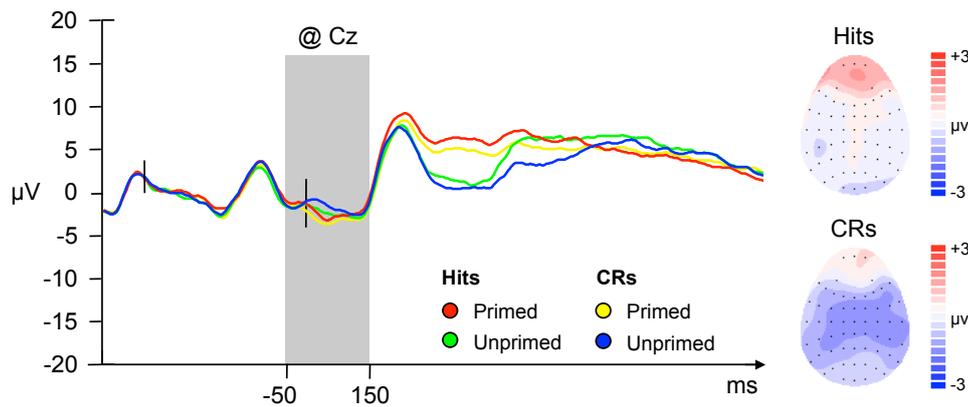


Figure 7.3: Priming @ Cz (-50-150ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode Cz. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Waveforms for primed correct rejections were more negative going than for unprimed correct rejections across frontal and central locations, with no difference between conditions for hits.

Despite failure to find interactions, inspection of the data suggests that the early negativity was strongest at central locations, with slightly larger effects over the right hemisphere. In support of this interpretation, subsidiary analysis at separate locations revealed significant main effects of condition extending from frontal to parietal locations ($p<0.05$ in all cases), and a significant interaction between condition, hemisphere and electrode [$F(1.1,35.5)=4.07$, $p=0.046$] at central locations. As can be seen in Figure 7.3 these results indicate the presence of a slight but widespread negativity for primed correct rejections that is stronger over the right hemisphere at central locations. Further examination of the data confirmed that priming effects for correct rejections were maximal at electrode

C2 ($t(31)=4.01$, $p<0.001$). In summary, the data demonstrated the presence of a widespread negativity for correct rejections extending from frontal to parietal locations with a focus over the right hemisphere at central locations, but this early negativity was not apparent in the data for hits.

7.4.1.2 Time window 250 to 500ms

From 250ms after target onset, waveforms for primed hits and correct rejections were more positive going than for unprimed hits and correct rejections across central and posterior locations, where the difference appeared slightly larger in magnitude for hits than for correct rejections (see Figure 7.4 for data from CPz). Initial analysis for hits revealed a significant main effect of condition [$F(1,31)=40.86$, $p<0.001$], along with interactions between condition, location and electrode [$F(2.5,79)=3.83$, $p=0.017$], and condition, hemisphere and electrode [$F(1.2,37.3)=9.46$, $p=0.002$]. Initial analysis for correct rejections produced a significant main effect of condition [$F(1,31)=55.13$, $p<0.001$], and significant interactions between condition and hemisphere [$F(1,31)=4.81$, $p=0.036$], and condition, location and electrode [$F(1.9,60.4)=4.02$, $p=0.024$]. As can be seen in Figure 7.4, these results reflect the presence of a positivity for primed hits and correct rejections over central and posterior locations that appears slightly stronger over the right hemisphere.

Table 7.5 shows the results of subsidiary analysis at separate locations for hits and correct rejections. Results for hits revealed interactions between condition and electrode, and condition hemisphere and electrode across locations, reflecting the presence of a widespread positivity for primed hits at superior electrode sites that appears slightly stronger over inferior sites in the right hemisphere. Follow up

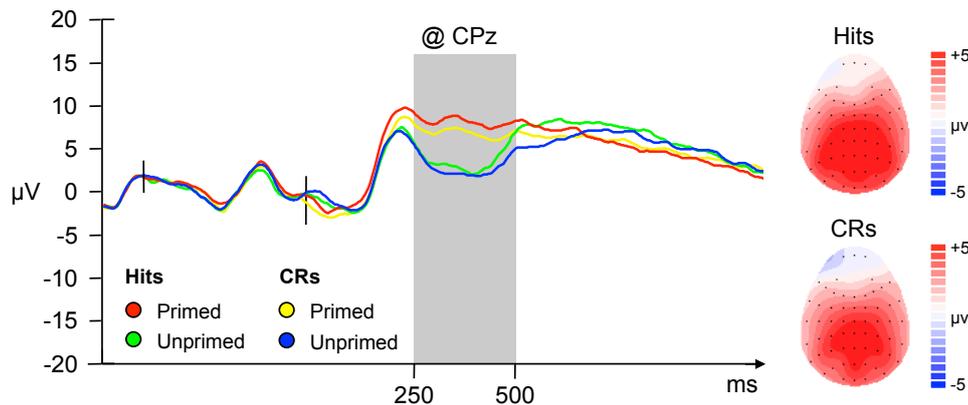


Figure 7.4: Priming @ CPz (250-500ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode CPz. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Waveforms for primed hits and correct rejections were more positive going than for unprimed hits and correct rejections across central and posterior locations, where the difference appeared slightly larger in magnitude for hits than for correct rejections.

analysis collapsed across locations confirmed this result, demonstrating slightly larger effects at inferior sites in the right hemisphere ($t(31)=2.13$, $p=0.041$) and that the difference between conditions was larger at superior sites than at medial ($t(31)=3.41$, $p=0.002$) or inferior sites ($t(31)=4.93$, $p<0.001$). Further examination of the data for hits confirmed that this priming effect was maximal at electrode CPz ($t(31)=7.48$, $p<0.001$).

Results for correct rejections revealed significant interactions between condition and electrode across locations, with interactions including the factor of hemisphere at central, centro-parietal and parietal locations, reflecting the presence of a widespread positivity for primed correct rejections at superior electrodes with a slight skew over the right hemisphere extending from central to parietal locations. Follow up analysis collapsed across locations and hemispheres again confirmed that effects were larger over superior sites than at medial ($t(31)=5.76$, $p<0.001$) or inferior sites ($t(31)=7.90$, $p<0.001$). Focused analysis on the data collapsed from central to parietal locations demonstrated that interactions be-

Table 7.5: Priming by location (250-500ms). Results of subsidiary analysis at separate locations for hits and correct rejections.

Hits (250-500ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=9.68, p=0.004$	$F(1,31)=19.59, p<0.001$	$F(1,31)=35.35, p<0.001$	$F(1,31)=52.90, p<0.001$	$F(1,31)=70.98, p<0.001$	$F(1,31)=86.93, p<0.001$
Cond*Hem	$F(1,31)=4.37, p=0.045$					
Cond*Elec	$F(1.1,34.4)=4.00, p=0.05$	$F(1.1,35)=13.30, p=0.001$	$F(1.1,33.7)=21.49, p<0.001$	$F(1.2,35.7)=22.12, p<0.001$	$F(1.3,38.9)=17.71, p<0.001$	$F(1.2,37.9)=31.48, p<0.001$
Cond*Hem*Elec	$F(1.5,47.8)=5.10, p=0.016$	$F(1.5,45.7)=3.94, p=0.038$	$F(1.2,37.4)=8.51, p=0.004$	$F(1.5,46.4)=5.32, p=0.014$	$F(1.5,48)=5.96, p=0.009$	$F(1.4,41.8)=6.04, p=0.011$
CRs (250-500ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=10.73, p=0.003$	$F(1,31)=26.50, p<0.001$	$F(1,31)=45.45, p<0.001$	$F(1,31)=64.66, p<0.001$	$F(1,31)=91.51, p<0.001$	$F(1,31)=102.63, p<0.001$
Cond*Hem			$F(1,31)=4.99, p=0.033$			
Cond*Elec	$F(1.2,36.1)=4.66, p=0.032$	$F(1.2,37.6)=20.26, p<0.001$	$F(1.2,37.3)=42.83, p<0.001$	$F(1.1,34.3)=45.17, p<0.001$	$F(1.2,35.8)=54.49, p<0.001$	$F(1.1,35.4)=75.19, p<0.001$
Cond*Hem*Elec				$F(1.3,40.5)=8.10, p=0.004$	$F(1.5,45.1)=5.13, p=0.017$	

tween condition, hemisphere and electrode were driven by slightly larger effects over inferior sites in the right hemisphere ($t(31)=2.23$, $p=0.033$). Further examination of the data confirmed that priming effects for correct rejections were also maximal at electrode CPz ($t(31)=8.32$, $p<0.001$).

The foregoing results suggest potential differences in the magnitude and distribution of priming effects for hits and correct rejections, but magnitude analysis contrasting effects for hits and correct rejections revealed no main effects or interactions including the factor of condition, confirming that the priming effects observed for hits and correct rejections were comparable in magnitude and distribution. In summary, during the 250-500ms time window primed hits and correct rejections were more positive going than unprimed hits and correct rejections. Priming effects were maximal at superior centro-parietal locations for hits and correct rejections and did not differ substantially in magnitude or distribution.

7.4.1.3 Time window 500 to 1100ms

From 500ms after target onset, waveforms for primed hits and correct rejections were more negative going than for unprimed hits and correct rejections at posterior locations in the left hemisphere, with the largest difference between conditions for hits (see Figure 7.5 for the data from PO3). Initial analysis for hits revealed a significant main effect of condition [$F(1,31)=4.48$, $p=0.043$], and significant interactions between condition and location [$F(5,155)=7.48$, $p=0.004$], and condition and electrode [$F(1.1,32.8)=6.25$, $p=0.016$]. Analysis for correct rejections produced a significant interaction between condition, location, hemisphere and electrode [$F(10,310)=2.55$, $p=0.04$]. As can be seen in Figure 7.5, these results

reflect the presence of a negativity for primed hits and correct rejections at posterior locations, that appears slightly larger over the left hemisphere.

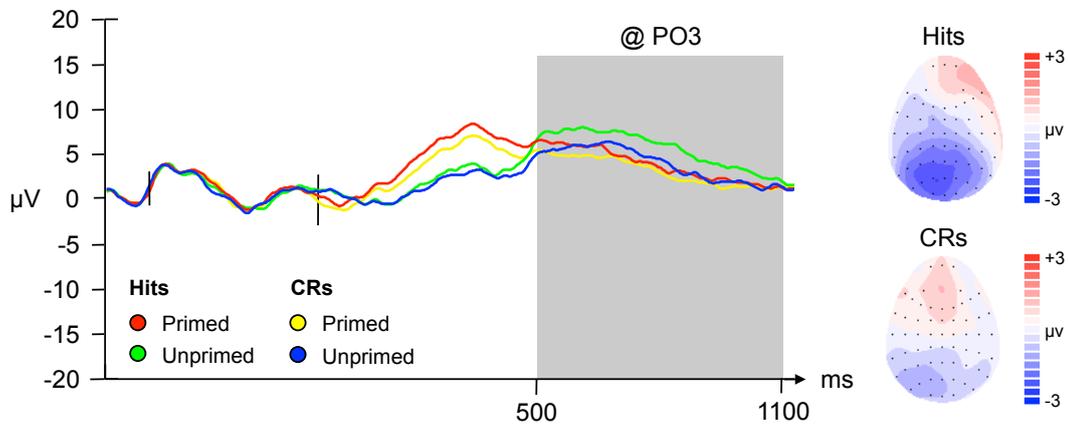


Figure 7.5: Priming @ PO3 (500-1100ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode PO3. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Waveforms for primed hits and correct rejections were more negative going than for unprimed hits and correct rejections at posterior locations, with the largest difference between conditions for hits.

Table 7.6 shows the results of subsidiary analysis at separate locations for hits and correct rejections. Results for hits demonstrated main effects of condition and interactions between condition and electrode extending from centro-parietal to parieto-occipital locations, with interactions including the factor of hemisphere at parietal and parieto-occipital locations. This pattern of results reflects the presence of a negativity for primed hits towards superior electrode sites across posterior locations, with larger effects over inferior sites in the the left hemisphere at parietal and parieto-occipital locations. Follow up analysis on the data collapsed from centro-parietal to parieto-occipital locations demonstrated that effects were larger over superior ($t(31)=2.77$, $p=0.009$) and medial sites ($t(31)=2.93$, $p=0.006$) than at inferior sites. Analysis collapsed over parietal and parieto-occipital locations confirmed that interactions including the factor of hemisphere reflected that effects were slightly larger over inferior sites in the left

Table 7.6: Priming by location (500-1100ms). Results of subsidiary analysis at separate locations for hits and correct rejections.

Hits (500-1100ms)	F	FC	C	CP	P	PO
Cond				$F(1,31)=5.53, p=0.041$	$F(1,31)=8.10, p=0.008$	$F(1,31)=11.60, p=0.002$
Cond*Hem						$F(1,31)=5.40, p=0.027$
Cond*Elec				$F(1.1,33.5)=4.03, p=0.05$	$F(1.1,34.9)=5.30, p=0.024$	$F(1.1,34.1)=13.06, p=0.001$
Cond*Hem*Elec					$F(1.3,38.8)=4.60, p=0.030$	
CRs (500-1100ms)	F	FC	C	CP	P	PO
Cond						$F(1,31)=4.82, p=0.036$
Cond*Hem						
Cond*Elec						
Cond*Hem*Elec						

hemisphere at these locations ($t(31)=2.06$, $p=0.048$). Further examination of the data demonstrated that priming effects for hits were maximal at electrode PO3 ($t(31)=4.28$, $p<0.001$).

Subsidiary analysis at separate locations for correct rejections revealed a significant main effect of condition at parieto-occipital locations, reflecting a slight negativity for primed correct rejections that did not differ across sites. Further examination of the data demonstrated that priming effects for correct rejections were maximal at electrode PO5 ($t(31)=2.47$, $p=0.019$). Magnitude analysis contrasting priming effects for hits and correct rejections revealed a significant interaction between test status and electrode [$F(1.1,33.4)=8.49$, $p=0.005$], reflecting a difference in the size of priming effects for hits and correct rejections over superior electrode sites, with greater negativity for hits. Topographic comparison performed on the rescaled data revealed no main effect or interactions including the factor of test status, suggesting that the observed effects for hits and correct rejections did not differ in distribution.

In summary, during the 500-1100ms time window primed hits and correct rejections were more negative going than unprimed hits and correct rejections at posterior locations. These late priming effects differed in magnitude but not in distribution, with larger effects over superior sites for hits, demonstrating that this late priming effect was modulated by exposure to words at study.

7.4.2 Priming 698ms SOA

Figure 7.6 shows grand average waveforms for hits and correct rejections in the unprimed and primed conditions. Visual inspection of the waveforms confirmed the presence of three priming related modulations. An early central negativity

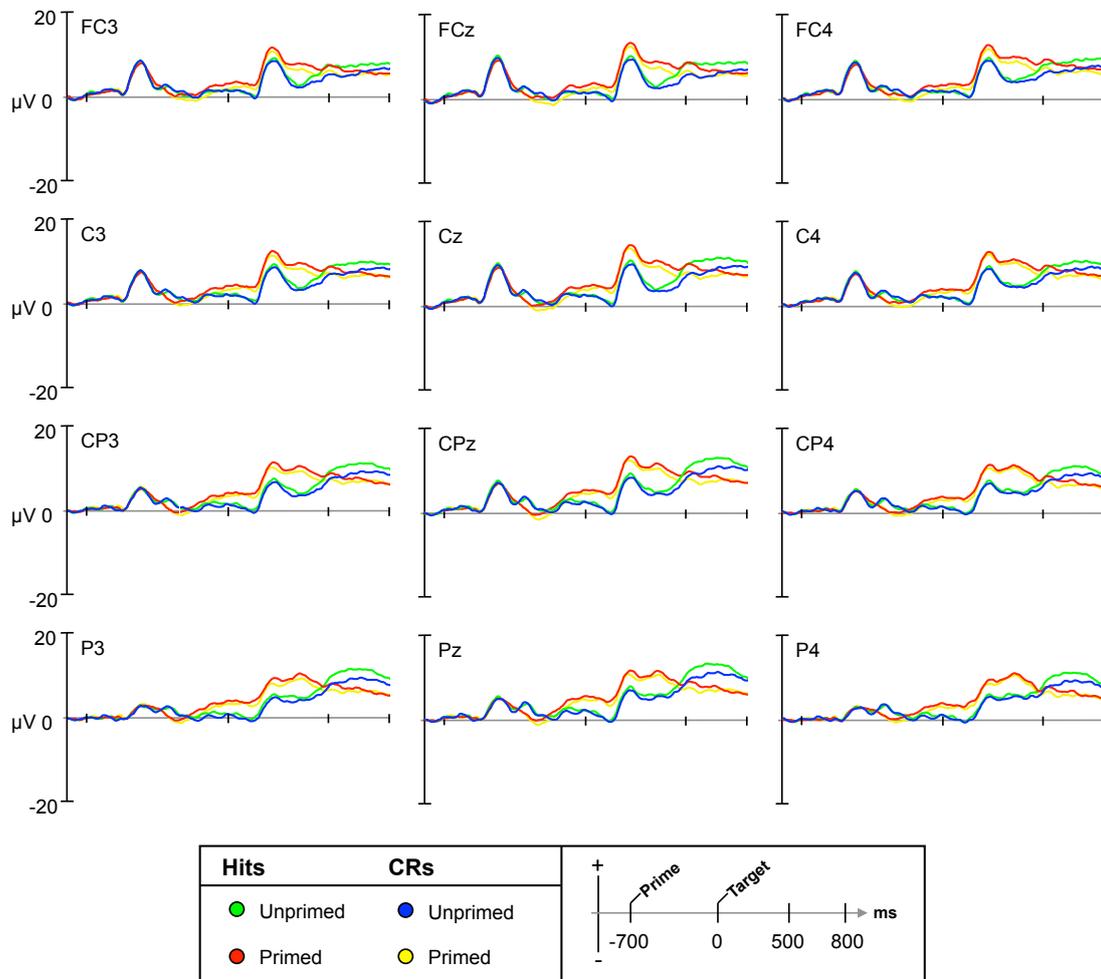


Figure 7.6: Priming effects 698ms SOA Grand average ERPs for hits and correct rejections in the unprimed and primed conditions with the 698ms prime-target SOA. Waveforms display the presence of three priming related modulations, an early central negativity, followed immediately by a widespread central positivity and a later posterior negativity for primed compared to unprimed words.

(-350 to -150ms), followed by a central positivity (-100-500ms), and a later posterior negativity (500-1100ms) for primed hits and correct rejections. The first level of analysis on the data was again designed to identify variations in priming effect across conditions and time windows, employing ANOVA with the factors of condition (unprimed, primed), location (Fz, FCz, Cz, CPz, Pz, POz) and time window (-350 to -150ms, -100-500ms, 500-1100ms). Results revealed significant interactions between condition, location and time window for hits [$F(2.5,77.7)=9.64$, $p<0.001$], and correct rejections [$F(2.1,66.2)=13.07$, $p<0.001$], providing strong evidence of variation in the pattern of priming effects across locations and time windows for hits and correct rejections. Follow up analysis was performed separately for hits and correct rejections on the data from each time window, using ANOVA with the factors of condition (unprimed, primed) and location (Fz, FCz, Cz, CPz, Pz, POz); the results of this analysis are summarised in Table 7.7.

Table 7.7: Priming ANOVAs by time window. Results of ANOVAs contrasting midline sites with the factors of condition and location over the three time windows chosen for analysis of priming effects.

		-350 to -150ms	-100-500ms	500-1100ms
Hits	Cond	-	$F(1,31)=51.96$, $p<0.001$	$F(1,31)=24.40$, $p<0.001$
	Cond*Loc	-	$F(1.3,42.1)=4.20$, $p=0.035$	$F(1.2,37.4)=8.37$, $p=0.004$
CRs	Cond	$F(1,31)=12.59$, $p=0.001$	$F(1,31)=48.38$, $p<0.001$	$F(1,31)=21.01$, $p<0.001$
	Cond*Loc	-	$F(1.8,56.4)=16.86$, $p<0.001$	$F(1.5,45.8)=18.79$, $p<0.001$

For hits the results demonstrated no main effect or interaction in the first time window, but did reveal main effects and interactions with the factor of location in the later two windows. Results for correct rejections revealed main effects of condition in all time windows and interactions between condition and location in the second and third time windows. This pattern of results is consistent with the

presence of priming effects that vary by location for hits and correct rejections in the later time windows and suggest a difference in the pattern of effects for hits and correct rejections in the first time window. Subsidiary analysis took the form of contrasts between the unprimed and primed conditions performed separately for hits and correct rejections, using ANOVA with the factors of condition (unprimed, primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior) and the results for each time window are reported separately in the following sections.

7.4.2.1 Time window -350 to -150ms

From 350ms after onset of the prime, waveforms for primed hits and correct rejections were more negative going than for unprimed hits and correct rejections across central and posterior locations (see Figure 7.7 for the data from CPz). Initial analysis for hits revealed no main effects or interactions including the factor of condition, demonstrating the absence of substantial priming effects for hits. Analysis for correct rejections produced a significant main effect of condition [$F(1,31)=13.28$, $p=0.001$], along with interactions between condition, location and hemisphere [$F(2.4,74.6)=5.19$, $p=0.005$], and condition, location and electrode [$F(3,93.8)=3.42$, $p=0.020$]. As can be seen in Figure 7.7, these results reflect the presence of a negativity for primed correct rejections over central locations at superior electrode sites, with a slight skew over the right hemisphere.

Table 7.8 shows the results of subsidiary analysis at separate locations for correct rejections. Results revealed significant main effects of condition across locations, interactions between condition and electrode extending from frontal to parietal locations and interactions involving the factor of hemisphere from cen-

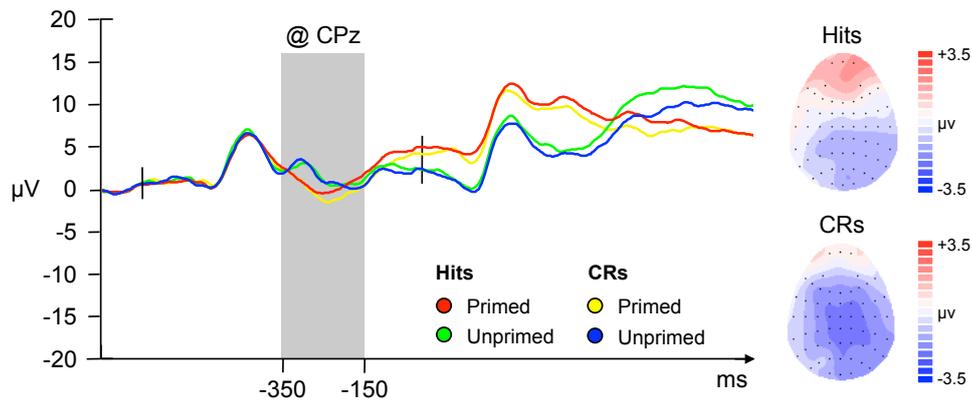


Figure 7.7: Priming @ CPz (-350 to -150ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode CPz. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Waveforms for primed hits and correct rejections were more negative going across central and posterior locations, with the largest difference between conditions for correct rejections.

tral to parieto-occipital locations. This pattern of results confirms the presence of a widespread negativity for primed correct rejections at superior electrode sites across locations, with a skew towards the right hemisphere over central and posterior locations. Follow up analysis on the data collapsed from frontal to parietal locations and across hemispheres confirmed that effects were larger over superior sites than at medial ($t(31)=2.84$, $p=0.008$), or inferior sites ($t(31)=2.92$, $p=0.006$). Collapsing the data over locations producing interactions including the factor of hemisphere and electrode sites confirmed the presence of stronger effects over the right hemisphere ($t(31)=2.87$, $p=0.007$) extending from central to parieto-occipital locations. Further examination of the data for correct rejections confirmed that the priming effect was maximal at electrode CPz ($t(31)=3.43$, $p=0.002$).

In summary, the data for hits did not produce significant priming effects despite evidence of a difference between conditions in the waveforms. Inspection of the data suggests that this lack of effect for hits may have been driven by the onset of an early old/new difference in the primed condition (see Section 7.4.6.1 for

Table 7.8: Priming for CRs by location (-350 to -150ms). Results of subsidiary analysis at separate locations for correct rejections.

CRs (500-1100ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=9.01, p=0.005$	$F(1,31)=11.04, p=0.002$	$F(1,31)=12.51, p=0.001$	$F(1,31)=12.36, p=0.001$	$F(1,31)=11.06, p=0.002$	$F(1,31)=10.86, p=0.002$
Cond*Hem				$F(1,31)=5.32, p=0.028$	$F(1,31)=9.67, p=0.004$	$F(1,31)=12.71, p=0.001$
Cond*Elec	$F(1.3,39.4)=8.68, p=0.003$	$F(1.1,34.6)=8.29, p=0.005$	$F(1.1,33.3)=7.69, p=0.008$	$F(1.1,34)=5.41, p=0.023$	$F(1,32.4)=4.14, p=0.049$	
Cond*Hem*Elec			$F(1.4,42.1)=3.74, p=0.048$	$F(1.3,40.2)=6.59, p=0.009$	$F(1.2,37.9)=6.95, p=0.008$	

data), increasing the level activity for primed hits and thus reducing the size of the difference between primed and unprimed hits. Data for correct rejections revealed a widespread negativity for primed words maximal at superior centroparietal sites, with a slight skew towards the right hemisphere over central and posterior locations.

7.4.2.2 Time window -100 to 500ms

From 100ms prior to target onset, waveforms for primed hits and correct rejections were more positive going than for unprimed hits and correct rejections across central and posterior locations (see Figure 7.8 for data from CPz). Initial analysis for hits revealed a significant main effect of condition [$F(1,31)=54.65$, $p<0.001$], along with significant interactions between condition and electrode [$F(1.1,34.5)=18.35$, $p<0.001$], and condition, location and hemisphere [$F(1.7,52)=6.62$, $p=0.004$]. Initial analysis for correct rejections also produced a significant main effect of condition [$F(1,31)=55.50$, $p<0.001$], along with significant interactions between condition and electrode [$F(1.1,33.6)=18.83$, $p<0.001$], and condition, location and hemisphere [$F(2.1,65.6)=4.66$, $p=0.011$]. As can be seen in Figure 7.8, these results reflect the presence of a positivity for primed hits and correct rejections towards superior electrode sites, with a focus over central and posterior locations, that appears slightly skewed over the right hemisphere towards frontal locations.

Table 7.9 shows the results of subsidiary analysis at separate locations for hits and correct rejections. Results for hits revealed main effects of condition and interactions between condition and electrode across locations, along with interactions between condition and hemisphere at frontal and fronto-central locations.

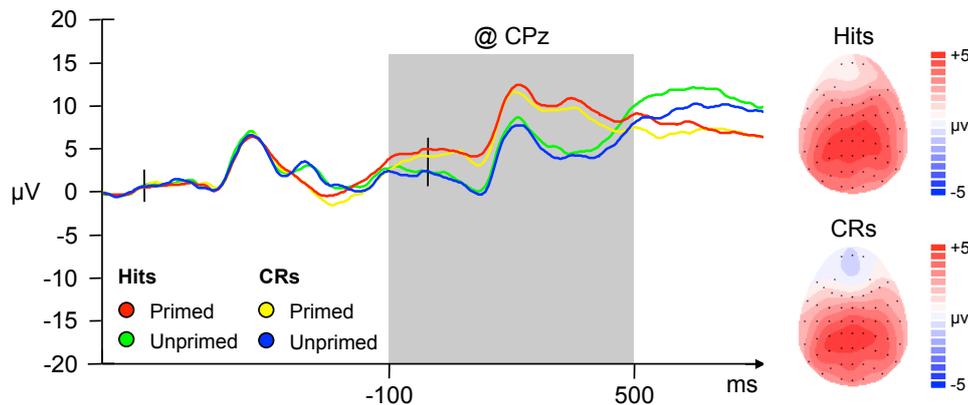


Figure 7.8: Priming @ CPz (-100 to 500ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode CPz. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Waveforms for primed hits and correct rejections were more positive going than for unprimed hits and correct rejections across central and posterior locations.

This pattern of results confirms the presence of a widespread positivity for primed hits at superior electrode sites over central and posterior locations, with a slight skew over the right hemisphere at frontal locations. Follow up analysis collapsed across locations and hemispheres confirmed the presence of larger effects over superior ($t(31)=4.29$, $p<0.001$), and medial sites ($t(31)=5.09$, $p<0.001$), than at inferior sites. Focused analysis on the data collapsed over frontal locations and electrodes confirmed the presence of larger effects over the right hemisphere ($t(31)=2.78$, $p=0.009$), on the outskirts of the priming effect for hits. Further examination of the data confirmed that effects for hits were maximal at electrode CPz ($t(31)=7.19$, $p<0.001$).

Analysis at separate locations for correct rejections revealed significant main effects and interactions between condition and electrode extending from fronto-central to parieto-occipital locations, along with a main effect and interaction between condition, hemisphere and electrode at frontal sites. The pattern of results is comparable to the outcome for hits demonstrating the presence of a widespread positivity for primed correct rejections at superior electrode sites over

Table 7.9: Priming by location (-100-500ms). Results of subsidiary analysis at separate locations for hits and correct rejections.

Hits (-100-500ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=25.41, p<0.001$	$F(1,31)=36.79, p<0.001$	$F(1,31)=47.92, p<0.001$	$F(1,31)=54.52, p<0.001$	$F(1,31)=51.52, p<0.001$	$F(1,31)=44.23, p<0.001$
Cond*Hem	$F(1,31)=9.31, p=0.005$	$F(1,31)=5.58, p=0.025$				
Cond*Elec	$F(1.2,36.2)=6.15, p=0.014$	$F(1.2,36.4)=16.88, p<0.001$	$F(1.1,35.1)=15.23, p<0.001$	$F(1.1,35.5)=13.74, p<0.001$	$F(1.1,34.8)=4.92, p=0.029$	$F(1.1,35.4)=15.01, p<0.001$
Cond*Hem*Elec						
CRs (-100-500ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=8.32, p=0.007$	$F(1,31)=24.15, p<0.001$	$F(1,31)=46.30, p<0.001$	$F(1,31)=72.88, p<0.001$	$F(1,31)=83.10, p<0.001$	$F(1,31)=72.78, p<0.001$
Cond*Hem						
Cond*Elec		$F(1.2,38.3)=9.48, p=0.002$	$F(1.1,34.1)=10.97, p=0.002$	$F(1.1,34.2)=14.35, p<0.001$	$F(1.1,33.9)=10.81, p=0.002$	$F(1.1,34.1)=27.20, p<0.001$
Cond*Hem*Elec	$F(1.6,50)=4.08, p=0.030$					

central and posterior locations, with a slight skew over the right hemisphere at frontal locations. Follow up analysis on the data collapsed from fronto-central to parieto-occipital locations again confirmed the presence of larger effects over superior ($t(31)=3.82$, $p=0.001$), and medial sites ($t(31)=4.27$, $p<0.001$), than at inferior sites. Further examination of the data confirmed that priming effects for correct rejections were also maximal at electrode CPz ($t(31)=7.62$, $p<0.001$). The results reported above for hits and correct rejections suggest no differences in the magnitude or distribution of priming effects. In support of this interpretation, magnitude analysis performed on the subtraction data revealed no main effect or interactions including the factor of condition, confirming that priming effects for hits and correct rejections were comparable.

In summary, during the -100 to 500ms time window the data for hits and correct rejections produced comparable effects, demonstrating the presence of a widespread positivity for primed words over superior sites extending from frontal to parieto-occipital locations, that was maximal for hits and correct rejections over centro-parietal locations.

7.4.2.3 Time window 500 to 1100ms

From 500ms after target onset, waveforms for primed hits and correct rejections were more negative going than for unprimed hits and correct rejections at posterior locations, with the largest difference between conditions for hits (see Figure 7.9 for the data from Pz). Initial analysis for hits revealed a significant main effect of condition [$F(1,31)=20.74$, $p<0.001$], and a significant interaction between condition, location and electrode [$F(3.1,95.6)=5.45$, $p=0.002$]. Analysis for correct rejections also produced a significant main effect of condition [$F(1,31)=22.09$,

$p < 0.001$], and a significant interaction between condition, location and electrode [$F(1.1,33.9)=8.05$, $p=0.006$]. As can be seen in Figure 7.9 these results reflect the presence of a negativity over superior electrode sites at posterior locations for hits and correct rejections.

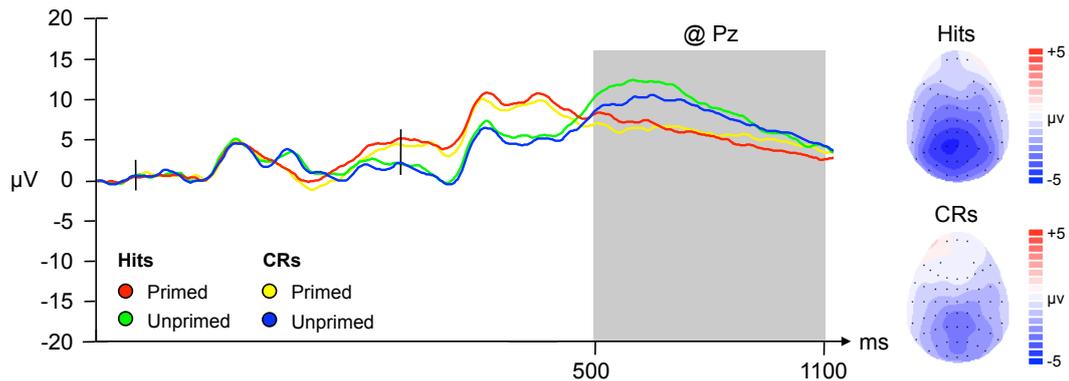


Figure 7.9: Priming @ Pz (500 to 1100ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode Pz. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections. Waveforms for primed hits and correct rejections were more negative going at posterior locations, with the largest difference between conditions for hits.

Table 7.10 shows the results of subsidiary analysis at separate locations for hits and correct rejections. Results for hits revealed significant main effects of condition across locations, and significant interactions between condition and electrode extending from fronto-central to parieto-occipital locations, indicating the presence of a negativity for primed hits at superior electrode sites. Follow up analysis on the data collapsed from fronto-central to parieto-occipital locations confirmed that effects were larger over superior sites than at medial ($t(31)=3.69$, $p=0.001$), or inferior sites ($t(31)=4.86$, $p < 0.001$). Further examination of the data confirmed that the priming effect for hits was maximal at electrode P1 ($t(31)=6.37$, $p < 0.001$). Results for correct rejections produced main effects of condition from fronto-central to parieto-occipital locations, and interactions between condition and electrode from central to parieto-occipital locations, reflecting the presence

Table 7.10: Priming by location (500-1100ms). Results of subsidiary analysis at separate locations for hits and correct rejections.

Hits (500-1100ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=5.46, p=0.026$	$F(1,31)=10.13, p=0.003$	$F(1,31)=18.54, p<0.001$	$F(1,31)=25.42, p<0.001$	$F(1,31)=31.46, p<0.001$	$F(1,31)=25.37, p<0.001$
Cond*Hem						
Cond*Elec		$F(1.2,38.5)=4.91, p=0.026$	$F(1.2,36.9)=11.71, p=0.001$	$F(1.1,37.1)=22.06, p<0.001$	$F(1.2,38.3)=28.49, p<0.001$	$F(1.2,36)=38.17, p<0.001$
Cond*Hem*Elec						
CRs (500-1100ms)	F	FC	C	CP	P	PO
Cond		$F(1,31)=7.82, p=0.009$	$F(1,31)=16.45, p<0.001$	$F(1,31)=24.18, p<0.001$	$F(1,31)=30.15, p<0.001$	$F(1,31)=33.91, p<0.001$
Cond*Hem						
Cond*Elec			$F(1.2,36.8)=4.12, p=0.043$	$F(1.2,35.6)=16.77, p<0.001$	$F(1.1,33.3)=19.16, p<0.001$	$F(1.1,34.4)=17.85, p<0.001$
Cond*Hem*Elec						

of a negativity for primed correct rejections with a similar distribution as was observed for hits, extending over central and posterior locations at superior electrode sites. Follow up analysis on the data collapsed from fronto-central to parieto-occipital locations confirmed that effects were larger over superior sites than at medial ($t(31)=4.54$, $p<0.001$) or inferior sites ($t(31)=4.10$, $p<0.001$). Further examination of the data confirmed that the priming effect for correct rejections was maximal at electrode Pz ($t(31)=5.65$, $p<0.001$).

The data suggest differences in the magnitude of effects for hits and correct rejections, with a stronger negativity evident for hits. Magnitude analysis performed on subtraction data revealed a marginally significant main effect of test status [$F(1,31)=4.14$, $p=0.051$], along with a significant interaction between test status and electrode [$F(1.3,38.8)=6.26$, $p=0.012$], reflecting a stronger effects over medial sites for hits. Topographic analysis performed on the rescaled data also revealed a significant interaction between test status and electrode [$F(1.3,38.8)=5.99$, $p=0.014$], indicating that effects for hits and correct rejections were driven by at least partially non overlapping sets of neural generators. In summary, during the 500-1100ms time window the data for hits and correct rejections demonstrated a priming related negativity maximal over parietal locations at superior electrode sites, that was larger in amplitude for hits than for correct rejections and also differed in distribution.

7.4.3 SOA comparisons

The next stage of analysis sought to compare the magnitude and distribution of priming effects reported in the previous sections across SOAs. Despite differences in the pre-target epoch timing across SOAs, the early negativity for both SOAs

occurs 350ms after prime onset facilitating comparison of this early effect. The late negativity reported for both SOAs occurs 500ms after target onset in both cases allowing direct comparison of this late priming effect. The widespread positivity present for hits and correct rejections at both SOAs differed in onset time and duration across SOAs. To facilitate comparison of the positive going priming effects across SOA, the much longer lasting effect for the 698ms SOA (-100-500ms) was split into two consecutive time windows (-100-250ms, 250ms-500ms) to allow direct comparison with the effect evident in the data for the 398ms SOA between 250-500ms. Results of magnitude and topographic comparison of the data for hits and correct rejections across SOAs for each time window are reported separately in the following sections.

7.4.3.1 Early negativity (350ms post-prime)

From 350ms after the onset of the prime words, waveforms for primed correct rejections were more negative going than for unprimed correct rejections for both SOAs, but as can be seen in Figure 7.10, the effects appeared to differ in size and distribution. Analysis contrasting the magnitude of effects for correct rejections across SOAs, using ANOVA with the factors of SOA (398ms, 698ms), Location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior), revealed significant interactions between SOA and electrode [$F(1,32.4)=5.02$, $p=0.031$], and SOA, location and hemisphere [$F(2.2,67.2)=7.03$, $p=0.001$]. Subsidiary analysis at separate locations identified significant interactions between SOA and electrode at frontal [$F(1.4,43.8)=4.00$, $p=0.038$], centroparietal [$F(1.1,33.2)=4.92$, $p=0.031$], and parietal locations [$F(1.1,33.8)=6.91$, $p=0.011$], along with significant interactions between SOA and hemisphere at

parietal [$F(1,31)=5.88$, $p=0.021$] and parieto-occipital locations [$F(1,31)=7.03$, $p=0.013$].

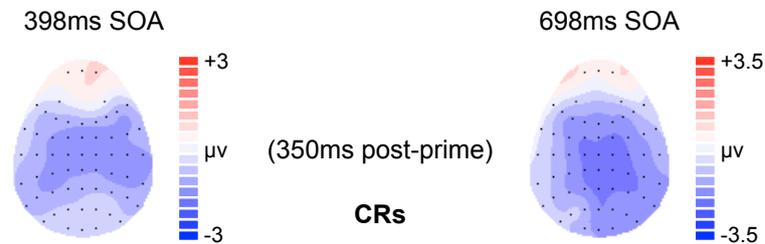


Figure 7.10: Early negativity (350ms post-prime). Topographic maps show the difference between the unprimed and primed correct rejections at each SOA. Primed correct rejections were more negative going than for unprimed correct rejections for both SOAs, but the effects appeared to differ in magnitude and distribution.

As can be seen in Figure 7.10, this pattern of interactions reflects greater negativity for the 698ms SOA over superior electrode sites at frontal, centro-parietal and parietal locations, and larger effects over the right hemisphere at parietal and parieto-occipital locations. Topographic analysis on the rescaled data revealed a significant interaction between SOA, location and hemisphere [$F(2,62.8)=6.08$, $p=0.004$], reflecting the recruitment of additional sets of neural generators in the right hemisphere at posterior locations for the 698ms SOA.

7.4.3.2 Post-target positivity (250-500ms)

To facilitate comparison of the positive going priming effects across SOA, the much longer lasting effect for the 698ms SOA (-100-500ms) was split into two consecutive time windows (-100-250ms, 250ms-500ms) to allow direct comparison with the effect evident in the data for the 398ms SOA between 250-500ms. Before investigating the size and distribution of effects for the 250-500ms time window across SOAs, the pattern of priming effects present in the new time windows for the 698ms SOA were analysed. Between -100-250ms waveforms for primed hits

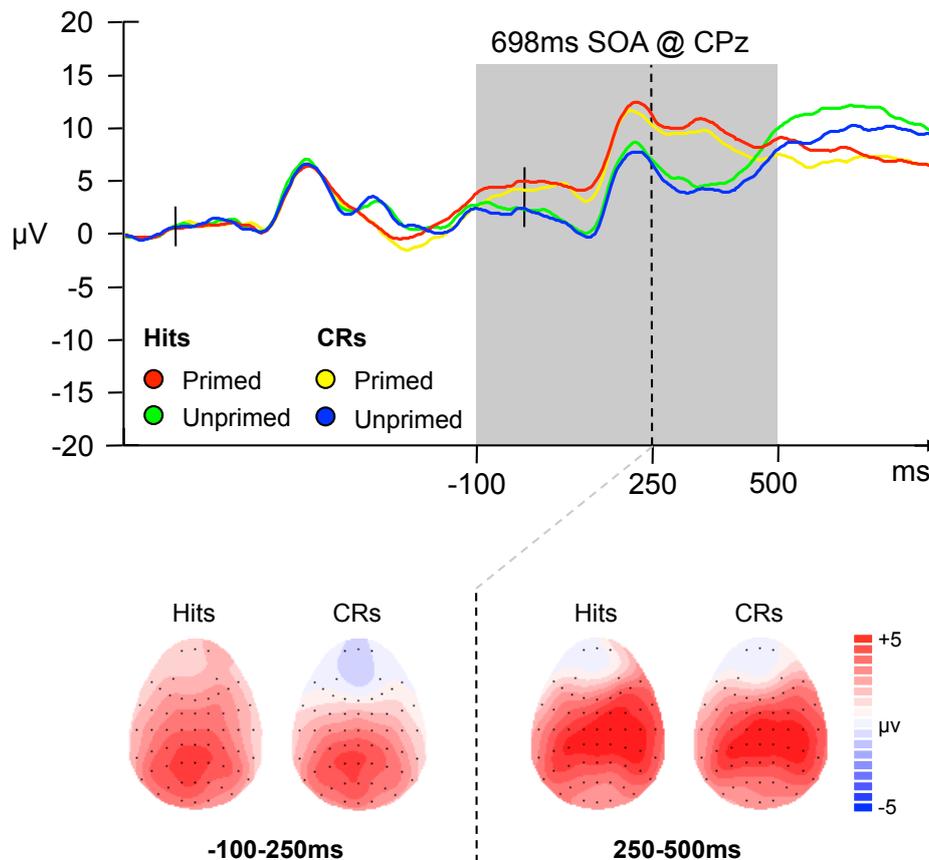


Figure 7.11: Priming @ CPz (-100-250ms & 250-500ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode CPz. Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections in each time window. Primed words were more positive going than unprimed words in both time windows, with the posterior distribution evident in the earlier window becoming more centrally focused over time.

and correct rejections were more positive going than for unprimed hits and correct rejections with a focus over posterior locations. Between 250-500ms waveforms for primed hits and correct rejections continued to be more positive for primed hits and correct rejections but appeared to become more centrally distributed, with stronger effects over the right hemisphere towards frontal locations (see Figure 7.11 for the data from CPz).

For the earlier window, initial analysis for hits revealed a significant main effect of condition [$F(1,31)=23.15$, $p<0.001$], along with significant interactions between condition and location [$F(1.2,37.4)=3.95$, $p=0.047$], and condition and electrode [$F(1.1,33.9)=18.97$, $p<0.001$]. Analysis for correct rejections produced a significant main effect of condition [$F(1,31)=24.24$, $p<0.001$], and a significant interaction between condition, location and electrode [$F(2.4,74.5)=4.24$, $p=0.013$]. As can be seen in Figure 7.11, these results reflect the presence of a positivity for primed words at posterior locations with a focus over superior electrode sites. For the later 250-500ms window, initial analysis for hits revealed a significant main effect of condition [$F(1,31)=72.95$, $p<0.001$], along with significant interactions between condition, location and hemisphere [$F(1.6,50.3)=7.16$, $p=0.003$], condition, location and electrode [$F(2.6,80.9)=5.58$, $p=0.003$], and condition, hemisphere and electrode [$F(1.2, 36.6)=4.86$, $p=0.028$]. Analysis for correct rejections produced a significant main effect of condition [$F(1,31)=85.10$, $p<0.001$], along with significant interactions between condition, location and hemisphere [$F(1.8,55.7)=4.30$, $p=0.022$], and condition, hemisphere and electrode [$F(1.1,34.7)=9.91$, $p=0.003$]. This pattern of results suggests the presence of a centrally distributed positivity for primed hits and correct rejections, with a skew over the right hemisphere towards anterior locations.

Table 7.11 displays the results of subsidiary analysis at separate locations for hits and correct rejections over the time windows of interest and demonstrates changes in the pattern of effects over time. For hits and correct rejections during the -100 to 250ms window the data evidenced the presence of a positivity for primed words at superior electrode sites with a focus over posterior locations. In the later window these positive priming effects for hits and correct rejections displayed a more central distribution, with a skew over the right hemisphere across

Table 7.11: Priming for 698ms SOA by location. Results of subsidiary analysis at separate locations for hits and correct rejections over the -100-250ms and 250-500ms time windows.

Hits (-100-250ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=13.41, p=0.001$	$F(1,31)=16.77, p<0.001$	$F(1,31)=19.98, p<0.001$	$F(1,31)=20.95, p<0.001$	$F(1,31)=21.51, p<0.001$	$F(1,31)=22.86, p<0.001$
Cond*Hem						
Cond*Elec	$F(1,2,36)=5.69, p=0.019$	$F(1,2,36.5)=13.32, p<0.001$	$F(1,2,35.9)=12.76, p=0.001$	$F(1,1,34.8)=14.55, p<0.001$	$F(1,1,33.7)=11.10, p=0.002$	$F(1,1,33.9)=17.50, p<0.001$
Cond*Hem*Elec						
CRs (-100-250ms)	F	FC	C	CP	P	PO
Cond		$F(1,31)=7.06, p=0.012$	$F(1,31)=19.46, p<0.001$	$F(1,31)=32.36, p<0.001$	$F(1,31)=39.36, p<0.001$	$F(1,31)=38.57, p<0.001$
Cond*Hem						
Cond*Elec		$F(1,2,36.8)=5.05, p=0.025$	$F(1,1,33.9)=8.19, p=0.006$	$F(1,1,33.6)=13.71, p=0.001$	$F(1,32.9)=16.20, p<0.001$	$F(1,1,33.1)=29.52, p<0.001$
Cond*Hem*Elec						
Hits (250-500ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=28.27, p<0.001$	$F(1,31)=56.45, p<0.001$	$F(1,31)=82.73, p<0.001$	$F(1,31)=86.85, p<0.001$	$F(1,31)=45.02, p<0.001$	$F(1,31)=18.79, p<0.001$
Cond*Hem	$F(1,31)=20.08, p<0.001$	$F(1,31)=18.85, p<0.001$	$F(1,31)=9.04, p=0.005$			
Cond*Elec		$F(1,1,35.5)=8.58, p=0.004$	$F(1,1,33.8)=6.66, p=0.012$			
Cond*Hem*Elec	$F(1,4,42.9)=4.71, p=0.025$	$F(1,5,47.6)=7.88, p=0.003$	$F(1,4,43.7)=5.09, p=0.019$			
CRs (250-500ms)	F	FC	C	CP	P	PO
Cond	$F(1,31)=27.09, p<0.001$	$F(1,31)=53.09, p<0.001$	$F(1,31)=78.53, p<0.001$	$F(1,31)=98.83, p<0.001$	$F(1,31)=66.57, p<0.001$	$F(1,31)=34.93, p<0.001$
Cond*Hem	$F(1,31)=10.19, p=0.003$	$F(1,31)=10.33, p=0.003$	$F(1,31)=9.72, p=0.004$			
Cond*Elec		$F(1,3,42.3)=14.38, p<0.001$	$F(1,2,35.9)=12.59, p=0.001$	$F(1,1,35.3)=8.72, p=0.004$		
Cond*Hem*Elec	$F(1,5,47.5)=7.06, p=0.004$	$F(1,4,43.2)=9.88, p=0.001$	$F(1,3,41.3)=11.63, p=0.001$	$F(1,1,35.6)=6.59, p=0.012$	$F(1,1,34.6)=4.07, p=0.047$	

frontal and central locations. The pattern of results reported above for hits and correct rejections during the 250 to 500ms time window for the 698ms SOA, appears similar to the pattern of effects identified for the 398ms SOA during the same time window (see Section 7.4.1.2 for data). The next level of analysis sought to contrast the magnitude and distribution of these effects across SOAs.

Figure 7.12 shows topographic maps of effects for hits and correct rejections at each SOA, and inspection of the data suggests that the effects differ in distribution across SOAs, with more anterior effects for the 698ms SOA. Magnitude analysis employing ANOVA with the factors of test status (old, new) SOA (398ms, 698ms), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior), revealed a significant interaction between SOA, location and hemisphere [$F(1.6,50)=4.17$, $p=0.029$], and SOA, location and electrode [$F(2.8,85.6)=4.65$, $p=0.006$]. Subsidiary analysis at separate locations revealed significant interactions between SOA and hemisphere at frontal [$F(1,31)=4.84$, $p=0.035$], fronto-central [$F(1,31)=5.53$, $p=0.025$], and central locations [$F(1,31)=4.61$, $p=0.040$], reflecting stronger effects over the right hemisphere at these locations for the 698ms SOA. Subsidiary analysis at posterior locations revealed significant interactions between SOA and electrode at centroparietal [$F(1.1,33.4)=6.60$, $p=0.013$], parietal [$F(1.1,32.9)=12.05$, $p=0.001$], and parieto-occipital locations [$F(1,32.5)=11.01$, $p=0.002$], reflecting stronger effects over medial and superior sites at these locations for the 398ms SOA.

The foregoing results suggest differences in the distribution of effects across SOAs. To investigate whether these differences reflect genuine changes in topography analysis was performed on difference waveforms for the 398ms and 698ms SOAs, using rescaled data. Results confirmed the presence of significant interactions between SOA, location and hemisphere [$F(1.6,49.4)=4.80$, $p=0.018$], and SOA,



Figure 7.12: Post-target positivity (250-500ms). Topographic maps show the difference between the unprimed and primed conditions for hits and correct rejections at each SOA. Primed hits and correct rejections were more positive going than unprimed correct rejections for both SOAs, but the effects appeared to differ slightly in distribution, with a slightly more anterior focus for hits and correct rejections at the 698ms SOA.

location and electrode [$F(2.8,86.9)=4.61, p=0.006$], indicating that effects for the 398ms and 698ms SOA were driven by partially non-overlapping sets of neural generators. As can be seen in figure 7.12, these findings confirm the presence of additional activation in the right hemisphere over anterior locations for the 698ms SOA, and additional posterior activation over medial and superior sites for the 398ms SOA.

7.4.3.3 Late negativity (500-1100ms)

From 500ms after the onset of the target words, waveforms for primed hits and correct rejections were more negative going than for unprimed hits and correct rejections at posterior locations for both SOAs. As can be seen in Figure 7.13, effects for hits were larger than effects for correct rejections at both SOAs, with no real differences in amplitude apparent across SOAs. Analysis contrasting the magnitude of effects for hits and correct rejections across SOAs, using ANOVA with the factors of test status (old, new), SOA (398ms, 698ms), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior), revealed a significant interaction between test status, SOA, location,

hemisphere and electrode [$F(4.1,129.4)=3.74$, $p=0.006$]. Subsidiary analysis contrasting effects for hits across SOAs revealed a significant main effect of SOA [$F(1,31)=10.68$, $p=0.003$], and an interaction between SOA, hemisphere and electrode [$F(1.2,35.9)=4.22$, $p=0.042$]. Analysis contrasting priming effects for correct rejections revealed a significant main effect of SOA [$F(1,31)=14.50$, $p=0.001$], and a significant interaction between SOA, location and electrode [$F(3,92.7)=4.27$, $p=0.007$].

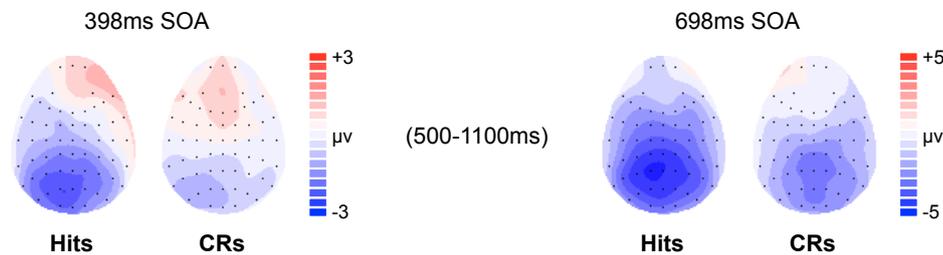


Figure 7.13: Late negativity (500-1100ms). Topographic maps show the difference between unprimed and primed conditions for hits and correct rejections at each SOA. Waveforms for primed hits and correct rejections were more negative going than for unprimed hits and correct at posterior locations for both SOAs, with larger effect for hits than for correct rejections.

As can be seen in Figure 7.13, these results reflect the presence of larger effects for hits at the 698ms SOA, with more widespread effects over the right hemisphere at medial sites across locations. Effects for correct rejections are also larger for the 698ms SOA, with the greatest difference over superior sites. The foregoing results suggest differences in the distribution of effects across SOAs. To investigate whether these differences reflect genuine changes in topography, analysis was performed on difference waveforms for the 398ms and 698ms SOAs, using rescaled data. Results revealed a significant 5-way interaction between SOA, test status, location, hemisphere and electrode [$F(4.5,139)=2.75$, $p=0.026$]. Subsidiary analysis contrasting priming effects for hits revealed a marginally significant interaction between SOA, hemisphere and electrode [$F(1.2,35.8)=3.94$,

$p=0.049$], reflecting the recruitment of additional generators for the 698ms SOA across locations in the right hemisphere. Analysis contrasting priming effects for correct rejections revealed significant interactions between SOA and electrode [$F(1.1,33.3)=6.45$, $p=0.014$], and SOA, location and hemisphere [$F(1.8,55)=4.22$, $p=0.024$], reflecting recruitment of additional sets of neural generators towards anterior locations in the right hemisphere for correct rejections.

7.4.4 Summary

For the 398ms SOA, the data demonstrated the presence of an early widespread negativity for correct rejections extending from frontal to parietal locations with a focus over the right hemisphere at central locations, but this early negativity was not apparent in the data for hits. Between 250-500ms primed hits and correct rejections were more positive going than unprimed hits and correct rejections at superior centro-parietal locations and did not differ substantially in magnitude or distribution. Between 500-1100ms primed hits and correct rejections were more negative going than unprimed hits and correct rejections at posterior locations. These late priming effects differed in magnitude but not in distribution, with larger effects over superior sites for hits, demonstrating that this late priming effect was modulated by exposure to words at study.

For the 698ms SOA, the data demonstrated the presence of an early widespread negativity for primed correct rejections maximal at superior centro-parietal sites, with a slight skew towards the right hemisphere over central and posterior locations, but data for hits again failed to produce significant priming effects. From 100ms prior to target onset primed hits and correct rejections produced comparable effects demonstrating a widespread positivity over superior sites extending

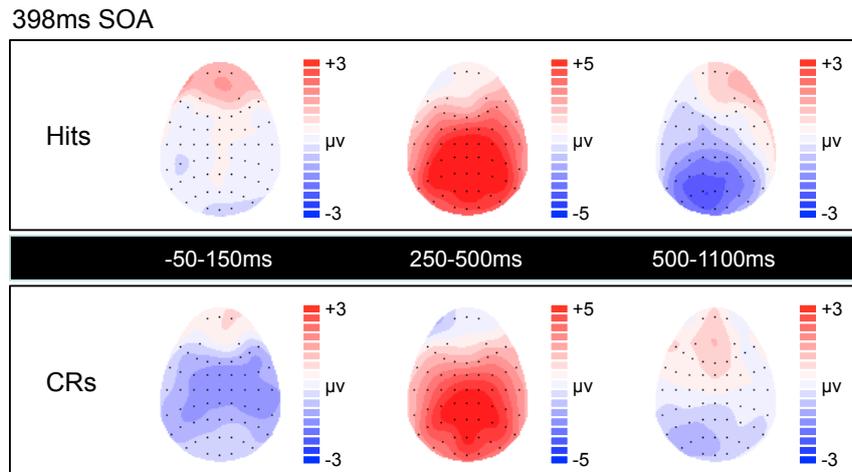


Figure 7.14: Priming topographic summary 398ms SOA. Topographic maps summarise differences between the unprimed and primed conditions for hits and correct rejections for the 398ms SOA.

from frontal to parieto-occipital locations, that were maximal for hits and correct rejections at centro-parietal locations. Between 500-1100ms, the data for hits and correct rejections demonstrated a priming related negativity maximal over parietal locations at superior electrode sites, that was larger in amplitude for hits than for correct rejections. Effects for hits and correct rejections and also differed in topography, confirming that effects were driven by partially non-overlapping sets of neural generators.

Comparison across SOAs of the early negativity for correct rejections onsetting 350ms after prime onset, confirmed the presence of greater negativity for the 698ms SOA over superior electrode sites at frontal, centro-parietal and parietal locations, and larger effects over the right hemisphere at parietal and parieto-occipital locations. Topographic analysis confirmed that effects for the 398ms and 698ms SOAs were driven by partially non-overlapping sets of neural generators, with additional activation at posterior locations in the right hemisphere for the 698ms SOA. To facilitate comparison of the positive going priming effects across SOA, the much longer lasting effect for the 698ms SOA (-100-500ms) was

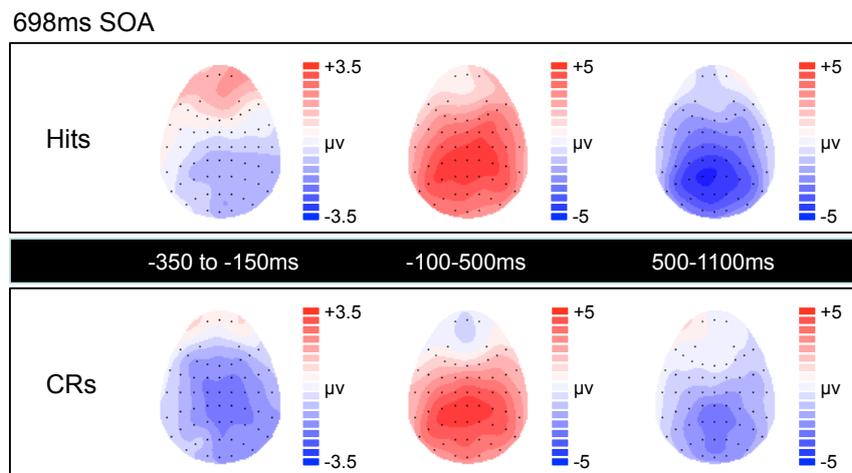


Figure 7.15: Priming topographic summary 698ms SOA. Topographic maps summarise differences between the unprimed and primed conditions for hits and correct rejections for the 698ms SOA.

split into two consecutive time windows (-100-250ms, 250ms-500ms) to allow direct comparison of this effect across SOAs. Comparison of these effects revealed the presence of larger effects over right-frontal locations for the 698ms SOA and larger effects over medial and superior sites at parietal and parieto-occipital locations for the 398ms SOA. Topographic analysis confirmed that these differences reflected a genuine change in distribution, with a more anterior right-sided focus for the 698ms SOA. For the late negativity, comparison across SOAs demonstrated the presence of larger effects for hits at the 698ms SOA, with more widespread effects over the right hemisphere at medial sites across locations. Priming effects for correct rejections are also larger for the 698ms SOA, with the greatest differences between SOAs over superior sites at posterior locations. Topographic analysis confirmed that priming effects for hits and correct rejections were driven by partially non-overlapping neural generators.

7.4.5 Memory 398ms SOA

Figures 7.16 and 7.17 show grand average ERPs time locked to the onset of the prime for hits and correct rejections, displayed separately for the unprimed and primed conditions. Visual inspection of the grand average waveforms shows that ERPs elicited in the unprimed condition were more positive going for hits than for correct rejections between 300-500ms and 500-800ms, with the greatest differences at anterior locations, and additional activity over left-parietal locations between 500-800ms. By contrast, waveforms in the primed condition were more positive going for hits than for correct rejections, but old/new effects exhibited a left-parietal focus between 300-500ms and a right-frontal focus between 500-800ms. For memory contrasts the data were analysed over -250-150ms, 300-500ms and 500-800ms time windows. While early old/new differences were not evident in the data for the 398ms SOA, this time window was included in the first stage of analysis for consistency.

The first level of analysis was designed to identify variations in old/new effects across conditions and time windows. Due to the presence of old/new effects with mid-frontal, left parietal and right frontal distributions, the data were submitted to ANOVA with the factors of test status (old, new), condition (unprimed, primed), location (F, FC, C, CP, P, PO), laterality (left: medial, midline, right: medial) and time window (-250-150ms, 300-500ms, 500-800ms), to capture all memory effects. Results revealed a significant main effect of test status [$F(1,31)=11.25$, $p=0.002$], and a significant five-way interaction between test status, condition, location, laterality and time window [$F(4.9,151.5)=5.16$, $p<0.001$]. The presence of this significant interaction provides strong evidence of

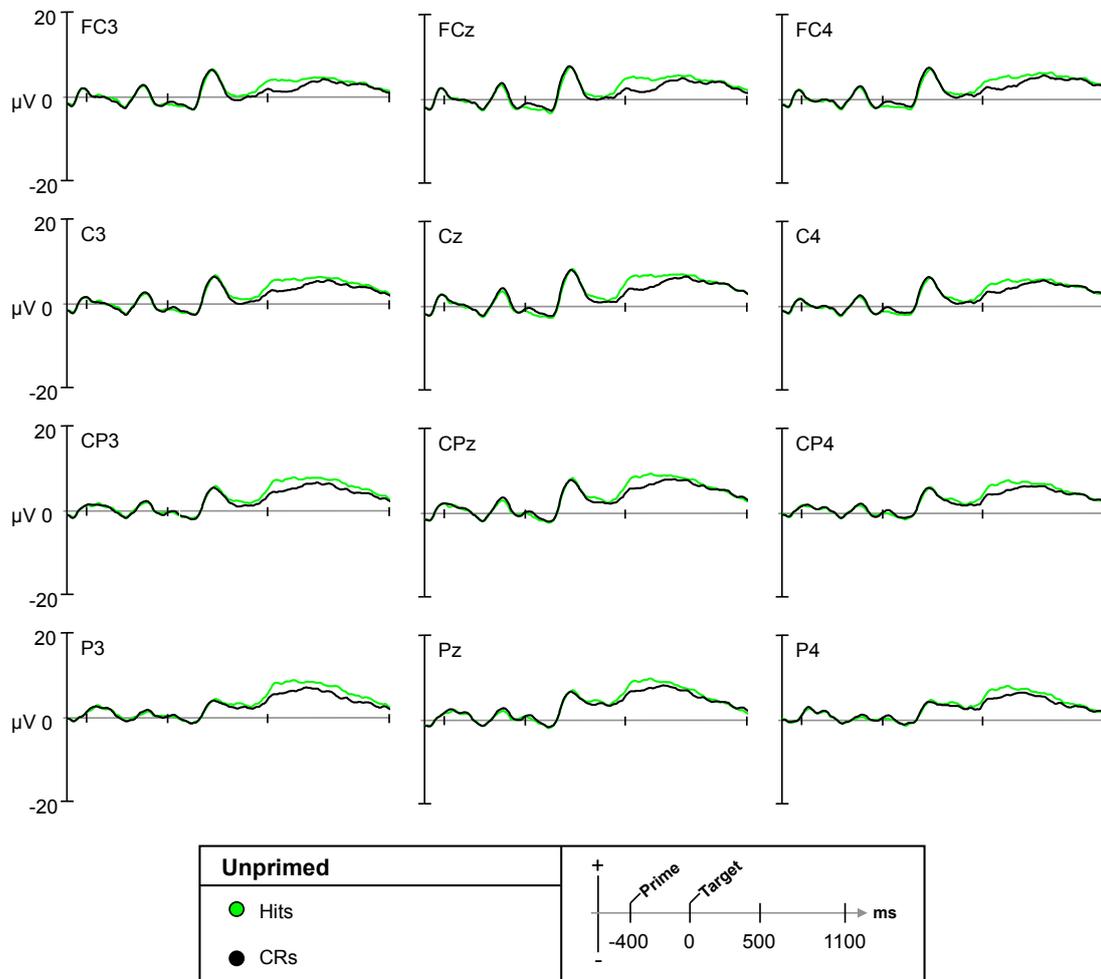


Figure 7.16: Memory effects for unprimed words 398ms SOA. Grand average ERPs for hits and correct rejections in the unprimed condition. Waveforms were more positive going for hits than for correct rejections between 300-500 and 500-800ms, with the greatest differences over anterior locations, and additional activity over left-parietal locations evident between 500-800ms.

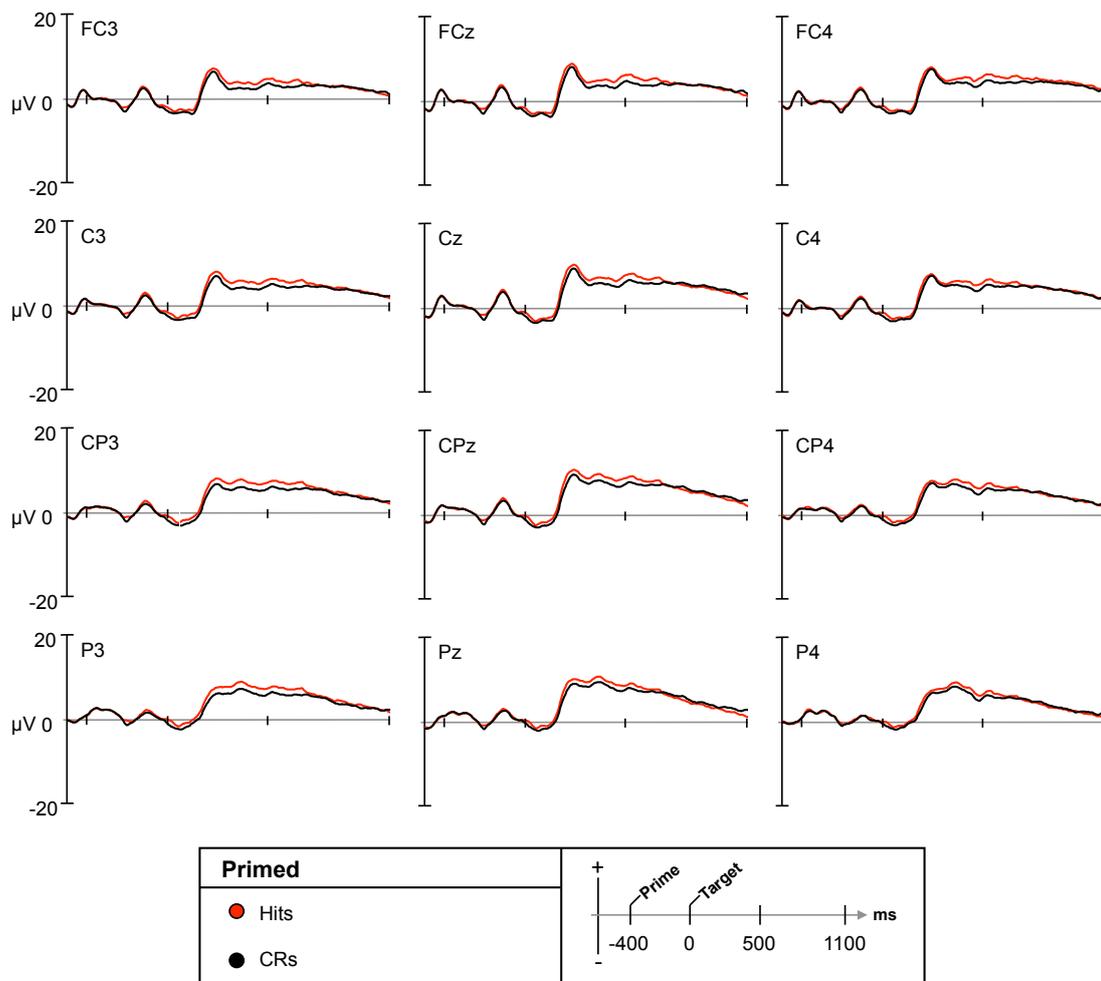


Figure 7.17: Memory effects for primed words 398ms SOA. Grand average ERPs for hits and correct rejections in the primed condition. Waveforms were slightly more positive going for hits than for correct rejections at left-parietal locations between 300-500ms and right-frontal locations between 500-800ms.

variation in the pattern of old/new effects across conditions, locations and time windows.

Table 7.12: Memory ANOVAs by time window. Results of ANOVAs with the factors of condition, test status, location and laterality for the three time windows chosen for analysis of old/new effects.

	-250-150ms	300-500ms	500-800ms
Test status	-	$F(1,31)=23.12, p<0.001$	$F(1,31)=16.84, p<0.001$
Test status*Cond*Loc*Lat	-	$F(3.4,106.2)=12.14, p<0.001$	$F(3.8,118.1)=9.60, p<0.001$

To further elucidate the pattern of memory related activity, a second level of analysis was performed separately on the data from each time window, using ANOVA with the factors test status (old, new), condition (unprimed, primed), location (F, FC, C, CP, P, PO) and laterality (left, midline, right). The results of this analysis are summarised in Table 7.12, and demonstrate that old/new effects were not present in the first time window, but were present in the later two windows and interacted with the factors of condition, location and laterality, suggesting variation in the pattern of old/new effects across conditions for each time window. Subsidiary analyses were performed on the average activity over three electrodes sites for four regions of interest: left-frontal (LF: F1, F3, F5), right-frontal (RF: F2, F4, F6), left-parietal (LP: P1, P3, P5) and right-parietal (RP: P2, P4, P6). The analysis took the form of contrasts between hits and correct rejections performed separately for each condition, using ANOVA with the factors of test status (old, new), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior); the results for each time window are reported separately in the following sections.

7.4.5.1 Time window 300 to 500ms

Between 300-500ms, waveforms for unprimed hits were more positive going than for unprimed correct rejections at frontal and central locations, with a slight skew over the left hemisphere. By contrast, waveforms for primed hits were more positive going than for primed correct rejections at left-parietal locations (see Figure 7.18 for data). Inspection of the data suggests that old/new differences onset earlier than 300ms for the primed condition, but to maintain consistency across experiments initial analysis will focus on the 300-500ms time window, before going on to identify the exact onset time of left-parietal effects for the primed condition. Initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,31)=5.28$, $p=0.029$], but no significant interactions including the factor of test status, reflecting the presence of a slight but widespread positivity for hits across locations. Further examination of the data confirmed that old/new effects for the unprimed condition were maximal at electrode C3 ($t(31)=2.44$, $p=0.020$).

Initial analysis for the primed condition revealed a significant main effect of test status [$F(1,31)=14.99$, $p=0.001$], and a significant interaction between test status, location and hemisphere [$F(1,31)=5.38$, $p=0.027$], reflecting the presence of an old/new difference at posterior locations in the left hemisphere. Subsidiary analysis at frontal locations revealed a significant main effect of test status [$F(1,31)=9.16$, $p=0.005$], but no interactions including the factor of test status, indicating a slight positivity for hits over frontal sites. Analysis at parietal locations revealed a significant main effect of test status [$F(1,31)=14.68$, $p=0.001$], and a significant interaction between test status and hemisphere [$F(1,31)=6.13$, $p=0.019$], confirming the presence of old/new effects for the primed condition

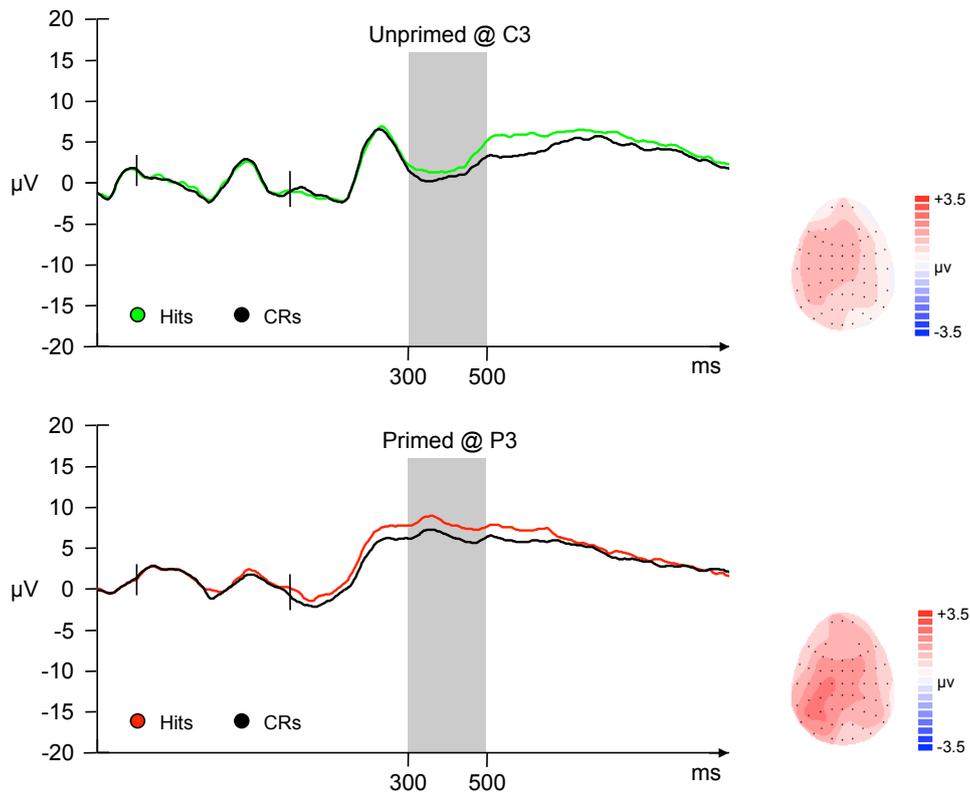


Figure 7.18: Memory (300-500ms). Grand average ERPs for hits and correct rejections in the unprimed condition at electrode C3 and primed condition at electrode P3. Topographic maps show the difference between the hits and correct rejections for both conditions. Waveforms for the unprimed condition displayed a slight positivity for hits over frontal and central locations, with a slight skew over the left hemisphere. Waveforms for the primed condition displayed the presence of an old/new difference at left-parietal locations.

with a left-parietal distribution. Follow up analysis on the data from parietal sites collapsed across electrodes supported this pattern of results, demonstrating the presence of larger effects over the left hemisphere ($t(31)=2.48$, $p=0.019$). Consistent with this pattern of results, further examination of the data confirmed that old/new effects for the primed condition were maximal at electrode CP3 ($t(31)=4.29$, $p<0.001$). While analysis so far has employed standard windows for identification of familiarity and recollection; inspection of the waveforms for the primed condition suggests that old/new differences are present at left-parietal locations earlier than 300ms after target onset.

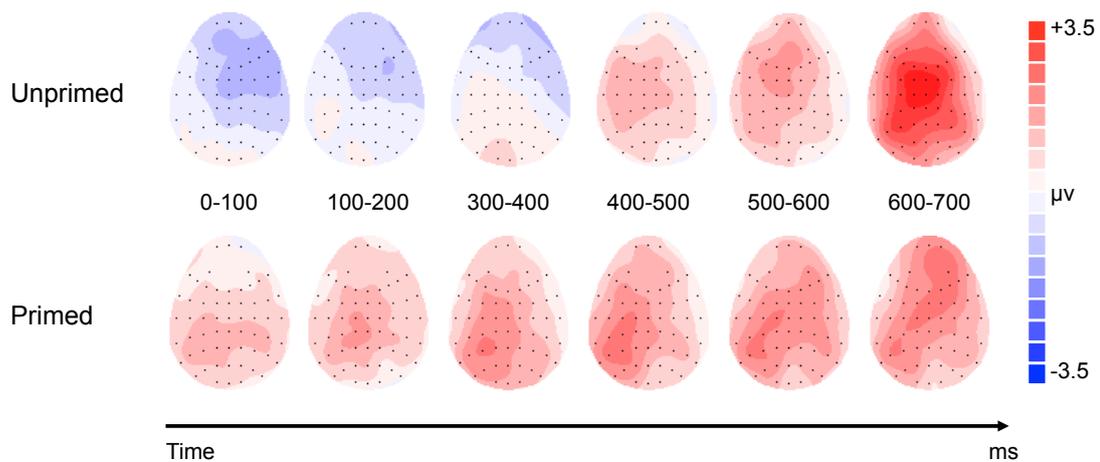


Figure 7.19: Topographic maps 0-700ms. Topographic maps showing the difference between the hits and correct rejections for both conditions between 0-700ms after target onset, split into the 100ms time bins that were used to establish the onset time of left-parietal old/new effects in the primed condition.

To establish a more precise onset time for the left-parietal old/new effect in the primed condition; the data were first split into six consecutive 100ms time bins starting from target onset. As can be seen in the topographic maps in Figure 7.19, data for the primed condition appears to exhibit a positivity for hits over left-parietal sites from as early as target onset. To demonstrate the presence of early onsetting LP effects, t-tests were performed contrasting activity for hits and correct rejections at electrode P3, for each time bin from 0-700ms. Onset time in this case was defined as the first window of three consecutive windows demonstrating the presence of significant differences between hits and correct rejections. Results confirmed a difference between hits and correct rejections for the primed condition emerging between 0-100ms after target onset ($t(31)=2.98$, $p=0.006$). Old/new effects for the unprimed did not exhibit a strong left-parietal distribution, appearing more centrally distributed. Analysis contrasting hits and correct rejections for the unprimed condition at electrode P3 confirmed that old/new differences for the unprimed condition did not emerge until between 500-600ms

after target onset ($t(31)=4.78$, $p<0.001$) on the outer edges of old/new effects present during this time window for the unprimed condition.

In summary, analysis for the unprimed condition demonstrated the presence of a slight positivity for hits across locations, that was maximal over medial central sites. Initial analysis for the primed condition confirmed the presence of old/new differences with a left-parietal distribution between 300-500ms. Further examination of the data demonstrated that significant old/new differences were present at left-parietal sites from target onset, evidencing the presence of very early on-setting left-parietal old/new effects for the primed condition that continued into the 300-500ms time window.

7.4.5.2 Time window 500 to 800ms

Between 500-800ms, waveforms for unprimed hits were more positive going than waveforms for unprimed correct rejections at mid-frontal locations, with additional activity apparent over left-parietal locations. Primed waveforms were more positive going for hits than for correct rejections over right-frontal and left-parietal locations (see Figure 7.20). Initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,31)=15.87$, $p<0.001$], and a significant interaction between test status and electrode [$F(1.2,35.7)=5.12$, $p=0.026$]. Despite failure to identify interactions including the factor of location, inspection of the data suggests the presence of mid-frontal activity combined with a spread over left-parietal locations. Subsidiary analysis at frontal locations revealed a main effect of test status [$F(1,31)=11.98$, $p=0.02$], and a significant interaction between test status and electrode [$F(1.1,34.1)=4.22$, $p=0.044$], indicating larger effects over superior sites at frontal locations. Analysis at parietal locations re-

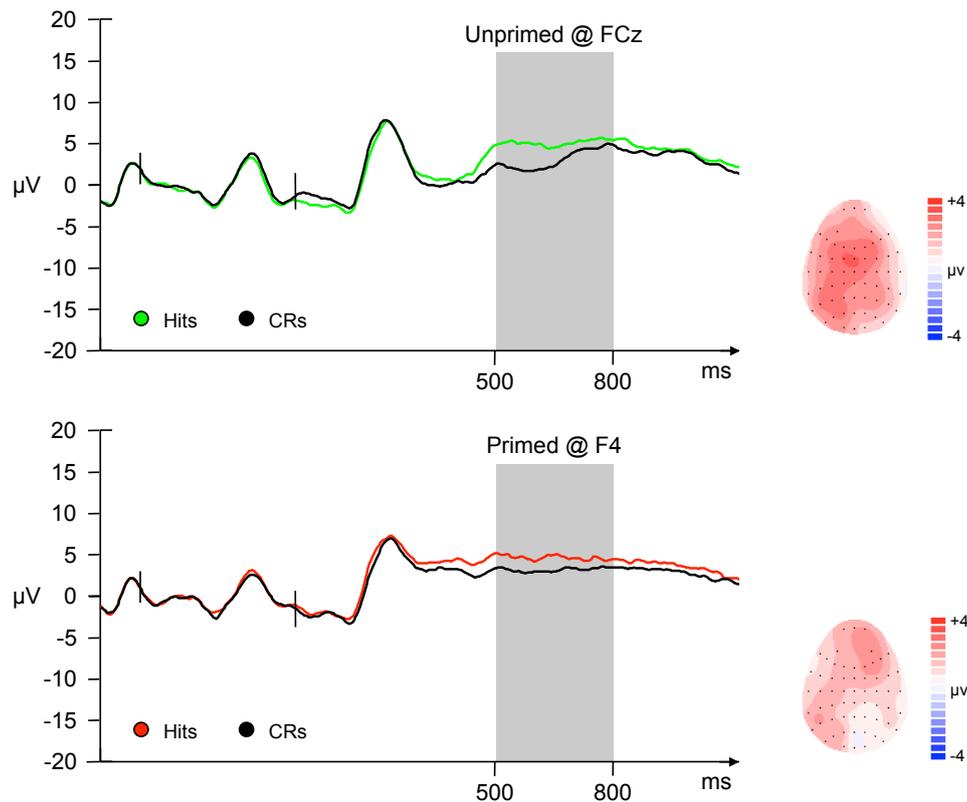


Figure 7.20: Memory (500-800ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at representative electrodes. Topographic maps show the difference between the hits and correct rejections for both conditions. Waveforms for unprimed hits were more positive going than for unprimed correct rejections at mid-frontal locations, with additional activity apparent over left-parietal locations. Primed waveforms were more positive going for hits than for correct rejections over right-frontal and left-parietal locations.

vealed a main effect of test status [$F(1,31)=14.13$, $p=0.001$], but no interactions including the factor of test status, indicating the presence of a slight positivity for hits across parietal locations. Consistent with the apparent frontal distribution of this effect, further examination of the data confirmed that old/new effects for the unprimed condition were maximal at electrode FCz ($t(31)=3.48$, $p=0.002$).

Initial analysis for the primed condition produced a significant main effect of test status [$F(1,31)=6.18$, $p=0.019$], and a significant interaction between test status, location, hemisphere and electrode [$F(1.6,50.8)=7.18$, $p=0.003$], reflecting the

continuation of left-parietal old/new effects for the 300-500ms time window, accompanied by additional activation at right-frontal locations. Subsidiary analysis at frontal locations revealed a significant main effect of test status [$F(1,31)=9.02$, $p=0.005$], and an interaction between test status and hemisphere [$F(1,31)=11.88$, $p=0.002$], indicating larger effects over the right hemisphere at frontal sites. Analysis at parietal locations revealed interactions between test status and hemisphere [$F(1,31)=8.48$, $p=0.07$], and test status and electrode [$F(1.1,34.4)=5.83$, $p=0.019$], indicating the presence of a slight positivity over medial sites at parietal locations in both hemispheres, but that is greater in magnitude over the left hemisphere. Consistent with the apparent right-frontal distribution, further examination of the data confirmed that old/new effects for the primed condition were maximal at electrode F4 ($t(31)=3.74$, $p=0.001$).

Magnitude analysis was performed on subtraction data to compare old/new effects for the primed and unprimed conditions, using ANOVA with the factors of condition (unprimed, primed), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed significant interactions between condition and electrode [$F(1.2,37.6)=9.25$, $p=0.003$], and condition, location and hemisphere [$F(1,31)=9.53$, $p=0.004$]. Subsidiary analysis at frontal locations revealed an interaction between condition and hemisphere [$F(1,31)=6.86$, $p=0.014$], and analysis at parietal locations produced a significant interaction between condition and electrode [$F(1.1,35.5)=7.95$, $p=0.006$]. As can be seen in Figure 7.20, these results suggest a difference in distribution at frontal sites, with old/new effects exhibiting a more right-sided focus in the primed condition. Topographic analysis contrasting the distribution of old/new effects revealed significant interactions between condition and electrode [$F(1.2,37.6)=9.52$, $p=0.002$], and condition, location and hemisphere [$F(1,31)=6.43$, $p=0.016$], confirmed that

memory effects evident between 500-800ms were supported by non-overlapping sets of neural generators. In summary, waveforms for hits were more positive going than waveforms for correct rejections in both conditions, but differed in distribution, with a focus over mid-frontal locations for the unprimed condition and over right-frontal locations for the primed condition.

7.4.5.3 Topographic analysis

The foregoing results suggest changes in the pattern of activity over time for the primed condition, with old/new effects exhibiting a left-parietal distribution between 300-500ms and a right-frontal distribution between 500-800ms. The next level of analysis was designed to contrast the distribution of old/new effects for the unprimed and primed conditions across time windows. Analysis was performed separately for each condition on rescaled data, using ANOVA with the factors of time window (300-500ms, 500-800ms), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). Analysis contrasting the distribution of effects for the unprimed condition revealed no main effect or interactions including the factor of time window, indicating that old/new differences present between 300-500ms reflect the onset of mid-frontal differences that

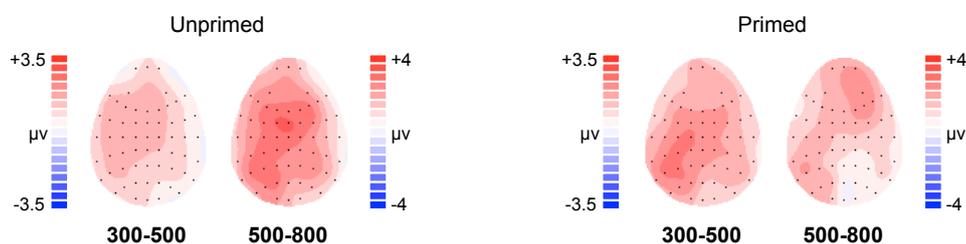


Figure 7.21: Memory over time 398ms SOA. Topographic maps show the difference between hits and correct rejections in the unprimed and primed conditions for the 398ms SOA. Old/new differences for the primed condition exhibited a shift over time from a left-parietal to a right-frontal distribution, but no substantial changes in the distribution were apparent for the unprimed condition.

become more evident during the 500-800ms time window and are driven by the same underlying neural generators. Analysis contrasting the distribution of effects over time for the primed condition revealed a significant interaction between time window and electrode [$F(1.2,36.5)=5.82$, $p=0.017$], confirming that effects for the primed condition were driven by partially non-overlapping sets of neural generators.

7.4.6 Memory 698ms SOA

Figures 7.22 and 7.23 show grand average ERPs time locked to the onset of the prime for hits and correct rejections, displayed separately for the unprimed and primed conditions. Visual inspection of the grand average waveforms shows that ERPs elicited in the unprimed condition were only more positive going for hits than for correct rejections between 300-500ms and 500-800ms, with the greatest differences at mid-frontal locations. Waveforms for the primed condition were more positive going for hits than for correct rejections from 250ms prior to target onset and between 300-500ms and 500-800ms. Effects were focused over fronto-polar and frontal locations from 250ms prior to target onset, over mid-frontal locations between 300-500ms, and over right-frontal locations between 500-800ms.

The first level of analysis on the data was designed to identify variations in old/new effects across conditions and time windows, employing ANOVA with the factors of test status (old, new), condition (unprimed, primed), location (F, FC, C, CP, P, PO), laterality (left: medial, midline, right: medial) and time window (-250-150ms, 300-500ms, 500-800ms). Results revealed a significant main effect of test status [$F(1,31)=13.31$, $p=0.001$], and a significant five-way

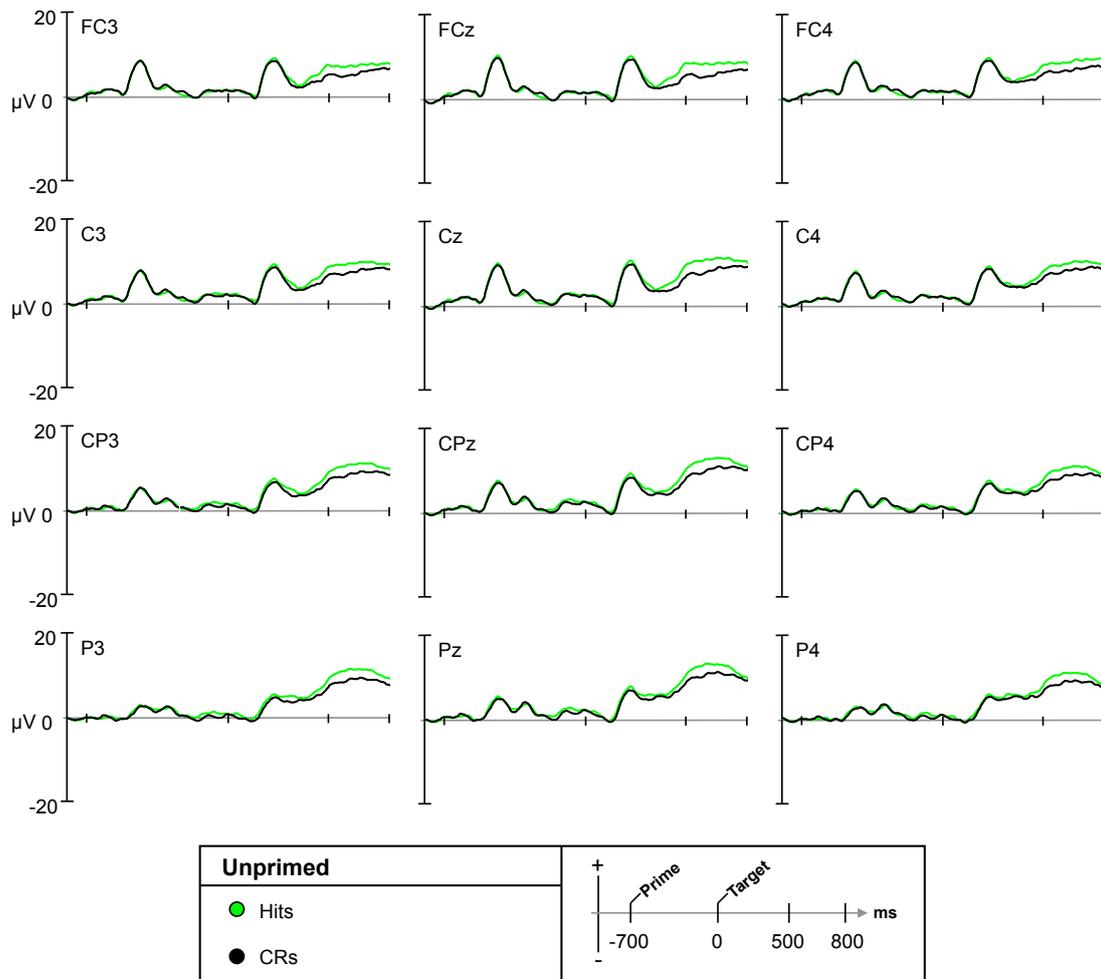


Figure 7.22: Memory effects for unprimed words 698ms SOA. Grand average ERPs for hits and correct rejections in the unprimed condition. Waveforms were more positive going for hits than for correct rejections between 300-500ms and 500-800ms, with the greatest differences at mid-frontal locations in both time windows.

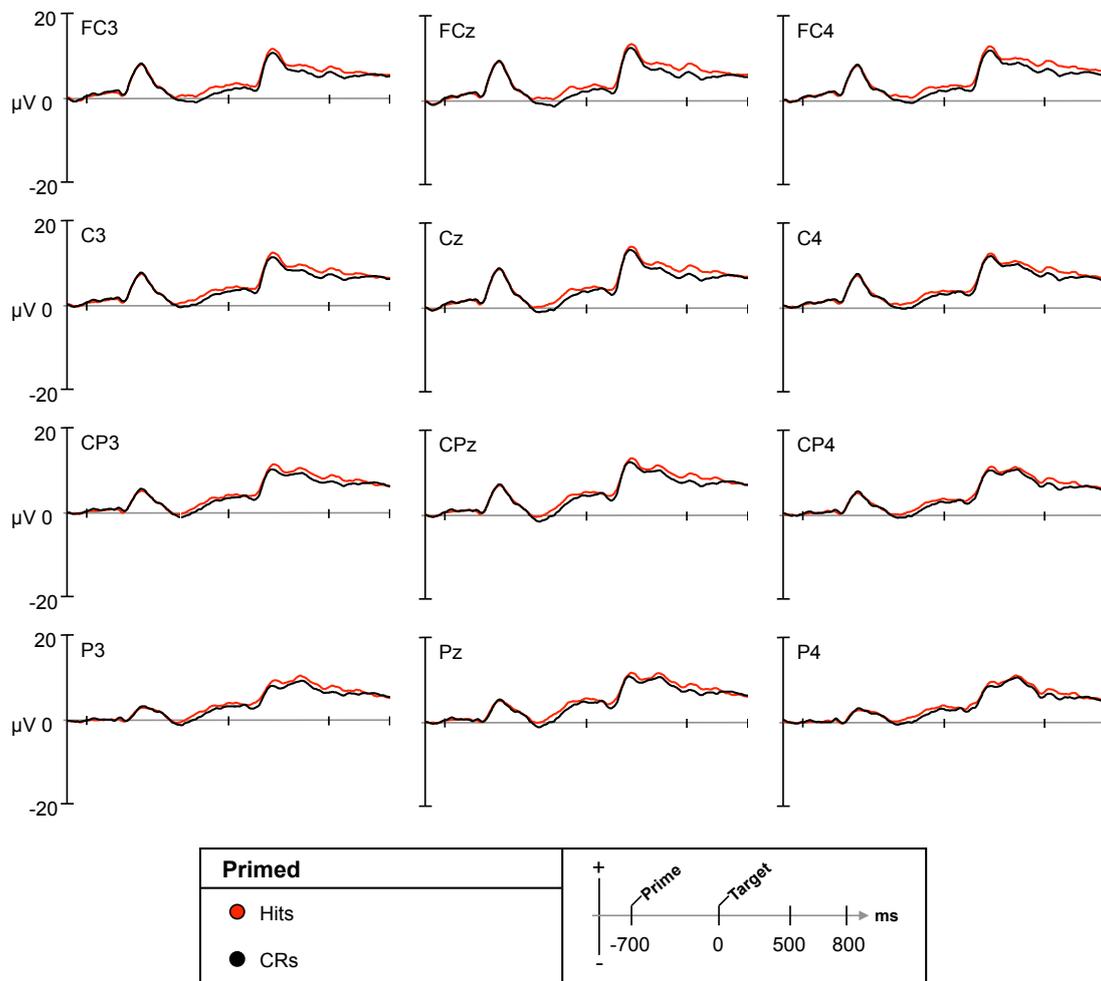


Figure 7.23: Memory effects for Primed words 698ms SOA. Grand average ERPs for hits and correct rejections in the primed condition. Waveforms for the primed condition were more positive going for hits than for correct rejections between -250-150ms, 300-500ms and 500-800ms. Old/new effects were focused over fronto-polar and frontal locations between -250-150ms, over mid-frontal locations between 300-500ms, and over right-frontal locations between 500-800ms

interaction between test status, condition, location, laterality and time window [$F(4.4,135.1)=3.33$, $p=0.010$]. The presence of this significant interaction provides strong evidence of variation in the pattern of old/new effects between conditions and across time windows. To elucidate the pattern of memory effects, a second level of analysis was performed separately on the data from each time window, using ANOVA with the factors of test status (old, new), condition (unprimed, primed), Location (F, FC, C, CP, P, PO) and laterality (left, midline, right). The results of this analysis are summarised in table 7.13, and demonstrate that old/new effects were present in all three time windows and suggest variation in the pattern of memory effects across conditions for each time window.

Table 7.13: Memory ANOVAs by time window. Results of ANOVAs with the factors of condition, test status and location and laterality for the three time windows chosen for analysis of old/new effects.

	-250-150ms	300-500ms	500-800ms
Test status	$F(1,31)=8.18$, $p=0.008$	$F(1,31)=13.18$, $p=0.001$	$F(1,31)=14.70$, $p=0.001$
Test*Cond*Loc*Lat	$F(2.7,83.6)=2.90$, $p=0.045$	$F(3.8,118.1)=4.06$, $p=0.005$	$F(4.5,138.5)=5.38$, $p<0.001$

Subsidiary analyses were performed on the average activity over three electrodes sites for four regions of interest: left-frontal (LF: F1, F3, F5), right-frontal (RF: F2, F4, F6), left-parietal (LP: P1, P3, P5) and right-parietal (RP: P2, P4, P6). The analysis took the form of contrasts between hits and correct rejections performed separately for each condition, using ANOVA with the factors of test status (old, new), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior); the results for each time window are reported separately in the following sections.

7.4.6.1 Time window -250 to 150ms

From 250ms prior to target onset, waveforms in the primed condition were more positive going for hits than for correct rejections over fronto-polar and frontal locations, but there was no evidence of old/new differences during the pre-target period for the unprimed condition (see Figure 7.24 for data from Fz). Importantly, initial analysis for the unprimed condition revealed a significant interaction between test status and location [$F(1,31)=6.51$, $p=0.016$], but subsidiary analysis at frontal and parietal locations failed to reveal main effects or interactions including the factor of test status, confirming the absence of substantial old/new differences for the unprimed condition during this time window. Initial analysis for the primed condition revealed a significant main effect of test status [$F(1,31)=19.04$, $p<0.001$], along with a significant interaction between test status and electrode [$F(1.1,32.8)=6.43$, $p=0.015$], and a marginally significant interaction between test status, location and electrode [$F(1.2,36.6)=3.70$, $p=0.056$], reflecting the presence of a positivity for hits that is maximal over superior sites at frontal locations.

For the primed condition, subsidiary analysis at frontal locations revealed a significant main effect of test status [$F(1,31)=18.04$, $p<0.001$], and a significant interaction between test status and electrode [$F(1.1,33.9)=8.80$, $p=0.005$], confirming the presence of a positivity for hits over superior sites at frontal locations. Analysis at parietal locations revealed a significant main effect of test status [$F(1,31)=7.54$, $p=0.010$], but no interactions including the factor of test status, indicating a slight positivity for hits across parietal sites. Further examination of the data confirmed that old/new effects for the primed condition were maximal at electrode F1 ($t(31)=3.95$, $p<0.001$). Due to absence of old/new effects for the

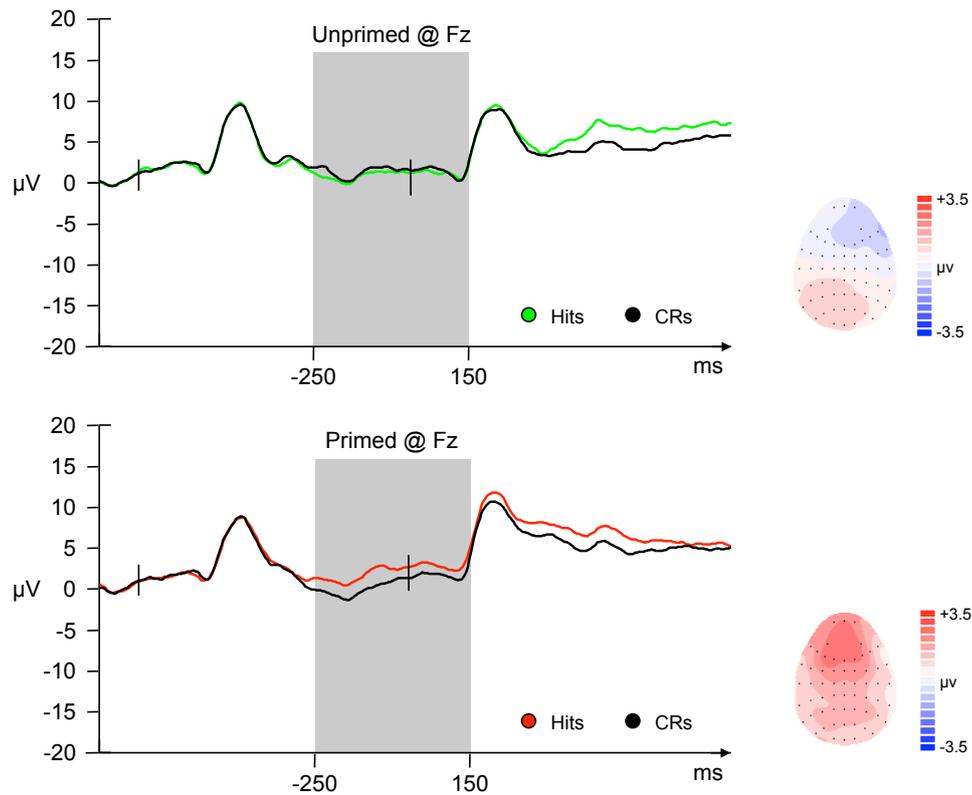


Figure 7.24: Memory @ Fz (-250-150ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at representative electrodes. Topographic maps show the difference between the hits and correct rejections for both conditions. Waveforms for primed hits were more positive going than waveforms for primed correct rejections over frontal sites, but there was no evidence of substantial old/new differences in the unprimed condition between -250-150ms.

unprimed condition it was not necessary to perform comparisons of magnitude across conditions. In summary, analysis for the unprimed condition confirmed the absence of early onsetting pre-target old/new differences. By contrast, analysis for the primed condition clearly demonstrated the presence old/new effect at frontal locations, onsetting 250ms prior to target onset (450ms post-prime) and continuing into the post-target period.

7.4.6.2 Time window 300 to 500ms

Between 300-500ms, waveforms for primed and unprimed hits were more positive going than for correct rejections at mid frontal locations (see Figure 7.25 for the data from FCz). Initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,31)=11.28$, $p=0.002$], and a significant interaction between test status, location and electrode [$F(1.3,38.8)=4.86$, $p=0.026$], reflecting the presence of a positivity for hits that is maximal towards superior sites at frontal locations. Subsidiary analysis at frontal locations revealed a significant main effect of test status [$F(1,31)=9.14$, $p=0.005$], along with a significant interaction between test status and electrode [$F(1.1,35.4)=8.44$, $p=0.005$], reflecting the presence of an old/new effect that is maximal towards superior sites at frontal locations. Analysis at parietal locations revealed a significant main effect of test status [$F(1,31)=6.35$, $p=0.017$], but no interactions including the factor of test status, indicating the presence of a slight positivity for hits across sites at parietal locations. Further examination of the data confirmed that old/new effects for the unprimed condition were maximal at electrode FC1 ($t(31)=3.83$, $p=0.001$).

Initial analysis for the primed condition also revealed a significant main effect of test status [$F(1,31)=7.68$, $p=0.009$], and a significant interaction between test status, location and electrode [$F(1.2,37.5)=10.66$, $p=0.001$], again reflecting the presence of a positivity for hits that is maximal towards superior sites at frontal locations. Subsidiary analysis at frontal locations revealed a significant main effect of test status [$F(1,31)=10.36$, $p=0.003$], and a significant interaction between test status and electrode [$F(1.1,34.8)=13.14$, $p=0.001$], demonstrating the presence of an old/new effect maximal over superior sites at frontal locations. Analysis at parietal locations revealed no main effect or interactions including the

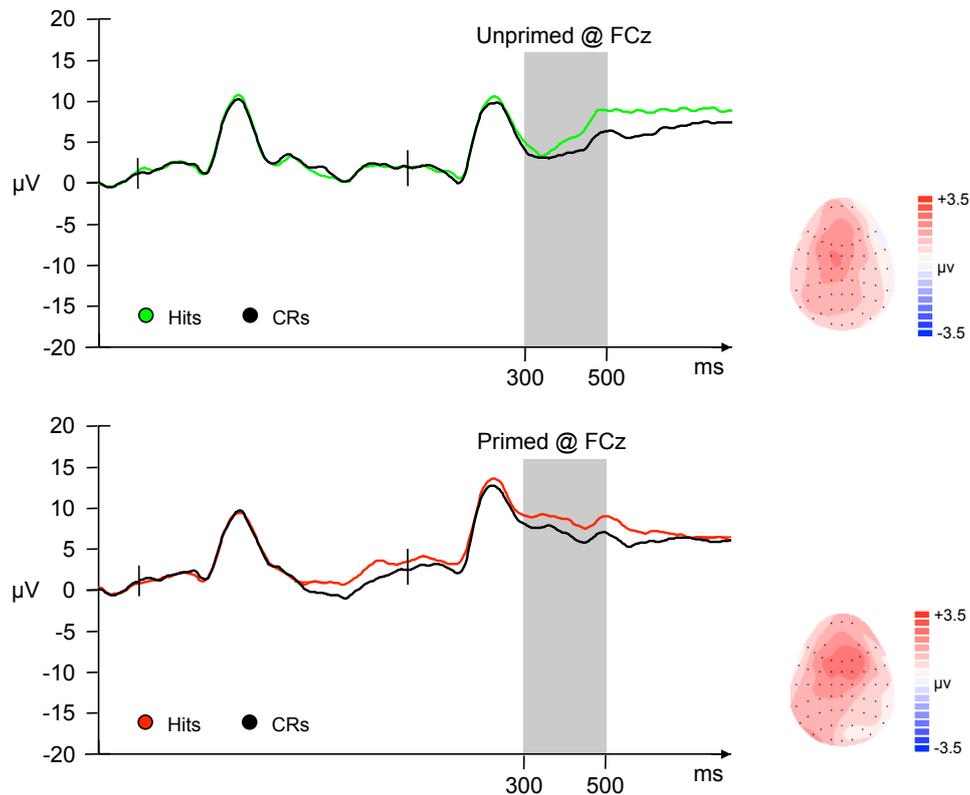


Figure 7.25: Memory @ FCz (300-500ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at electrode FCz. Topographic maps show the difference between hits and correct rejections for both conditions. Mid-frontal old/new effects were evident for both conditions during the 300-500ms time window, and appeared similar in magnitude and distribution across conditions.

factor of test status, confirming the absence of old/new effects at parietal locations. Further examination of the data confirmed that old/new effects for the primed condition were maximal at electrode FC2 ($t(31)=3.28$, $p=0.003$).

Magnitude analysis was performed on subtraction data to compare the amplitude of old/new effects for the primed and unprimed conditions, using ANOVA with the factors of condition (unprimed, primed), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed no main effect or interactions including the factor of condition, indicating that memory effects for the unprimed and primed conditions did not differ substantially in

magnitude or distribution between 300-500ms. In summary, between 300-500ms mid-frontal old/new effects were evident in both conditions and did not differ in magnitude or distribution, demonstrating that FN400 signals were unaffected by the priming manipulation.

7.4.6.3 Time window 500 to 800ms

Between 500-800ms, waveforms in the unprimed condition were more positive going for hits than for correct rejections at mid-frontal locations. By contrast, old/new effects evident for the primed condition exhibited a right-frontal focus (see Figure 7.26 for data). Initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,31)=14.33$, $p=0.001$], and a significant interaction between test status location and electrode [$F(1.1,35.7)=4.05$, $p=0.047$], reflecting the presence of a positivity for hits that is larger over superior sites at mid-frontal locations. Subsidiary analysis at frontal locations revealed a significant main effect of condition [$F(1,31)=9.05$, $p=0.005$], and a significant interaction between test status and electrode [$F(1.1,35.2)=10.66$, $p=0.002$], indicating the continuation and strengthening of old/new differences at superior mid-frontal locations. Analysis at parietal locations revealed a significant main effect of test status [$F(1,31)=15.35$, $p<0.001$], and a significant interaction between test status and electrode [$F(1.1,34.5)=5.65$, $p=0.020$], reflecting the presence of a slight positivity for hits over superior sites in both hemispheres. Further examination of the data demonstrated that old/new effects for the unprimed condition were maximal at electrode FCz ($t(31)=3.63$, $p=0.001$).

Initial analysis for the primed condition revealed significant interactions between test status, location and hemisphere [$F(1,31)=5.33$, $p=0.028$], and test status,

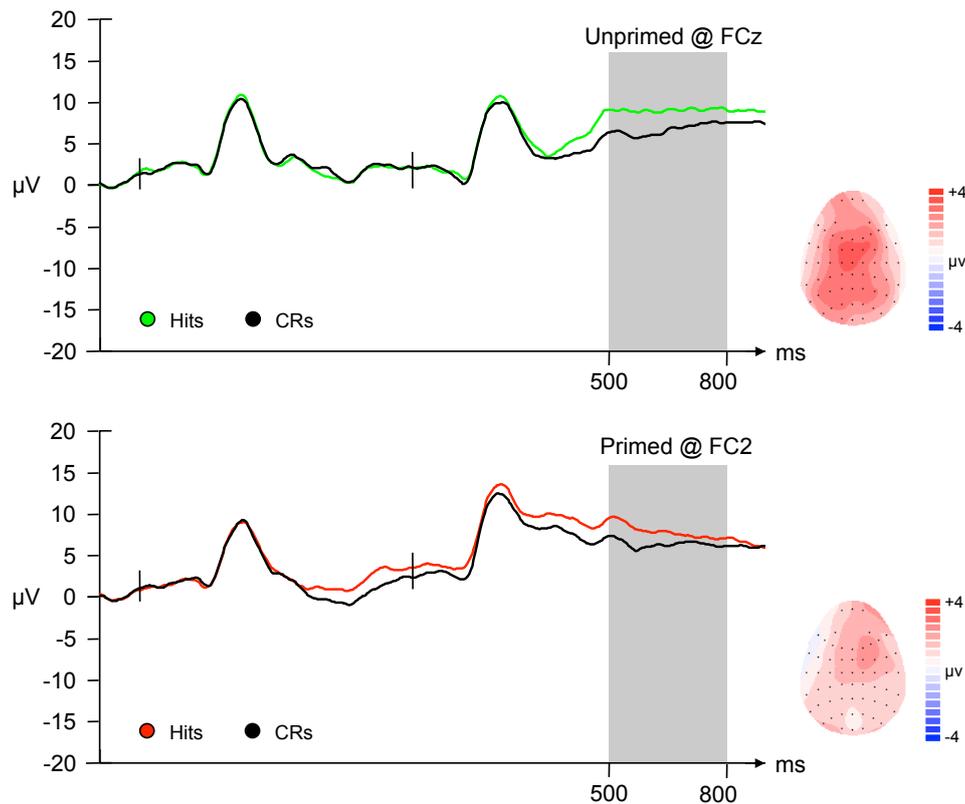


Figure 7.26: Memory (500-800ms). Grand average ERPs for hits and correct rejections in the unprimed and primed conditions at representative electrodes. Topographic maps show the difference between the hits and correct rejections for both conditions. Frontal old/new effects were evident in both conditions, with a left-sided distribution for the primed condition and a focus over superior sites for the unprimed condition.

location and electrode [$F(1.2,37.9)=5.32$, $p=0.024$], reflecting the presence of a positivity for primed hits towards inferior sites at right-frontal locations. Subsidiary analysis at frontal sites revealed a significant main effect of test status [$F(1,31)=4.66$, $p=0.039$], along with interactions between test status and hemisphere [$F(1,31)=7.44$, $p=0.010$], and test status and electrode [$F(1.1,34)=4.32$, $p=0.042$], reflecting the presence of a positivity for hits maximal over superior sites in the right hemisphere at frontal locations. Analysis at parietal locations revealed no main effects or interactions including the factor of test status, confirming the absence of substantial old/new differences at parietal locations.

Further examination of the data supported this pattern of results, demonstrating that old/new effects for the primed condition were maximal at electrode FC2 ($t(31)=2.62$, $p=0.013$).

Magnitude analysis was performed on subtraction data to compare the amplitude of old/new effects for the primed and unprimed conditions, using ANOVA with the factors of condition (unprimed, primed), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). Initial analysis failed to identify a main effect or interactions including the factor of condition. Inspection of the data strongly suggested a difference in the distribution of memory effects across conditions, so the analysis was repeated contrasting fronto-central and parietal sites to better capture the maxima of frontal effects. Results revealed significant interaction between condition and electrode [$F(1.3,40.7)=5.61$, $p=0.016$], indicating a difference in distribution, with old/new effects for the unprimed condition focused over superior sites and effects for the primed condition exhibiting a skew towards medial sites in the right hemisphere. Subsidiary analysis was performed on the rescaled data to investigate whether these differences reflected genuine changes in distribution across conditions. Results also revealed a significant interaction between condition and electrode [$F(1.3,41.2)=3.82$, $p=0.046$], confirming that old/new effects present for the unprimed and primed conditions were driven by partially non-overlapping sets of neural generators.

In summary, analysis for the unprimed condition demonstrated the continuation of mid-frontal old/new effects into the 500-800ms time window. Analysis for the primed condition also suggested the presence of an old/new difference at frontal sites with a focus over the right hemisphere. Topographic analysis confirmed that old/new effects for the unprimed and primed conditions were driven by partially non-overlapping sets of neural generators.

7.4.6.4 Topographic analysis

The foregoing results suggest changes in the pattern of memory related activity over time for the primed condition, with old/new effects exhibiting a mid-frontal distribution between 300-500ms, followed by a right-frontal distribution between 500-800ms. The next level of analysis was designed to contrast the distribution of old/new effects for the unprimed and primed conditions across time windows. Analysis was performed separately for each condition and time window contrast, using ANOVA with the factors of time window (window1, window2), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). Analysis contrasting the distribution of memory effects between 300-500ms and 500-800ms for the unprimed condition revealed no main effect or interactions including the factor of time window, confirming that mid-frontal old/new effects evident in both time windows, were driven by the same underlying neural generators.

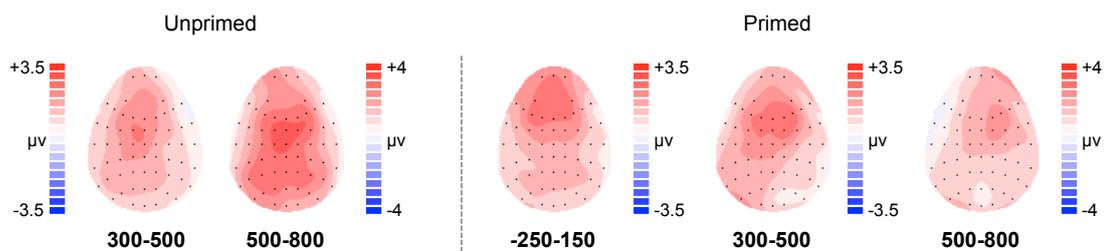


Figure 7.27: Memory over time 698ms SOA. Topographic maps show the difference between hits and correct rejections in the unprimed and primed conditions for the 698ms SOA. Old/new differences for the primed condition exhibited a shift over time from a mid-frontal to a right-frontal distribution, but no substantial changes in the distribution were apparent for the unprimed condition.

Analysis contrasting old/new effects evident between -250-150ms and 300-500ms for the primed condition revealed a significant interaction between time window, location, hemisphere and electrode [$F(1.4,42.9)=4.68$, $p=0.025$], suggesting that

effects were driven by partially non-overlapping neural generators across time windows. As can be seen in Figure 7.27, the early positivity has a more anterior distribution encompassing fronto-polar sites, and as a result the previous analysis may have failed to adequately capture this early anterior effect. More focused analysis was performed contrasting three strings of frontal electrodes (fronto-polar: FP1, FPz, FP2; frontal: F1, Fz, F2; fronto-central: FC1, FCz, FC2), using ANOVA with the factors of time window (-250-150ms, 300-500ms), location (fronto-polar, frontal, fronto-central) and electrode (left, mid, right). Results revealed no main effect or interactions including the factor of time window, indicating that mid-frontal effects in both time windows were driven by the same underlying neural generators. Contrasting old/new effects for the primed condition between 300-500ms and 500-800ms revealed a significant interaction between time window, hemisphere and electrode [$F(1,31)=8.37$, $p=0.004$], demonstrating that the mid-frontal old/new effect between 300-500ms and the later right-frontal effect between 500-800ms were driven by at least partially non-overlapping sets of neural generators.

7.4.7 SOA comparisons

The next stage of analysis sought to compare the magnitude and distribution of priming effects reported in the previous sections across SOAs for each time window. Contrasts took the form of within condition comparisons across SOAs for the 300-500ms and 500-800ms time windows. Results of magnitude and topographic analyses on the data across SOA for each time window are reported separately in the following sections.

7.4.7.1 300-500ms

Between 300-500ms, unprimed hits were more positive going than unprimed correct rejections over frontal and central locations for both SOAs. Data for the primed condition demonstrated a difference in distribution across SOA, with a left-parietal old/new difference evident for the 398ms SOA, in contrast to a mid-frontal old/new difference for the 698ms SOA (see Figure 7.28 for topographic maps). Analysis contrasting the magnitude of memory effects across SOAs for the unprimed condition, using ANOVA with the factors of SOA (398ms, 698ms), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior), revealed no significant main effect or interactions including the factor of SOA, indicating that old/new effects did not differ in magnitude or distribution across SOAs.

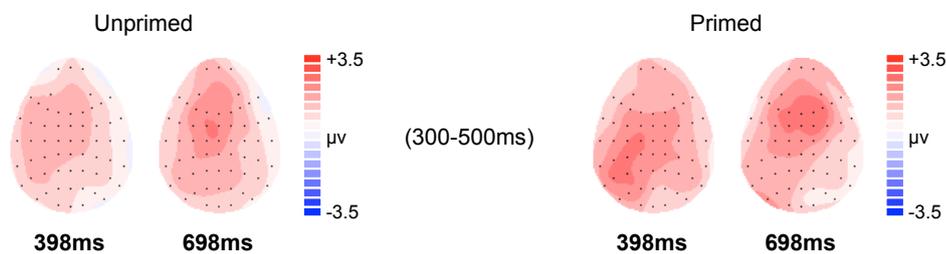


Figure 7.28: Memory effects (300-500ms). Topographic maps show the difference between unprimed and primed hits and correct rejections. Old/new effects in the unprimed condition were present over frontal and central locations across SOAs. Old/new effects in the primed condition demonstrated a difference in distribution across SOAs, with a left-parietal focus for the 398ms SOA, and a mid-frontal focus for the 698ms SOA.

Contrasting the magnitude of memory effects across SOAs for the primed condition revealed a significant interaction between SOA, location and hemisphere [$F(1,31)=6.36$, $p=0.017$], reflecting the presence of stronger old/new effects at frontal sites with a slight skew over the right hemisphere for the 698ms SOA, and stronger effects over left-parietal locations for the 398ms SOA. To inves-

tigate whether these differences reflect a genuine change in topography across SOAs analysis was performed on rescaled data, using ANOVA with the factors of SOA (398ms,698ms), location (frontal, parietal) and electrode (inferior, mid, superior). Results also revealed a significant interaction between SOA, location and hemisphere [$F(1,31)=5.89$, $p=0.021$], confirming that old/new effects for the primed condition varied as a function of SOA and were driven by partially non-overlapping sets of neural generators.

7.4.7.2 500-800ms

Between 500-800ms, old/new differences appeared similar in magnitude and distribution across SOAs, with mid-frontal effects evident for the unprimed condition and right-frontal effects evident for the primed condition (see Figure 7.29 for topographic maps).

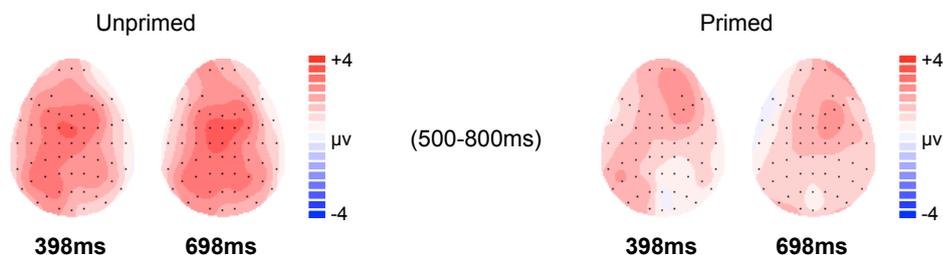


Figure 7.29: Memory effects (500-800ms). Topographic maps show the difference between unprimed and primed hits and correct rejections at each SOA. Old/new differences appeared similar in magnitude and distribution across SOAs, with mid-frontal effects evident for the unprimed condition and right-frontal effects evident for the primed condition

Analysis contrasting the magnitude of effects across SOAs for the unprimed condition revealed no significant main effect or interactions including the factor of SOA, confirming that mid-frontal memory effects did not differ in magnitude or distribution across SOAs. Contrasting memory effects for the primed condition

across SOAs revealed no significant main effect or interactions, confirming that right-frontal effects did not differ in magnitude or distribution across SOAs.

7.4.8 Summary

For the 398ms SOA, the data demonstrated the presence of old/new differences between 300-500ms and 500-800ms in both conditions. Analysis for the unprimed condition demonstrated the presence of a slight positivity for hits across locations, that was maximal over medial central sites between 300-500ms, followed by a mid-frontal positivity between 500-800ms. Contrasting these early and late effects for the unprimed condition demonstrated the absence of differences in magnitude or distribution across time windows, suggesting that the 300-500ms time window captures the onset of mid-frontal effects evident during the 500-800ms time window. Analysis for the primed condition confirmed the presence of old/new differences with a left-parietal distribution between 300-500ms, followed by differences over right-frontal locations between 500-800ms. Further examination of the data demonstrated that significant old/new differences were present at left-parietal sites from target onset in the primed condition, and continued into the 300-500ms time window. Contrasting effects for the 300-500ms and 500-800ms time windows for the primed condition confirmed that old/new effects differed in distribution, with a focus over left-parietal locations between 300-500ms, and over right-frontal locations between 500-800ms. Comparison of memory effects across conditions for each time window identified the presence of a difference in the magnitude and distribution of effects in the 500-800ms time window, confirming that effects were driven by non-overlapping sets of neural generators.

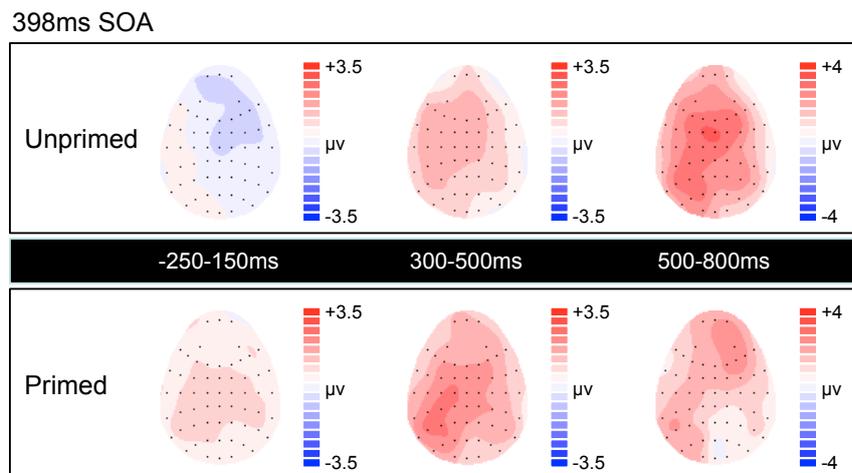


Figure 7.30: Memory topographic summary 398ms SOA. Topographic maps summarise differences between hits and correct rejections for the unprimed and primed conditions over time.

For the 698ms SOA the data demonstrated the presence of old/new differences for the unprimed condition between 300-500ms and 500-800ms, with a mid-frontal distribution in both windows. Contrasting these early and late memory effects for the unprimed condition failed to reveal differences in magnitude or distribution over time, confirming that effects in the 500-800ms time window reflected a continuation of mid-frontal effects evident between 300-500ms. Analysis for the primed condition demonstrated the presence of three memory related effects, starting with an additional pre-target positivity for hits at frontal sites, onsetting 250ms prior to target words and continuing into the post-target period. This early memory effect was followed by a mid-frontal positivity between 300-500ms and then a right-frontal positivity between 500-800ms.

Contrasting effects for the primed condition over time failed to reveal differences in the magnitude or distribution during the -250-150ms and 300-500ms time windows, but did confirm differences for the 300-500ms and 500-800ms time windows, demonstrating that mid-frontal old/new effects between 300-500ms and right-frontal effect between 500-800ms were driven partially non-overlapping sets of

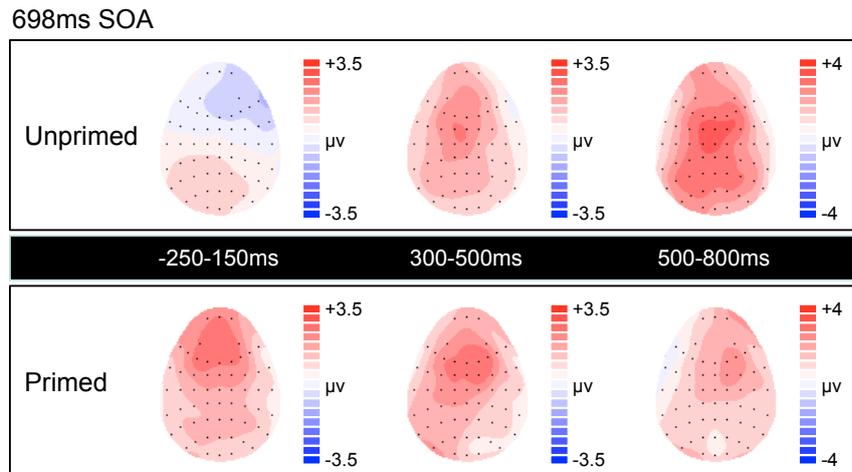


Figure 7.31: Memory topographic summary 698ms SOA. Topographic maps summarise differences between hits and correct rejections for the unprimed and primed conditions over time.

neural generators. Comparison of memory effects across conditions for each time window demonstrated no difference in magnitude or distribution of mid-frontal effects during the 300-500ms time window, but did reveal a between condition difference in the later window, confirming mid-frontal effects in the unprimed condition and right-frontal effects in the primed condition were driven by partially non-overlapping sets of neural generators.

Comparison across SOAs demonstrated no difference in the magnitude or distribution of old/new effects for the unprimed condition between 300-500ms or 500-800ms, exhibiting a largely mid-frontal distribution across SOAs and time windows. Comparison across SOAs for the primed condition confirmed the absence of differences in magnitude or distribution of right-frontal effects evident during the 500-800ms time window, but did reveal a difference in the magnitude and distribution of old/new effects evident between 300-500ms. Analysis demonstrated the presence of stronger old/new effects at frontal sites with a slight skew over the right hemisphere for the 698ms SOA, in contrast to larger effects over left-parietal locations for the 398ms SOA. Topographic analysis confirmed that these

differences reflected a genuine change in the distribution of memory effects as a function of SOA. These findings demonstrate a difference in process engagement across SOAs during the 300-500ms time window, with left-parietal effects previously associated with recollection evident for the 398ms SOA, and mid-frontal differences previously linked to familiarity evident for the 698ms SOA.

7.5 Discussion

The main aim of the current experiment was to investigate mechanisms driving the absence of FN400 old/new effects reported in the first data chapter, in an attempt to identify factors that determine whether retrieval will be implicit or explicit. In addition, we sought to investigate N400 effects observed in the first experiment, in an attempt to delineate lexical and post-lexical interpretations of the observed outcome. Response time data demonstrated faster responses for primed words across SOAs, with larger effects overall for the 698ms SOA. Despite significantly larger facilitation effects on response times for the 698ms SOA, the SOA manipulation did not directly influence the pattern of memory performance. However, in contrast to the previous experiments, the behavioural data demonstrated a slight increase in false alarm rates and a slightly more liberal response bias for the primed condition, resulting in poorer discrimination for primed words. The Remember/Know data also demonstrated a slight increase in the raw proportion of R and K false alarms for the primed condition, but analysis on corrected estimates of familiarity and recollection failed to support this result. These findings suggest that while the SOA manipulation did not produce measurable changes in behavioural performance, beyond the expected increase in facilitation on response times, inclusion of the longer SOA appears to

have driven a change in retrieval processing. The ERP results are illuminating in this respect, and as such, we will return to this issue in more detail after discussion of the ERP data.

Contrasting ERPs for primed and unprimed words shown with the standard SOA revealed the presence of three priming related modulations; an early central negativity (-50-150ms) that was only evident for correct rejections, followed by a centro-parietal positivity (250-500ms) for primed hits and correct rejections, and a later (500-1100ms) negativity over posterior locations for primed hits and correct rejections. In short, the data displayed a very similar pattern of priming effects to those observed in the first experiment: N400 effects did not differ substantially in magnitude or distribution, and the late negativity was again modulated by study exposure, being larger in magnitude for hits than for correct rejections. Contrasting ERPs for primed and unprimed words shown with the longer SOA again revealed the presence of three priming related modulations: an early central negativity (-350 to 150ms) that was only significant for correct rejections, followed by long lasting centro-parietal positivity (-100-500ms) for primed hits and correct rejections that did not differ in magnitude or distribution, and a later negativity (500-1100ms) over posterior locations for primed hits and correct rejections, that was again larger in magnitude for hits. In essence, the most notable difference in priming effects across SOAs was the apparent modulation of the N400, which onset earlier and was longer in duration for the 698ms SOA.

Comparison of N400 effects across SOAs over the 250-500ms time window, where the effect was observed for the standard SOA, revealed that the N400 had a more anterior distribution for the longer SOA. In a recent study, Eddy and Holcomb (2010) manipulated prime-target SOA in a semantic categorization task using pictures, and found that increasing the SOA between prime-target pairings did

not modulate the size of N400 effects, but did result in a more anterior focus at longer SOAs. On this basis, the authors concluded that increasing SOA duration does not encourage in-depth high level processing of the prime to occur. However, the longest duration used was 470ms, which is substantially shorter than the SOA employed here, and it is plausible that the use of pictures and semantic categorization is not directly comparable to the use of words within a recognition task, so an increase in high-level semantic processing cannot be ruled out in the current experiment. In addition, N400 effects in the current study for the 698ms SOA persisted for 600ms, suggesting that an increase in semantic processing of the prime may be indexed by an increase in the duration of the N400 rather than by differences in amplitude in this case.

For memory effects, contrasting ERPs for unprimed hits and correct rejections at both SOAs revealed a similar pattern of results. Old/new effects with a largely mid-frontal distribution were present during the 300-500ms time window and continued into the 500-800ms time window for both SOAs. Data for the primed condition shown with the standard SOA exhibited old/new differences with a left-parietal distribution between 300-500ms, replicating the findings from the second experiment, followed by differences over right-frontal locations between 500-800ms. Further examination of the data demonstrated that old/new differences at left-parietal locations were evident within 100ms of target onset. For the longer SOA, data for the primed condition demonstrated the presence of three memory related effects, starting with an additional pre-target positivity for hits with a fronto-polar distribution, onsetting 250ms prior to target words, and continuing into the post-target period. This early memory effect was followed by a mid-frontal positivity between 300-500ms, and then a right-frontal positivity between 500-800ms. In essence, the most notable differences were the presence of

left-parietal old/new effects for the short SOA, in contrast to mid-frontal old/new effects for the longer SOA between 300-500ms, and the presence of an additional fronto-polar old/new effect for the longer SOA.

A number of studies have reported an early onsetting fronto-polar old/new effect, with a similar distribution to the one found here for primed words at the longer SOA (Curran & Dien, 2003; Diana, Vilberg & Reder, 2005; Duarte et al., 2004; Friedman, 2004; Tsivilis, Otten & Rugg, 2001). The functional significance of this early effect, which usually appears between 100-300ms after stimulus onset, remains unclear. Tsivilis et al. (2001) suggested that it could reflect a priming effect unrelated to recognition, or that it may reflect early access to information concerning prior exposure to an item that contributes to recognition. More recently, Diana et al. (2005) have suggested that it reflects the initiation of a memory search. The current data appear to support the latter suggestion; the effect onsets 450ms post-prime which falls outside time windows normally associated with priming (i.e., P150, N250, P325), and is not consistent with the normal timing and distribution of N400 effects. Therefore, we interpret this effect as reflecting initiation of a memory search prior to target onset as a result of the match between study exposure and presentation of the prime, which is in turn predictive of the upcoming target.

As noted earlier, the SOA manipulation also caused differential process engagement during the 300-500ms for primed words, with left-parietal effects evident for the shorter SOA, and mid-frontal old/new effects supporting recognition for the longer SOA. Based on the extended N400 effect observed for the longer SOA, it appears that an increase post-lexical semantic processing does result in familiarity based retrieval, while the shorter SOA elicits less semantic elaboration and promotes recollection. However, the first experiment demonstrated the absence

of FN400 and left-parietal effects with an SOA of 398ms, therefore the presence of early-onsetting left-parietal effects in the current study for the short SOA suggests that the inclusion of the longer SOA indirectly influenced process engagement by changing the strength of evidence available from the prime. Specifically, presenting short and long SOA trials randomly intermixed appears to promote direct and automatic access to memory traces for short SOA trials, while excessive semantic elaboration appears to produce interference, leading to a sense of familiarity rather than recollection. Therefore, it could be argued that combining evidence from lexical and post-lexical processing serves as a more effective cue for retrieval of contextual information than post-lexical processing in isolation.

In addition to the effects discussed above, the current study revealed the presence of right-frontal old/new effects between 500-800ms for primed words at both SOAs, that were not apparent in the data from the previous experiments. These right-frontal old/new effects did not differ in magnitude or distribution as a function of SOA, but their presence may be illuminating in understanding the reduction in discrimination for primed words in the current study. As noted earlier (see Chapter 3, Section 3.1.3), right-frontal old/new effects have been found in a number of recognition memory experiments (e.g., Hayama et al., 2008; Schloerscheidt & Rugg, 2004; Wilding & Rugg, 1996; Woodruff et al., 2006), but the exact functional significance of this effect remains unclear, although most commonly related to monitoring the products of retrieval. For example, Wilding and Rugg (1996) reported larger right-frontal effects for correct than for incorrect source judgements, but right-frontal effects have also been found in the absence of correct source judgements (Trott et al., 1999), suggesting that they are not directly related to accuracy. In the current context, the fact that right-frontal effects were only present for primed items suggests that they may reflect the at-

tribution of fluency to prior exposure. As a result, the reduction in discrimination found in the current study could be driven by additional processing related to attribution, that was not observed in our earlier studies, potentially accounting for the difference in findings.

7.5.1 Summary

The main aims of the current experiment were to identify factors that determine whether retrieval will be implicit or explicit, and to investigate the processing nature of the N400, by manipulating the prime-target SOA. The findings clearly demonstrated that increasing the SOA modulated the N400, which onset earlier and was longer in duration. However, randomly intermixing short and long SOA trials had a number of unexpected consequences. The pattern of memory results in the ERP data for the short SOA failed to replicate the findings of the first experiment, demonstrating the presence of early onset left-parietal old/new differences, and in contrast to the first two experiments, memory performance was lower for the primed condition. Recent research has discovered that priming is highly sensitive to context effects. For example, Taylor and Henson (2012) contrasted repetition and conceptual primes in intermixed blocks during a masked priming paradigm, finding an increase in the proportion of remember responses for studied words that were preceded by conceptual primes, but not for words preceded by repetition primes. However, the authors failed to replicate their results when conceptual blocks were not intermixed with repetition blocks. Therefore, it seems that one of the factors determining how retrieval will proceed is the comparative degree of fluency between items in recognition tasks.

Chapter 8

ERP 4

8.1 Introduction

The main aim of the current study was to query the relationship between N400 priming effects and FN400 effects associated with familiarity. Recently it has been suggested that the N400 and FN400 may be functionally equivalent (Voss & Federmeier, 2011), and while the other experiments reported in this thesis suggest that this view is not entirely appropriate, further manipulation of the N400 effect would facilitate assessment of this claim more directly. In essence, the current experiment sought to establish whether the FN400 old/new effect is impacted by changes in the N400. Based on the findings of the previous study, we reasoned that introducing an additional manipulation that varied the comparative degree of priming across conditions would modulate the N400 and promote reliance on familiarity, allowing changes in both components to be assessed simultaneously. To achieve this goal the current study matched the design of the first experiment but introduced a third partial prime condition, where prime items consisted of a

repetition of the target word with the first letter removed, reducing the degree of semantic overlap between prime and target words.

Partial-word priming is normally used to enable manipulation of the degree of informativeness of prime words (Davis, 2003), and clear differences in the size of priming effects on response times have been observed as a function of the specific position of the letter that is removed. For example, Grainger and Jacobs (1993) contrasted facilitation effects for five letter partial prime words where the first, third or fifth letters were removed. The authors found that removing the last letter of the prime produced greater facilitation effects than removing the first or third letters and concluded that these results confirmed the presence of a word-initial superiority effect (also see Humphreys, Evett & Quinlan, 1990). However, it is also important to note that letter position effects interact with the level of ambiguity created by removing specific letters in words, based on the number of potential candidates for completion. For example, Hinton, Liversedge and Underwood (1998) contrasted facilitation effects in a lexical decision task where four letter words either had one (unambiguous) or three (ambiguous) potential completions, finding that priming effects were larger for unambiguous than for ambiguous words. The stimuli used in the current thesis were not prepared with this manipulation in mind, and the intention in the current experiment was not to elicit competition between lexical representations. Therefore, removing the first letter was considered to be the best option for controlling effects of ambiguity and reducing facilitation effects.

In addition to behavioural research demonstrating changes in facilitation effects for partial primes, ERP research employing masked priming has demonstrated that partial repetition modulates the amplitude of N400 effects, with full primes being more positive going than partial primes, which in turn are more positive

going than unrelated primes (Holcomb & Grainger, 2006). As noted earlier, the absence of FN400 effects for stimuli that do not support semantic processing, for example geometric patterns (Voss & Paller, 2009) and novel faces (MacKenzie & Donaldson, 2007), has opened up debate on whether FN400 effects during recognition memory tests arise from conceptual priming, and as such should not be considered functionally dissociable from N400 effects (Voss & Federmeier, 2011). Moreover, it has been argued that the logic applied to dissociate familiarity and recollection has greatly contributed to the misattribution of the FN400 as a generic marker of pure familiarity, by identifying neural correlates of familiarity on the basis of exclusion (Paller et al., 2007). In essence, neural signals of familiarity are often identified by demonstrating that they are not influenced by factors that influence neural signals associated with recollection, making the link between the FN400 and familiarity indirect, and leaving open the possibility that FN400 effects could, at least in part, reflect the operation of conceptual priming.

Based on this view, it would appear that factors that modulate N400 repetition effects should also influence FN400 effects during recognition tests. Specifically, manipulating the ease of semantic integration between prime and target pairings to reduce the magnitude of N400 effects, could potentially influence the magnitude of FN400 potentials, if both are sensitive to the degree of conceptual priming. It is difficult to predict exactly how the relationship between N400 and FN400 potentials will unfold on the basis of the existing literature, which is reasonably limited at this stage, but there are two logical predictions that can be made within the context of the current masked priming paradigm. Firstly, if N400 and FN400 potentials are functionally equivalent, reductions in the N400 would be expected to be matched by reductions in FN400 potentials. Alternatively, if

N400 and FN400 potentials are functionally independent, then manipulating the ease of semantic integration between prime and target pairings should modulate N400 potentials, but leave FN400 potentials largely unaffected. The current experiment sought to differentiate between these predictions by employing partial primes at test to modulate N400 effects and to assess the consequences for FN400 potentials.

8.2 Methods

Stimulus materials and procedures were identical to those reported in chapter 4, but with the addition of a partial prime condition. In the partial prime condition the first letter of each prime word was removed to reduce the degree of semantic overlap between prime and target words. The assignment of words to the three conditions was again fully counterbalanced across participants. The number of words in each test list remained 120 and included 40 trials for each condition, across the entire experiment participants viewed 160 trials for each of the three conditions (80 old, 80 new). Thirty-seven undergraduate psychology students from the University of Stirling participated in the experiment. Seven participants were excluded due to excessive EEG artefacts, resulting in insufficient ERP trials for critical contrasts (<16 trials). The remaining thirty participants comprised of 18 females and 12 males with a mean age of 22 (range=18-35; SD=4.70).

8.3 Behavioural results

In total 75% of participants reported being unaware of the existence of the masked prime, 13% reported that they detected flickering on the screen but were unable

to detect any of the words, and the remaining 12% reported that they were aware of seeing the word blank appear before the onset of the target on a few trials, but again none of the participants reported being aware of the repetition of the target words. Initial examination of the behavioural data as a function of reported awareness confirmed no differences in the pattern of results for participants who reported being aware of flickering on the screen or aware of the word blank compared to unaware participants, and as a result the data were analysed collapsed across awareness categories. Table 8.1 shows a summary of memory performance measures for the current experiment and suggests a slight increase in performance for old items in the primed condition accompanied by an increase in discrimination and bias.

Table 8.1: Memory performance. Percentage of correct responses, discrimination and bias measures for the unprimed, part primed and primed conditions (standard error of the mean). Data demonstrate an increase in mean accuracy and for the primed condition compared to the unprimed and part primed conditions. Bias measures were conservative across conditions, but were slightly less conservative for primed words.

	Correct %		Discrimination	
	Old	New	Pr	Br
Unprimed	52.58 (2.85)	75.35 (2.78)	0.28 (0.02)	0.34 (0.04)
Part primed	51.13 (2.93)	77.11 (2.65)	0.28 (0.02)	0.32 (0.04)
Primed	56.67 (3.25)	75.12 (2.97)	0.32 (0.02)	0.37 (0.04)

Importantly, analysis confirmed that participants were able to discriminate between old and new words in all three conditions (paired t-tests comparing hits and false alarms for the three conditions were significant [$p < 0.001$] in all comparisons). Mean accuracy data were submitted to analysis using ANOVA with the factors of condition (unprimed, part primed, primed), and test status (old, new). Results revealed a significant main effect of condition [$F(1,29)=3.47$, $p=0.038$], and a significant interaction between condition and test status [$F(1,29)=8.63$,

$p=0.001$]. Subsidiary analysis confirmed that this interaction reflected an increase in mean accuracy for old words in the primed condition compared to the unprimed ($t(29)=3.44$, $p=0.002$), and part primed conditions ($t(29)=3.48$ $p=0.002$). Discrimination scores increased slightly for the primed condition compared to the unprimed ($t(29)=2.20$, $p=0.036$), and part primed conditions ($t(29)=2.20$, $p=0.036$), but this did not survive correction for multiple comparisons. Response bias was conservative across conditions, but demonstrated a slightly less conservative bias in the primed compared to the part primed condition ($t(29)=3.29$, $p=0.003$), and did not differ between the unprimed and primed conditions. Overall, the pattern of results demonstrate a slight increase in mean accuracy and a slightly less conservative bias for primed compared to part primed words, but no substantial difference in discrimination rates across conditions.

Table 8.2: Response by RK. Mean percentage of all response types split by test status and condition (standard error of the mean). The data demonstrate a slight increase in the raw proportion of K hits in the primed condition, and a reduction in R false alarms in the part primed condition.

		Remember	Know	New
Old	Unprimed	28.30 (3.04)	24.28 (2.42)	47.42 (2.85)
	Part primed	28.61 (3.07)	22.52 (2.30)	48.87 (2.93)
	Primed	29.93 (3.67)	26.74 (2.71)	43.33 (3.25)
New	Unprimed	11.06 (2.24)	13.60 (1.88)	75.35 (2.78)
	Part primed	8.62 (1.88)	14.27 (2.06)	77.11 (2.65)
	Primed	11.01 (2.11)	13.87 (2.09)	75.12 (2.97)

Table 8.2 shows the breakdown of responses by RK judgement for old and new words in the unprimed, part primed and primed conditions. The data suggest a slight increase in the raw proportion of K hits in the primed condition, and a reduction in R false alarms in the part primed condition. ANOVA contrasting RK responses including the factors of condition (unprimed, part primed,

primed), test status (Hits, FAs) and response type (Remember, Know) produced a significant main effect of condition [$F(2,58)=8.78$, $p<0.001$], along with a significant interaction between condition and test status [$F(2,58)=3.65$, $p=0.032$], and a marginally significant interaction between condition, test status and response type [$F(2,58)=3.02$, $p=0.056$]. Follow up t-tests demonstrated an a slight increase in the proportion of K hits for the primed compared to the part primed condition ($t(29)=2.94$, $p=0.006$), and a decrease in the proportion of R false alarms for the part primed compared to the primed ($t(29)=3.65$, $p=0.001$), and unprimed ($t(29)=3.11$, $p=0.004$) conditions.

Table 8.3: IRK estimates of recollection and familiarity. Average corrected estimates of familiarity and recollection (standard error of the mean). The data demonstrate a reduction in corrected estimates of familiarity for the part primed condition, while estimates of recollection were unaffected by the priming manipulation.

	Rec.	Fam.
Unprimed	0.17 (0.02)	0.18 (0.02)
Part primed	0.20 (0.02)	0.15 (0.02)
Primed	0.19 (0.03)	0.21 (0.02)

Table 8.3 shows the IRK estimates of familiarity and recollection calculated as described in Chapter 4, and the data suggest lower levels of familiarity in the part primed condition. ANOVA with the factors of condition (unprimed, primed) and retrieval process (familiarity, recollection), revealed a significant main effect of condition [$F(2,58)=3.72$, $p=0.030$], and a significant interaction between condition and retrieval process [$F(2,58)=4.51$, $p=0.015$]. Follow up t-tests confirmed the presence of greater levels of familiarity for primed ($t(29)=3.24$, $p=0.003$), and unprimed words ($t(29)=2.23$, $p=0.034$), compared to part primed words, but no difference in levels of recollection across conditions. Overall, this pattern of results confirms that reported levels of recollection were unaffected by the priming

manipulation, while levels reported familiarity were slightly higher for primed than for part primed words.

Table 8.4: Response times (ms). Mean response time data for correct responses split by test status (A) and the magnitude of the difference between unprimed response times and those for the part primed and primed conditions (B) split by test status (standard error of the mean). The data demonstrate a graded reduction in response times, with the fastest responses in the primed condition, but no difference in magnitude for hits and correct rejections.

(A)	Old (Hits)	New (CRs)
Unprimed	994.90 (35.65)	945.89 (41.83)
Part primed	971.26 (39.61)	924.03 (42.05)
Primed	926.06 (40.05)	889.93 (45.37)
(B)	Old (Hits)	New (CRs)
Part primed	23.65 (13.11)	21.86 (8.81)
Primed	68.84 (14.10)	55.96 (13.13)

Table 8.4 shows the response time data for hits and correct rejections in the unprimed, part primed and primed conditions, and the magnitude of the difference between the unprimed condition, and the part primed and primed conditions. Response times were faster for primed and part primed words compared to unprimed words for hits and correct rejections, with the primed condition producing the greatest decrease in response times. ANOVA including the factors of condition (unprimed, part primed, primed) and test status (old, new) confirmed the presence of a significant main effect of condition [$F(2,58)=21.06$, $p<0.001$], but no interaction between condition and test status, indicating that the observed differences in response times were comparable for hits and correct rejections.

Follow up t-tests on the mean RT data collapsed across test status revealed faster response times for part primed ($t(29)=3.00$, $p=0.002$) and primed words ($t(29)=5.53$, $p<0.001$) compared to unprimed words. Reaction times were also

significantly faster for primed words compared to part primed words ($t(29)=3.98$, $p<0.001$). While the subtraction data suggested a trend towards greater priming for hits than for correct rejections in the primed condition (12.88 ms), ANOVA on the difference between the unprimed and both priming conditions produced only a main effect of condition [$F(1,29)=15.84$, $p<0.001$]. This result reflects a greater degree of facilitation on reaction times for the primed words than for part primed words, with no difference in the degree of priming effects within conditions for hits and correct rejections.

8.3.1 Summary

In Summary, the accuracy data demonstrated a slight increase in mean accuracy for studied words in the primed condition compared with words in the part primed and unprimed conditions, and a slightly less conservative bias for primed compared to part primed words, but no substantial difference in discrimination rates across conditions. Analysis of the RK data demonstrated a slight increase in the proportion K hits in the primed compared to the part primed condition, and a reduction in R false alarms for the part primed condition. Corrected estimates of familiarity and recollection revealed an increase in levels of familiarity for the primed compared to the part primed condition. Response time data demonstrated a graded reduction in response times for part primed and primed words compared to unprimed words, with the fastest responses in the primed condition, but did not reveal differences in the magnitude of facilitation effects across hits and correct rejections.

8.4 ERP results

To examine priming and memory effects, grand average ERPs were formed for hits and correct rejections in the unprimed, part primed and primed conditions. Visual inspection of the waveforms again confirmed the presence of an early priming effect onsetting before the onset of the target words, as a result the -500-1500ms epoch, which includes the onset of the prime, was chosen to capture all effects in the current experiment. The mean number of trials contributing to waveforms for hits was 37 for the unprimed condition, 36 for the part primed condition and 39 for the primed condition. The mean number of trials contributing to waveforms for correct rejections was 54 for the unprimed and part primed conditions and 52 for the primed condition.

8.4.1 Priming contrasts

Figure 8.1 and 8.2 show grand average waveforms for hits and correct rejections in the unprimed, part primed and primed conditions. Visual inspection of the waveforms confirmed the presence of three priming related modulations for both hits and correct rejections, with differences in the pattern of effects across hits and correct rejections. For hits the data indicate the presence of an early graded negativity between -100-150ms, with part primed hits more negative going than primed hits, which were in turn more negative going than unprimed hits. This early effect was followed by a graded positivity between 250-500ms, with primed hits more positive going than part primed hits, which were in turn more positive going than unprimed hits. From around 500ms after target onset until the end of the epoch, waveforms for hits were more negative going for primed and part primed hits than for unprimed hits at posterior locations. The data for cor-

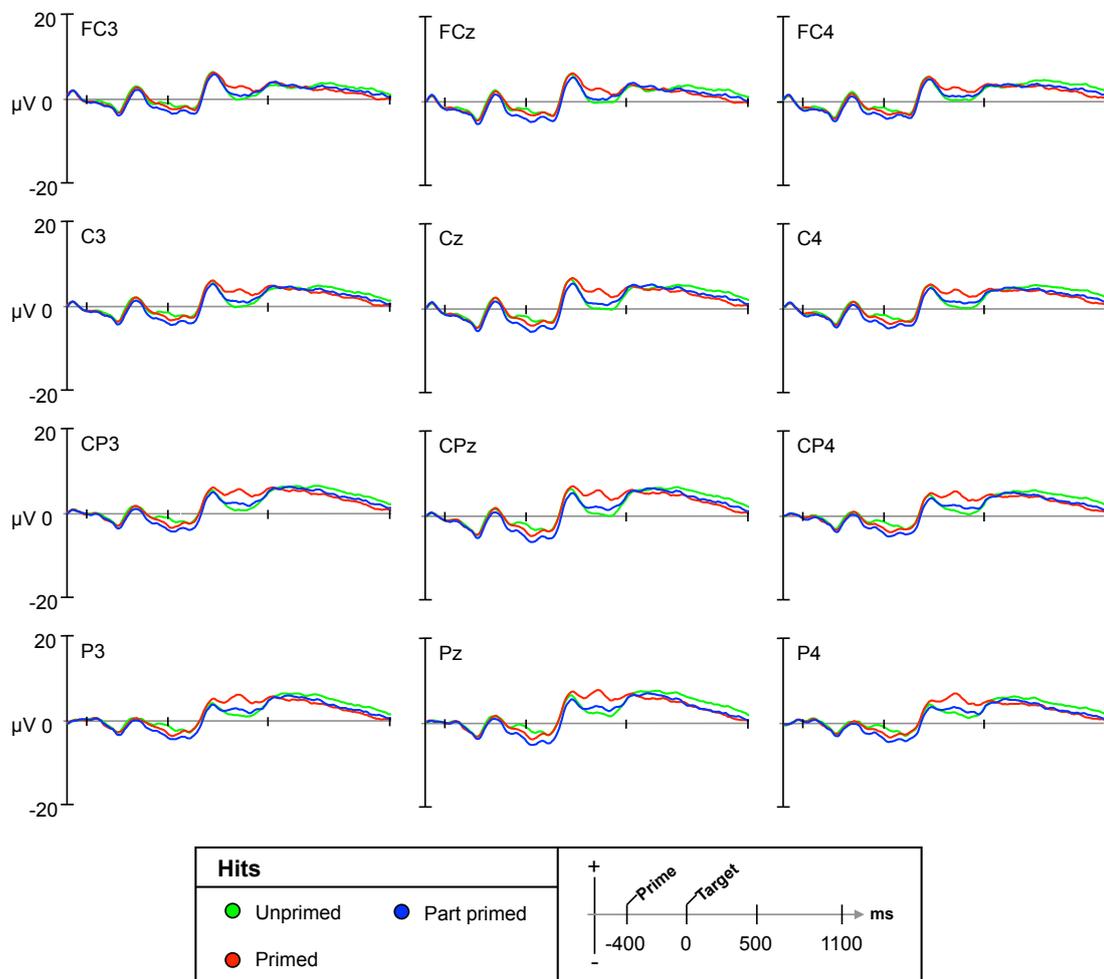


Figure 8.1: Priming effects for hits. Grand average ERPs for hits in the unprimed, part primed and primed conditions. The data demonstrated the presence of three priming related modulations: (i) an early graded posterior negativity that was most negative for the part primed condition (ii) a later graded posterior positivity between 250-500ms, with primed hits more positive going than part primed hits, which were in turn more positive going than unprimed hits (iii) and a late negativity at posterior locations between 500-1100ms for primed and part primed hits compared to unprimed hits.

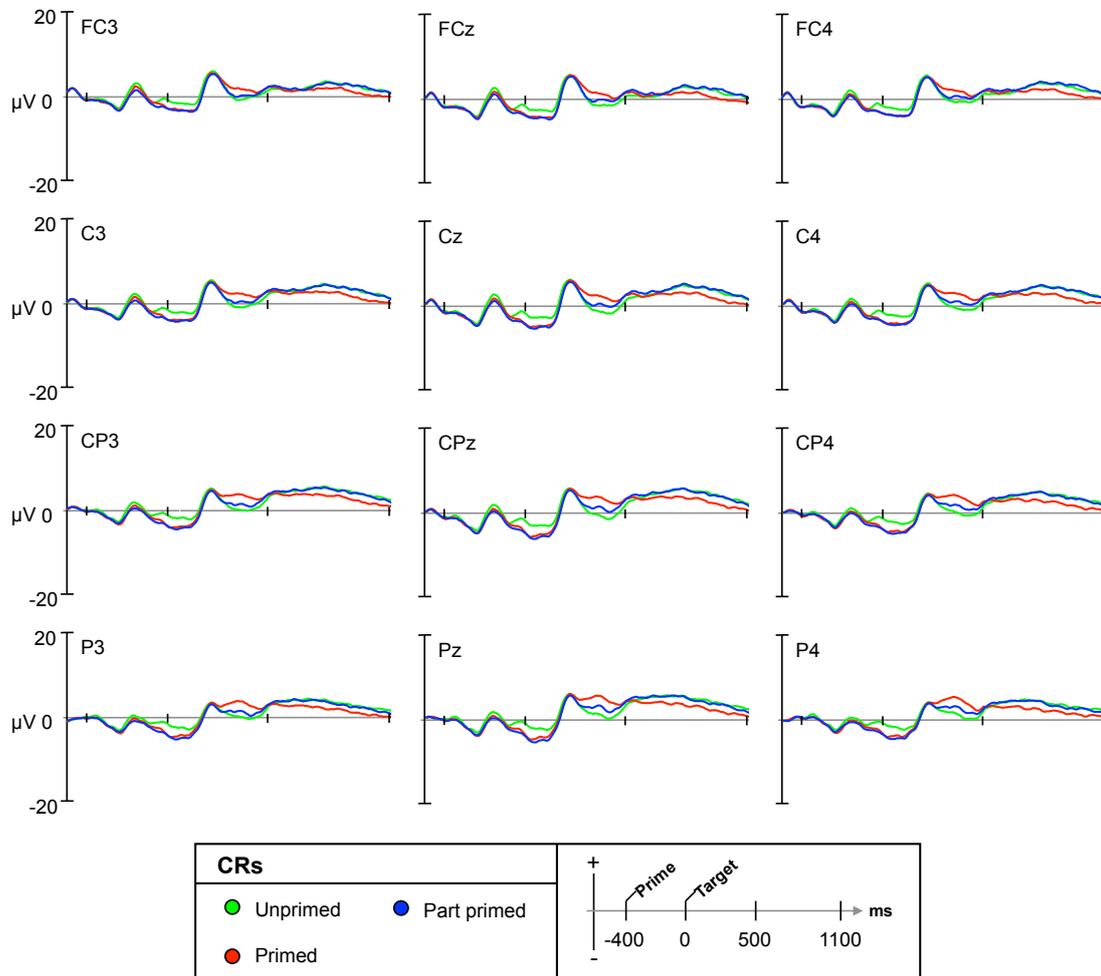


Figure 8.2: Priming effects for CRs. Grand average ERPs for correct rejections in the unprimed, part primed and primed conditions. The data demonstrated the presence of three priming related modulations: (i) an early posterior negativity that was equally more negative going for the primed and part primed conditions (ii) a later graded posterior positivity between 250-500ms, with primed hits more positive going than part primed hits, which were in turn more positive going than unprimed hits (iii) and a late negativity at posterior locations between 500-1100ms for primed correct rejections compared to part primed and unprimed correct rejections.

rect rejections demonstrated the presence of the same graded posterior positivity between 250-500ms, but differs from the data for hits in pattern of effects in the part primed condition for the early and late negativities. In contrast to the graded effect evident in the data for hits, in the early time window, waveforms for primed and part primed correct rejections were equally more negative going than waveforms for unprimed correct rejections. In contrast to more negative going activity for primed and part primed hits than for unprimed hits at posterior locations for hits, the data for correct rejections indicate more negative going activity for primed compared to part primed and unprimed correct rejections.

Visual inspection of the data suggested that the early negativity in the current experiment onset slightly earlier than in the previous experiments. As a result the standard time window was altered to capture this difference, and the time windows chosen for analysis of priming effects were -100-150ms, 250-500ms and 500-1100ms, maintaining consistency across experiments for the later windows. To separate priming contrasts from memory contrasts the data for hits and correct rejections were analysed independently. The first level of analysis on the data was designed to identify variations in priming effects across conditions and time windows, employing ANOVA with the factors of condition (unprimed, part primed, primed), location (Fz, FCz, Cz, CPz, Pz, POz) and time window (-100-150, 250-500, 500-800). Results for hits revealed a significant main effect of condition [$F(2,58)=6.75$, $p=0.002$], along with a significant interaction between condition, location and time window [$F(3.8,110.1)=14.09$, $p<0.001$]. Analysis for correct rejections also revealed a significant interaction between condition, location and time window [$F(4.4,127.8)=16.13$, $p<0.001$]. The presence of these interactions provides strong evidence of variation in the pattern of priming effects across locations and time windows for hits and correct rejections.

Table 8.5: Priming ANOVAs by time window. Results of ANOVAs contrasting midline sites with the factors of condition and location over the three time windows chosen for analysis of priming effects.

		-100-150ms	250-500ms	500-1100ms
Hits	Cond	$F(2,58)=15.67, p<0.001$	$F(2,58)=38.56, p<0.001$	$F(2,58)=4.70, p=0.013$
	Cond*Loc	$F(2.8,80.1)=3.02, p=0.038$	$F(2.7,77.5)=11.26, p<0.001$	-
CRs	Cond	$F(2,58)=27.71, p<0.001$	$F(2,58)=29.61, p<0.001$	$F(2,58)=9.53, p<0.001$
	Cond*Loc	$F(2.4,70.2)=4.46, p=0.010$	$F(2.7,78.6)=7.46, p<0.001$	$F(2.8,80.4)=3.25, p=0.029$

A second level of analysis was performed separately for hits and correct rejections on the data from each time window, using ANOVA with the factors of condition (unprimed, part primed, primed) and location (Fz, FCz, Cz, CPz, Pz, POz). The results of this analysis are summarised in Table 8.5, and confirm that priming effects were present in each time window for hits and correct rejections, interacting with the factor of location for all contrasts except for hits during the 500-1100ms time window. Subsidiary analysis took the form of paired contrasts between each condition performed separately for hits and correct rejections, using ANOVA with the factors of contrast (unprimed vs primed / unprimed vs part primed / primed vs part primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior), and the results for each time window and contrast are reported separately in the following sections.

8.4.1.1 Time window -100-150ms

From 100ms prior to the onset of target words, waveforms for primed and part primed hits were more negative going than waveforms for unprimed hits at posterior locations, with the greatest degree of negativity for part primed hits (see Figure 8.3 for data from CPz). Initial analysis contrasting unprimed and primed hits produced no main effects or interactions including the factor of condition,

demonstrating that the effect apparent in the data did not reach significance. Contrasting unprimed and part primed hits revealed a significant main effect of condition [$F(1,29)=20.22$, $p<0.001$], and a significant interaction between condition, location and electrode [$F(2.9,85.2)=4.00$, $p=0.011$]. As can be seen in Figure 8.3, these results reflect the presence of a negativity for part primed hits over superior sites at posterior locations. Comparison of primed and part primed hits also produced a main effect of condition [$F(1,29)=14.51$, $p=0.001$], and a significant interaction between condition, location and electrode [$F(3.4,98.6)=2.96$, $p=0.030$]. As can be seen in Figure 8.3, these results again reflect that part primed hits were more negative going than primed hits over superior sites extending from fronto-central to parietal locations.

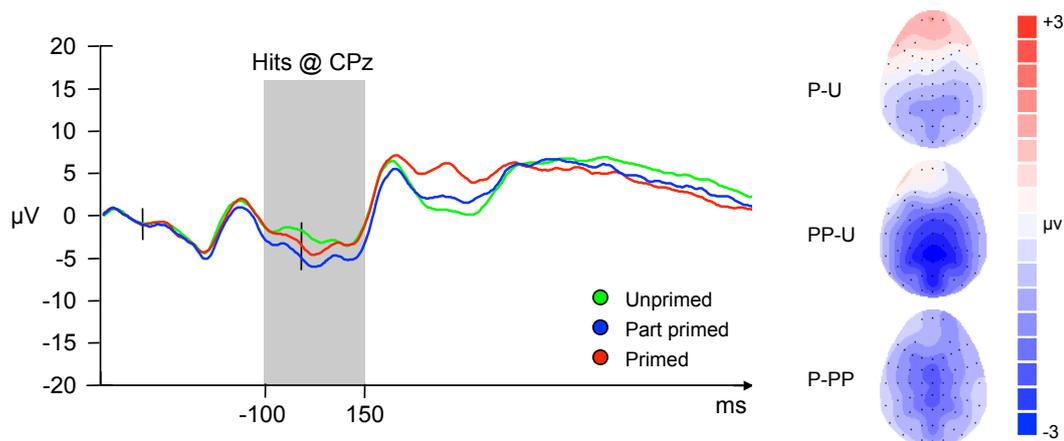


Figure 8.3: Priming for hits (-100-150ms). Grand average ERPs for hits in the unprimed, part primed and primed conditions at electrode CPz. Topographic maps show the difference between conditions for paired contrasts. Waveforms for primed and part primed hits were more negative going than waveforms for unprimed hits at posterior locations, with the greatest degree of negativity for part primed hits.

Table 8.6 shows the results of subsidiary analysis at separate locations for the significant contrasts reported above for hits. Results revealed significant main effects of condition and significant interactions between condition and electrode extending from frontal to parieto-occipital locations for both contrasts, indicating

Table 8.6: Priming contrasts by location (-100-150ms). Results of subsidiary analysis at separate locations for contrasts producing significant priming effects, shown separately for hits and correct rejections.

Hits (PP/U)	F	FC	C	CP	P	PO
Cond	$F(1,29)=6.84, p=0.014$	$F(1,29)=12.66, p=0.001$	$F(1,29)=20.74, p<0.001$	$F(1,29)=24.85, p<0.001$	$F(1,29)=27.90, p<0.001$	$F(1,29)=17.13, p<0.001$
Cond*Hem						
Cond*Elec	$F(1.2,36.3)=12.18, p=0.001$	$F(1.2,34.8)=17.28, p<0.001$	$F(1.1,32.8)=18.24, p<0.001$	$F(1.2,33.4)=26.85, p<0.001$	$F(1.1,30.9)=32.39, p<0.001$	$F(1.2,35.9)=32.95, p<0.001$
Cond*Hem*Elec						
Hits (P/PP)	F	FC	C	CP	P	PO
Cond	$F(1,29)=7.79, p=0.009$	$F(1,29)=10.52, p=0.003$	$F(1,29)=13.64, p=0.001$	$F(1,29)=14.60, p=0.001$	$F(1,29)=15.66, p<0.001$	$F(1,29)=10.62, p=0.003$
Cond*Hem						
Cond*Elec	$F(1.1,32.6)=4.58, p=0.036$	$F(1.1,31.7)=8.22, p=0.006$	$F(1.1,32.9)=13.52, p=0.001$	$F(1.2,34.4)=22.72, p<0.001$	$F(1.12,33.9)=31.20, p<0.001$	$F(1.2,35.3)=15.62, p<0.001$
Cond*Hem*Elec						

the presence of priming effects for hits that were maximal towards superior sites across locations. The preceding analysis failed to elucidate the interaction with location reported for hits in the first level of analysis; to better characterize the location of effects, activity from midline sites (Fz, Cz, Pz) was compared for each significant contrast using paired samples t-tests. Results of analysis contrasting part primed and unprimed hits demonstrated the presence of larger effects over central ($t(29)=3.36$, $p=0.002$), and parietal sites ($t(29)=3.15$, $p=0.004$) than at frontal sites. Consistent with this pattern of results, further examination of the data confirmed that the difference between part primed and unprimed hits was maximal at electrode CPz ($t(29)=5.56$, $p<0.001$). Analysis contrasting priming effects at midline sites for primed and part primed hits failed to reveal significant differences across locations, confirming the presence of a negativity for part primed hits extending from frontal to parietal locations. Further examination of the data confirmed that the difference between primed and part primed hits was maximal at electrode FCz ($t(29)=3.85$, $p=0.001$).

The foregoing results suggest variation in the magnitude of effects across contrasts, with larger effects over posterior locations for part primed compared to unprimed hits, and effects with a more anterior distribution for part primed compared to primed hits. The next level of analysis was performed on difference waveforms to compare the magnitude of priming effects, using ANOVA with the factors of contrast (part primed-unprimed, primed-part primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Analysis revealed a significant main effect of contrast [$F(1,29)=24.54$, $p<0.001$], and a significant interaction between contrast, location and electrode [$F(3.5,100.6)=4.90$, $p=0.002$], reflecting larger effects over posterior locations across medial and inferior sites for part primed compared to unprimed hits than

for part primed compared to primed hits. To investigate whether these differences in magnitude reflect genuine changes in topography, analysis was performed on rescaled data, using ANOVA with the factors of contrast (part primed-unprimed, primed-part primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Analysis also revealed a significant interaction between contrast, location and electrode [$F(3.6, 103.3)=4.71, p=0.002$], demonstrating that effects were driven by partially non-overlapping sets of neural generators.

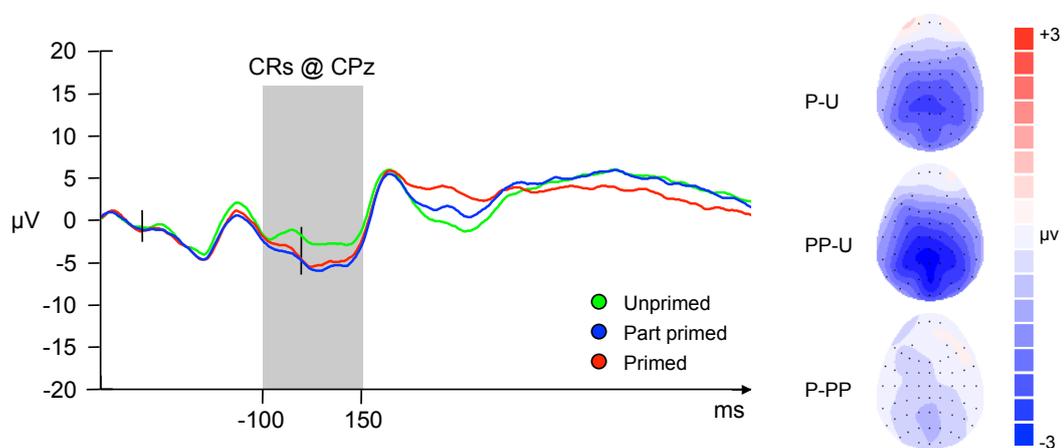


Figure 8.4: Priming for CRs (-100-150ms). Grand average ERPs for correct rejections in the unprimed, part primed and primed conditions at electrode CPz. Topographic maps show the difference between conditions for paired contrasts. Waveforms for primed and part primed words were more negative going than waveforms for unprimed words at posterior locations, with no apparent differences between the primed and part primed conditions.

For correct rejections, waveforms for primed and part primed words were more negative going than waveforms for unprimed words at posterior locations, with no apparent differences between the primed and part primed conditions (see Figure 8.4 for the data from CPz). Initial analysis contrasting unprimed and primed correct rejections produced a significant main effect of condition [$F(1,29)=33.36, p<0.001$], and significant interactions between condition and location [$F(1.4,41.7)=5.47, p=0.014$], and condition and electrode [$F(1.1,31.3)=14.89, p<0.001$]. As

can be seen in Figure 8.4, these results reflect the presence of a negativity for primed words towards superior sites over central and parietal locations. Analysis comparing unprimed and part primed correct rejections revealed a main effect of condition [$F(1,29)=42.85$, $p<0.001$], and a significant interaction between condition, location and electrode [$F(2.6,74.1)=3.28$, $p=0.032$], reflecting the presence of a negativity for part primed words at superior sites over central and posterior locations. Finally, analysis contrasting primed and part primed correct rejections confirmed the absence of priming difference, producing no main effects or interactions including the factor of condition.

Table 8.6 shows the results of subsidiary analysis at separate locations for primed and part primed compared to unprimed correct rejections. Results for primed correct rejections revealed significant main effects of condition across locations, and interactions between condition and electrode extending from frontal-central to parieto-occipital locations. Results for part primed correct rejections revealed significant main effects and interactions between condition and electrode across locations. The preceding analysis again failed to elucidate the interaction with location reported in the first level of analysis. Analysis contrasting priming effects at midline sites (Fz, Cz, Pz) for primed correct rejections demonstrated the presence of larger differences over central ($t(29)=3.17$, $p=0.004$), and parietal locations ($t(29)=2.92$, $p=0.007$), than at frontal locations. Consistent with this pattern of results, further examination of the data confirmed that the difference between primed and unprimed correct rejections was maximal at electrode CPz ($t(29)=6.12$, $p<0.001$). Analysis contrasting priming effects at midline sites for part primed correct rejections again revealed larger effects over central ($t(29)=3.07$, $p=0.005$), and parietal locations ($t(29)=2.27$, $p=0.031$), than at frontal locations. Further examination of the data confirmed that the difference

Table 8.7: Priming contrasts by location (-100-150ms). Results of subsidiary analysis at separate locations for contrasts producing significant priming effects, shown separately for hits and correct rejections.

CRs (P/U)	F	FC	C	CP	P	PO
Cond	$F(1,29)=11.56, p=0.002$	$F(1,29)=23.72, p<0.001$	$F(1,29)=31.99, p<0.001$	$F(1,29)=35.15, p<0.001$	$F(1,29)=35.66, p<0.001$	$F(1,29)=28.68, p<0.001$
Cond*Hem						
Cond*Elec		$F(1.2,34.1)=6.01, p=0.016$	$F(1.1,32.9)=12.39, p=0.001$	$F(1.2,34.5)=15.09, p<0.001$	$F(1.2,35.5)=13.96, p<0.001$	$F(1.1,30.72)=20.24, p<0.001$
Cond*Hem*Elec						
CRs (PP/U)	F	FC	C	CP	P	PO
Cond	$F(1,29)=15.33, p=0.001$	$F(1,29)=27.39, p<0.001$	$F(1,29)=39.82, p<0.001$	$F(1,29)=45.32, p<0.001$	$F(1,29)=48.13, p<0.001$	$F(1,29)=45.45, p<0.001$
Cond*Hem						
Cond*Elec	$F(1.2,34.9)=8.49, p=0.004$	$F(1.3,37.7)=14.73, p<0.001$	$F(1.3,36.6)=27.64, p<0.001$	$F(1.2,34.4)=26.14, p<0.001$	$F(1.2,33.5)=23.74, p<0.001$	$F(1.1,32.2)=35.47, p<0.001$
Cond*Hem*Elec						

between part primed and unprimed correct rejections was also maximal at electrode CPz ($t(29)=6.90$, $p<0.001$).

Figure 8.5 shows a summary of the data for the -100-150ms time window at a representative electrode site, along with topographic maps of significant contrasts for hits and correct rejections. The next level of analysis was designed to compare the magnitude of effects for part primed compared to unprimed words for hits and correct rejections, as this contrast was significant in both cases. Analysis was performed on difference waveforms, using ANOVA with the factors of test status (old, new), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed no main effect or interactions including the factor of test status, indicating that effects did not differ in magnitude or distribution for hits and correct rejections.

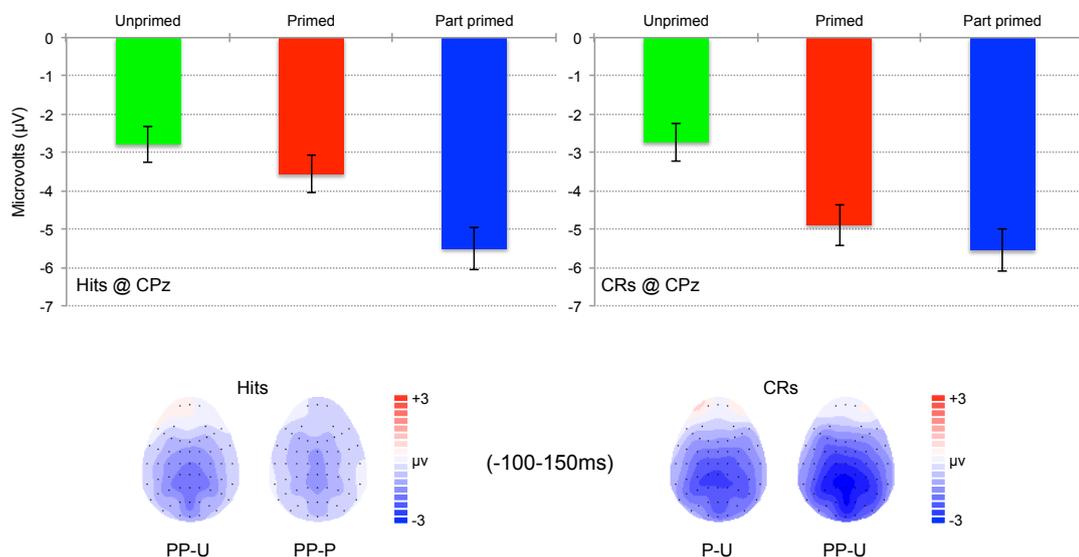


Figure 8.5: Summary data (-100-150ms). Bar charts display the amplitude of activity for hits and correct rejections in the unprimed, part primed and primed conditions at a representative electrode (error bars show S.E.M). Topographic maps show the distribution of priming effects for significant contrasts.

In summary, analysis of the priming data during this early time window revealed a different pattern of results for primed hits and correct rejections. In the data for hits, primed words did not differ from unprimed words, while in the data for correct rejections both priming conditions were equally more negative going at superior centro-parietal locations than waveforms for the unprimed condition. Magnitude analysis contrasting effects for part primed compared to unprimed hits and correct rejections confirmed the presence of a centro-parietal negativity that was equivalent in magnitude and distribution.

8.4.1.2 Time window 250-500ms

From 250ms after onset of target words, waveforms for primed hits were more positive going than for part primed hits, which were in turn more positive going than waveforms for unprimed hits, with the largest differences between conditions evident at posterior locations (see Figure 8.6 for the data from CPz). Initial analysis contrasting unprimed and primed hits revealed a significant main effect of condition [$F(1,29)=69.00$, $p<0.001$], along with significant interactions between condition, location and electrode [$F(2.5,72.7)=5.49$, $p=0.003$], and condition, hemisphere and electrode [$F(1.4,40.7)=8.45$, $p=0.003$]. Results of subsidiary analysis at separate locations are shown in Table 8.8, and confirmed the presence of interactions between condition, hemisphere and electrode extending from frontal to parietal locations, and interactions between condition and electrode extending from fronto-central to parieto-occipital sites. As can be seen in Figure 8.6, these results reflect the presence of a widespread positivity for primed hits compared to unprimed hits that is maximal over superior sites, but with a slight skew over the right hemisphere. Consistent with this pattern of results,

further examination of the data confirmed that the difference between primed and unprimed hits was maximal at electrode CPz ($t(29)=8.42$, $p<0.001$).

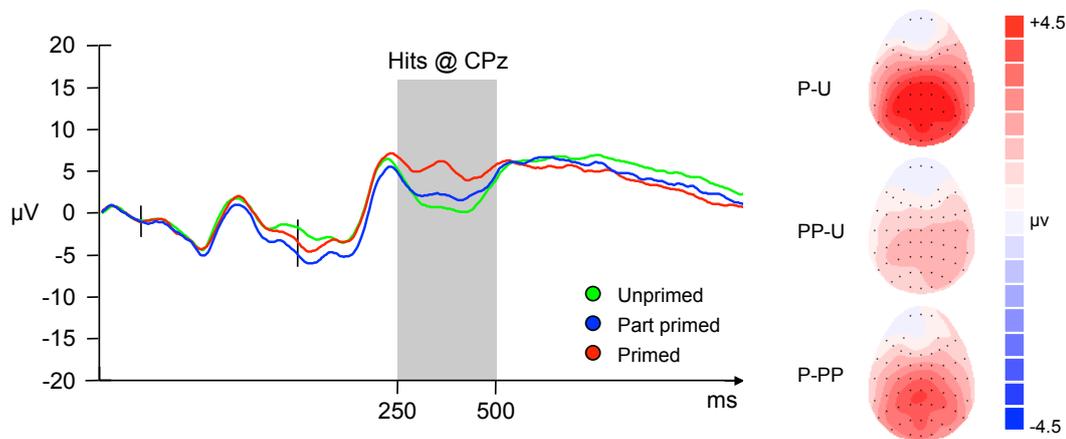


Figure 8.6: Priming for hits (250-500ms). Grand average ERPs for hits in the unprimed, part primed and primed conditions at electrode CPz. Topographic maps show the difference between conditions for paired contrasts. Waveforms for primed hits were more positive going than for part primed hits, which were in turn more positive going than waveforms for unprimed hits, with the largest differences between conditions evident over posterior locations.

Initial analysis contrasting unprimed and part primed hits produced a significant main effect of condition [$F(1,29)=12.30$, $p=0.001$], but no significant interactions including the factor of condition, reflecting the presence of a slight but widespread positivity for hits across locations. Analysis comparing primed and part primed hits revealed a significant main effect of condition [$F(1,29)=30.63$, $p<0.001$], and a significant interaction between condition, location and electrode [$F(2.7,76.8)=4.23$, $p=0.011$]. Results of subsidiary analysis at separate locations are shown in Table 8.8, and demonstrated the presence of main effects and interactions between condition and electrode extending from fronto-central to parieto-occipital locations. As can be seen in Figure 8.6, these results reflect the presence of a positivity for primed hits compared to part primed hits over superior electrode sites at posterior locations. Further examination of the data confirmed that

the difference between primed and part primed hits was maximal at electrode CPz ($t(29)=6.19$, $p<0.001$).

Inspection of the data for hits suggests variation in the magnitude of effects across contrasts, with the largest difference between primed and unprimed hits. To investigate this, the next level of analysis was performed on difference waveforms, using ANOVA with the factors of contrast (primed-unprimed, part primed-unprimed, primed-part primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Analysis revealed a significant main effect of contrast [$F(2,58)=11.93$, $p<0.001$], and significant interactions between condition and location [$F(1.8,50.8)=3.42$, $p=0.046$], and condition and electrode [$F(1.3,37.3)=6.45$, $p=0.010$], confirming the presence of differences in magnitude across contrasts. To characterize this difference paired contrasts were performed on subtraction data for each effect. Analysis comparing the size of the difference between primed and part primed words and the unprimed baseline revealed a significant main effect of contrast [$F(1,29)=30.63$, $p<0.001$], and a significant interaction between contrast, location and electrode [$F(2.7,76.8)=4.23$, $p=0.011$], reflecting larger differences for primed compared to part primed hits over posterior locations at superior electrode sites.

Analysis of effects for primed compared to unprimed, and primed compared to part primed hits revealed a significant main effect of contrast [$F(1,29)=12.30$, $p<0.001$], but no interactions including the factor of contrast, confirming the presence of a larger difference between primed and unprimed hits than between primed and part primed hits. Analysis of effects for part primed compared to unprimed, and part primed compared to primed hits revealed a marginally significant interaction between condition and electrode [$F(1.1,31.2)=4.07$, $p=0.050$], suggesting a difference in the distribution of effects. To investigate whether these

Table 8.8: Priming contrasts for Hits by location (250-500ms). Results of subsidiary analysis for hits at separate locations for all contrasts producing significant priming effects, shown separately for each contrast.

Hits (P/U)	F	FC	C	CP	P	PO
Cond	$F(1,29)=10.69, p=0.003$	$F(1,29)=33.13, p<0.001$	$F(1,29)=58.77, p<0.001$	$F(1,29)=69.20, p<0.001$	$F(1,29)=74.23, p<0.001$	$F(1,29)=81.00, p<0.001$
Cond*Hem						
Cond*Elec		$F(1.3,36.4)=13.89, p<0.001$	$F(1.2,34.2)=24.58, p<0.001$	$F(1.1,31.89)=25.69, p<0.001$	$F(1.1,30.9)=17.10, p<0.001$	$F(1.2,35.6)=23.65, p<0.001$
Cond*Hem*Elec	$F(1.5,43.4)=5.23, p=0.016$	$F(2,58)=4.37, p=0.017$	$F(1.6,47)=4.73, p=0.019$	$F(1.4,41.4)=5.86, p=0.011$	$F(1.2,35.4)=5.10, p=0.024$	
Hits (P/PP)	F	FC	C	CP	P	PO
Cond		$F(1,29)=11.37, p=0.002$	$F(1,29)=24.29, p<0.001$	$F(1,29)=37.48, p<0.001$	$F(1,29)=44.09, p<0.001$	$F(1,29)=44.50, p<0.001$
Cond*Hem						
Cond*Elec		$F(1.1,33.2)=7.84, p=0.007$	$F(1.1,31.6)=16.32, p<0.001$	$F(1,30.4)=16.73, p<0.001$	$F(1.1,30.8)=12.62, p=0.001$	$F(1.3,37.3)=10.15, p=0.001$
Cond*Hem*Elec						

differences in magnitude identified above reflect genuine changes in topography, analysis was performed on rescaled data using ANOVA with the factors of contrast (primed-unprimed, part primed-unprimed, primed-part primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed no main effects or interactions including the factor of contrast, suggesting that priming effects for all three contrasts for hits were supported by the same sets of underlying neural generators.

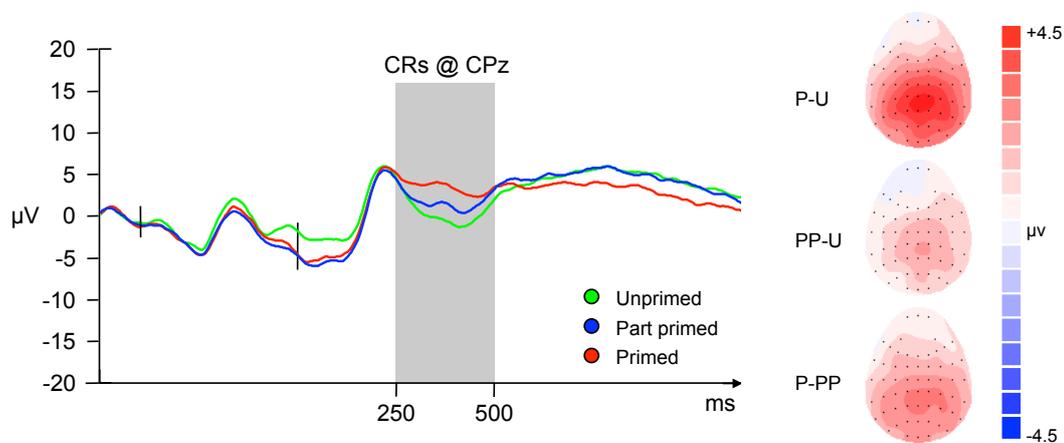


Figure 8.7: Priming for CRs (250-500ms). Grand average ERPs for correct rejections in the unprimed, part primed and primed conditions at electrode CPz. Topographic maps show the difference between conditions for paired contrasts. Waveforms for primed correct rejections were more positive going than for part primed correct rejections, which were in turn more positive going than waveforms for unprimed correct rejections, with the largest differences between conditions evident over posterior locations.

For correct rejections, the pattern of effects at posterior locations appeared identical to the pattern for hits, waveforms for primed words were more positive going than for part primed words, which were in turn more positive going than waveforms for unprimed words (see Figure 8.7 for the data from CPz). Initial analysis contrasting unprimed and primed correct rejections revealed a main effect of condition [$F(1,29)=38.03$, $p<0.001$], along with a significant interaction between condition, hemisphere and electrode [$F(1.1,30.9)=7.66$, $p=0.008$], and

a marginally significant interaction between condition, location and electrode [$F(2.8,81.5)=2.75$, $p=0.051$]. Results of subsidiary analysis at separate locations are shown in Table 8.8, and confirmed the presence of interactions between condition and electrode across locations, and significant interactions including the factor of hemisphere extending from frontal to parietal locations. As can be seen in Figure 8.7, these results reflect the presence of a posterior positivity for primed correct rejections over superior sites, that is slightly skewed over the right hemisphere at the locations identified. Further examination of the data confirmed that the difference between primed and unprimed correct rejections was maximal at electrode Pz ($t(29)=7.78$, $p<0.001$).

Analysis comparing unprimed and part primed correct rejections produced a significant main effect of condition [$F(1,29)=7.92$, $p=0.009$], along with a significant interaction between condition, location and electrode [$F(2.8,80.3)=3.18$, $p=0.032$], and a marginally significant interaction between condition and hemisphere [$F(1,29)=4.16$, $p=0.051$]. Subsidiary analysis at separate locations revealed main effects of condition from central to parieto-occipital locations, interactions including the factor of electrode across locations, and interactions including the factor of hemisphere at frontal and fronto-central locations (see Table 8.9 for results). As can be seen in Figure 8.7, these results reflect the presence of a posterior positivity for part primed correct rejections over superior sites, with a slight skew over the right hemisphere at frontal sites on the outskirts of the effect. Further examination of the data confirmed that difference between the part primed and unprimed correct rejections was maximal at electrode CPz ($t(29)=3.92$, $p<0.001$).

Analysis contrasting primed and part primed correct rejections revealed a main effect of condition [$F(1,29)=23.72$, $p<0.001$], along with significant interactions

Table 8.9: Priming contrasts for CRs by location (250-500ms). Results of subsidiary analysis for correct rejections at separate locations for all contrasts producing significant priming effects, shown separately for each contrast.

CRs (P/U)	F	FC	C	CP	P	PO
Cond	$F(1,29)=8.21, p=0.008$	$F(1,29)=17.44, p<0.001$	$F(1,29)=31.78, p<0.001$	$F(1,29)=43.16, p<0.001$	$F(1,29)=48.68, p<0.001$	$F(1,29)=40.16, p<0.001$
Cond*Hem	$F(1,29)=5.92, p=0.021$	$F(1,29)=9.80, p=0.004$	$F(1,29)=7.01, p=0.013$	$F(1,29)=5.52, p=0.026$	$F(1,29)=4.58, p=0.041$	
Cond*Elec	$F(1.2,33.4)=11.50, p=0.001$	$F(1.3,37)=17.29, p<0.001$	$F(1.2,34.8)=29.71, p<0.001$	$F(1.2,34.5)=33.69, p<0.001$	$F(1.1,31.6)=31.55, p<0.001$	$F(1.3,36.7)=33.16, p<0.001$
Cond*Hem*Elec	$F(1.3,38.7)=5.63, p=0.015$	$F(1.3,36.4)=5.57, p=0.018$	$F(1.2,33.9)=9.33, p=0.003$		$F(1.1,32.8)=7.64, p=0.007$	
CRs (PP/U)	F	FC	C	CP	P	PO
Cond			$F(1,29)=9.22, p=0.005$	$F(1,29)=11.33, p=0.002$	$F(1,29)=11.46, p=0.002$	$F(1,29)=6.81, p=0.014$
Cond*Hem	$F(1,29)=4.96, p=0.034$	$F(1,29)=4.59, p=0.041$				
Cond*Elec		$F(1.3,38)=5.66, p=0.015$	$F(1.2,33.5)=9.45, p=0.003$	$F(1.1,31.4)=12.34, p=0.001$	$F(1.1,31.2)=13.53, p=0.001$	$F(1.2,34.2)=11.76, p=0.001$
Cond*Hem*Elec	$F(2,58)=6.16, p=0.004$					
CRs (PP/P)	F	FC	C	CP	P	PO
Cond	$F(1,29)=4.70, p=0.038$	$F(1,29)=9.25, p=0.005$	$F(1,29)=19.67, p<0.001$	$F(1,29)=28.47, p<0.001$	$F(1,29)=30.96, p<0.001$	$F(1,29)=31.46, p<0.001$
Cond*Hem						
Cond*Elec	$F(1.3,37.2)=6.30, p=0.011$	$F(1.2,35.8)=6.81, p=0.009$	$F(1.2,33.6)=4.84, p=0.030$	$F(1.1,32)=4.45, p=0.039$	$F(1.1,32.6)=6.01, p=0.017$	$F(1.4,39.2)=10.50, p=0.001$
Cond*Hem*Elec						

between condition and location [$F(1.4,39.4)=6.74$, $p=0.008$], and condition and electrode [$F(1.1,32.3)=10.12$, $p=0.002$]. Subsidiary analysis at separate locations revealed significant main effects of condition and significant interactions between condition and electrode across locations (see Table 8.9 for results). As can be seen in Figure 8.7, these results reflect the presence of a widespread positivity for primed correct rejections over superior electrode sites that appears maximal over posterior locations. Consistent with this interpretation of results, further examination of the data confirmed that the difference between primed and part primed correct rejections was maximal at electrode Pz ($t(29)=5.46$, $p<0.001$).

Inspection of the data for correct rejections also suggests variation in the magnitude of effects across contrasts, with the largest difference between primed and unprimed correct rejections. To investigate this, the next level of analysis was performed on difference waveforms, using ANOVA with the factors of contrast (primed-unprimed, part primed-unprimed, primed-part primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Analysis revealed a significant main effect of contrast [$F(2,58)=8.25$, $p=0.001$], and a significant interaction between contrast and electrode [$F(1.4,39.6)=4.84$, $p=0.024$], confirming the presence of differences in magnitude across contrasts. To characterize this difference, paired contrasts were performed on subtraction data for each effect. Analysis comparing the size of the difference between primed and part primed words and the unprimed baseline revealed a significant main effect of contrast [$F(1,29)=23.73$, $p<0.001$], along with significant interactions between contrast and location [$F(1.4,39.4)=6.74$, $p=0.008$], and contrast and electrode [$F(1.1,32.3)=10.12$, $p=0.002$], reflecting larger differences for primed than for part primed correct rejections at superior sites over posterior locations.

Analysis of effects for primed compared to unprimed, and primed compared to part primed correct rejections revealed a significant main effect of contrast [$F(1,29)=7.92$, $p=0.009$], along with a significant interaction between contrast, location and electrode [$F(2.7,80.3)=3.18$, $p=0.001$], reflecting the presence of larger difference over posterior locations for primed vs. unprimed than for primed vs. part primed correct rejections. Analysis of effects for part primed compared to unprimed, and part primed compared to primed correct rejections revealed no significant main effect or interactions including the factor of contrast, indicating that priming effects did not differ substantially in magnitude or distribution. To investigate whether these differences in magnitude identified above reflect genuine changes in topography, analysis was performed on rescaled data using ANOVA with the factors of contrast (primed-unprimed, part primed-unprimed, primed-part primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed no main effects or interactions including the factor of contrast, suggesting that priming effects for all three contrasts for hits were supported by overlapping sets of underlying neural generators.

Figure 8.8 shows a summary of the data for the 250-500ms time window at a representative electrode site, along with topographic maps of significant priming effects for hits and correct rejections. The next level of analysis on the data was designed to compare the magnitude and distribution of effects for hits and correct rejection across all three priming contrasts. Magnitude analysis was performed separately for each contrast on difference waveforms, using ANOVA with the factors of test status (old, new), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Analysis contrasting the magnitude of effects across hits and correct rejections for primed compared to unprimed

words revealed no main effects or interactions including the factor of test status, indicating that the size of the difference between primed and unprimed words was comparable in magnitude and distribution for hits and correct rejections. Analysis contrasting the magnitude of effects across hits and correct rejections for part primed compared to unprimed words again revealed no main effects or interactions, demonstrating that effects were again comparable for hits and correct rejections.

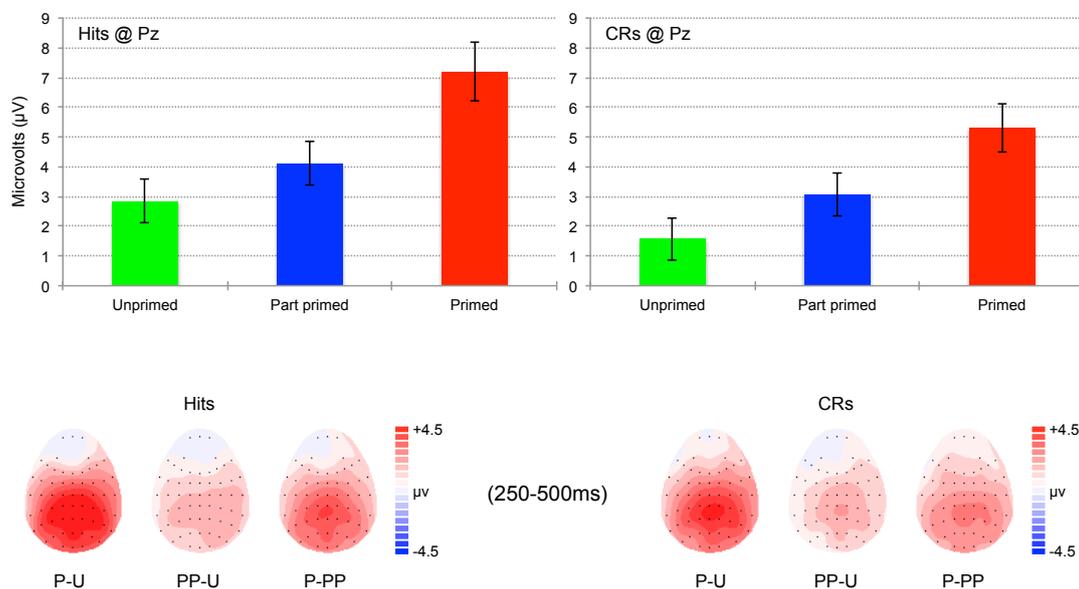


Figure 8.8: Summary data (250-500ms). Bar charts display the amplitude of activity for hits and correct rejections in the unprimed, part primed and primed conditions at a representative electrode (error bars show S.E.M). Topographic maps show the distribution of effects for significant contrasts.

Contrasting the magnitude of effects across hits and correct rejections for primed compared to part primed words did reveal a significant interaction between test status, location and electrode [$F(3.7,108)=3.17$, $p=0.019$], reflecting the presence of larger differences for hits over superior sites at posterior locations. To investigate whether this difference in magnitude reflected a genuine change in topography, analysis was performed on rescaled data using ANOVA with the fac-

tors of test status (old, new), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed no main effects or interactions including the factor of test status, indicating that effects were driven by overlapping sets of neural generators.

In summary, analysis of the priming data during the 250-500ms time window revealed a similar pattern of results for hits and correct rejections. Overall, the data demonstrated a graded priming effect for hits and correct rejections over centro-parietal locations, with primed waveforms more positive going than part primed waveforms, which were in turn were more positive going than unprimed waveforms. Magnitude comparisons for hits and correct rejections across contrasts revealed a larger difference between part primed and primed words for hits than for correct rejections, the size and distribution of all other effects were comparable for hits and correct rejections.

8.4.1.3 Time window 500 to 1100ms

From around 500ms after target onset, waveforms for primed and part primed hits appeared more negative going than waveforms for unprimed hits at posterior locations (see Figure 8.9 for data from POz). Initial analysis contrasting unprimed and primed hits revealed a significant main effect of condition [$F(1,29)=8.78$, $p=0.006$], and a significant interaction between condition and electrode [$F(1.1,31.2)=6.79$, $p=0.012$], reflecting the presence of a negativity for primed hits towards superior sites across locations. Inspection of the data suggests that this difference is largest over posterior sites and further examination of the data confirmed that the difference between primed and unprimed hits was maximal at electrode Pz ($t(29)=3.28$, $p=0.003$). Initial analysis contrasting part

primed and unprimed hits revealed a marginally significant main effect of condition [$F(1,29)=3.97$, $p=0.056$], and a significant interaction between condition and electrode [$F(1.1,31.3)=4.41$, $p=0.041$], reflecting the presence of a slight negativity for hits over superior sites across locations. Inspection of the data again suggested that effects had a posterior focus, and consistent with this interpretation of the data, further examination confirmed that the difference between part primed and unprimed hits was also maximal at electrode Pz ($t(29)=2.88$, $p=0.007$). Initial analysis contrasting primed and part primed confirmed the absence of differences between conditions, revealing no significant main effect or interactions with the factor of condition.

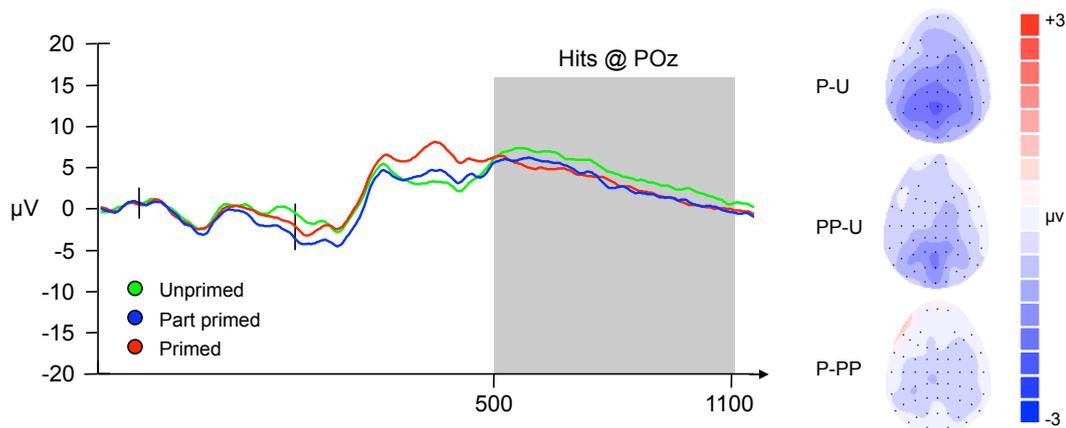


Figure 8.9: Priming for hits (500-1100ms). Grand average ERPs for hits in the unprimed, part primed and primed conditions at electrode POz. Topographic maps show the difference between conditions for paired contrasts. Waveforms for primed and part primed hits were more negative going than waveforms for unprimed hits at posterior locations.

Inspection of the data for hits suggests a slight variation in the magnitude of the differences identified for primed and part primed hits compared to the unprimed baseline, with the largest difference between primed and unprimed hits. To investigate the next level of analysis was performed on difference waveforms, using ANOVA with the factors of contrast (primed-unprimed, part primed-unprimed),

location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed no main effect or interactions including the factor of contrast, indicating that effects for the primed and part primed conditions did not differ in magnitude or distribution between 500-1100ms, with waveforms for both conditions equally more negative going than waveforms in the unprimed condition at posterior locations.

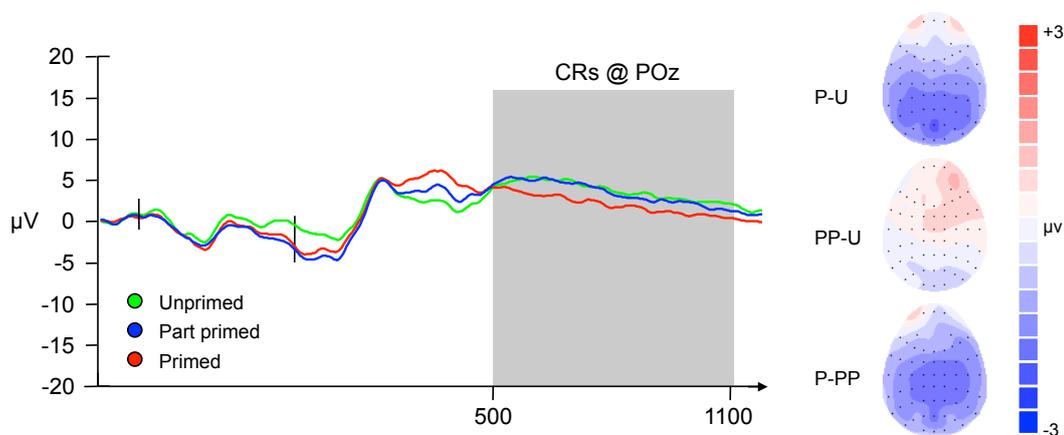


Figure 8.10: Priming for CRs (500-1100ms). Grand average ERPs for correct rejections in the unprimed, part primed and primed conditions at electrode POz. Topographic maps show the difference between conditions for paired contrasts. Waveforms for primed correct rejections were more negative going than waveforms for part primed and unprimed correct rejections over central and posterior locations.

The data for correct rejections displayed a different pattern of results during the 500-1100ms time window, with waveforms for primed correct rejections more negative going than waveforms for part primed and unprimed correct rejections over posterior locations (see Figure 8.10 for data from POz). Initial analysis contrasting primed and unprimed correct rejections revealed a significant main effect of condition [$F(1,29)=15.01$, $p=0.001$], and a significant interaction between condition and location [$F(1.4,39.4)=5.05$, $p=0.021$]. Subsidiary analysis at separate locations revealed a significant main effect of condition extending from fronto-central to parieto-occipital locations ($p<0.05$ in all cases), reflecting

the presence of a negativity for primed correct rejections across these locations. Inspection of the data suggests that this difference has a focus over posterior sites; subsidiary analysis contrasting activity at midline sites (Fz, Pz) confirmed this interpretation of the data, demonstrating the presence of larger effects at parietal sites than at frontal sites ($t(29)=2.22$, $p=0.035$). Consistent with this pattern of results, further examination of the data confirmed that the difference between primed and unprimed correct rejections was maximal at electrode POz ($t(29)=5.54$, $p<0.001$).

Initial analysis comparing unprimed and part primed correct rejections revealed an interaction between condition and location [$F(1.3,37.1)=4.08$, $p=0.041$]. Subsidiary analysis at separate locations failed to reveal significant main effects or interactions including the factor of condition, indicating the absence of substantial differences between part primed and unprimed correct rejections during the 500-1100ms time window. Initial analysis contrasting primed and part primed correct rejections revealed a significant main effect of condition [$F(1,29)=13.87$, $p=0.001$], but no interactions including the factor of condition, reflecting the presence of a widespread centrally distributed negativity for primed correct rejections across sites and locations. Consistent with this interpretation of the results, further examination of the data confirmed that the difference between primed and part primed correct rejections was maximal at electrode C2 ($t(29)=4.00$, $p<0.001$).

Inspection of the data for correct rejections suggests variation in the magnitude of differences identified for primed correct rejections when contrasted with part primed and unprimed correct rejections. To investigate the potential differences in magnitude that may indicate differences in distribution, the next level of analysis was performed on difference waveforms, using ANOVA with the factors of

contrast (primed-unprimed, primed-part primed), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed a significant main effect of contrast [$F(1,29)=7.92$, $p=0.009$], and a significant interaction between contrast, location and electrode [$F(2.8,80.3)=3.18$, $p=0.032$]. As can be seen in Figure 8.10, these results reflect the presence of larger differences for primed compared to part primed correct rejections over frontal and central locations. To establish whether this difference in magnitude reflected a genuine change in topography, analysis was performed on rescaled data using ANOVA with the factors of test status (old, new), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed no main effects or interactions including the factor of test status, indicating that effects in both cases were driven by overlapping sets of underlying neural generators.

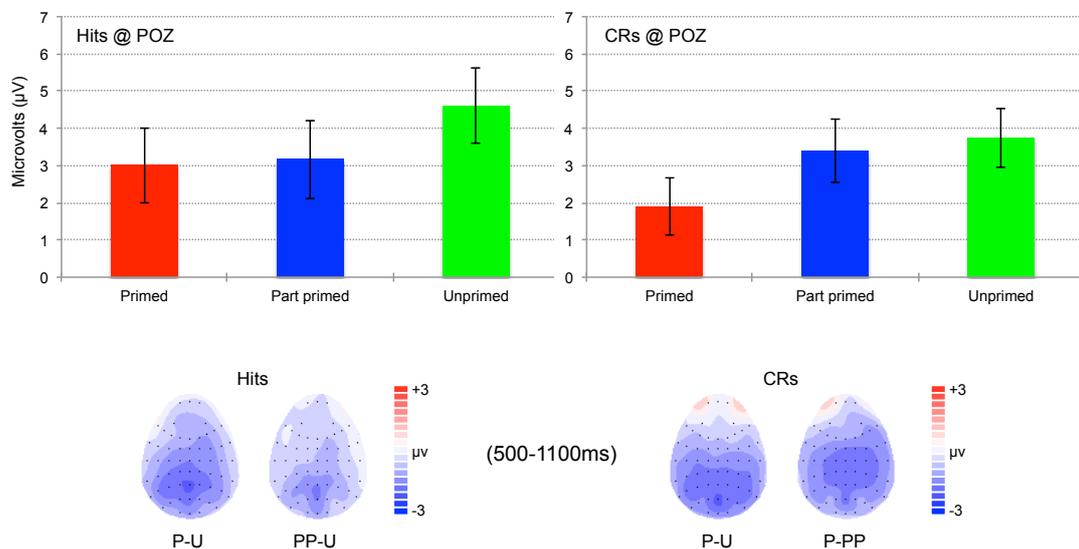


Figure 8.11: Summary data (500-1100ms). Bar charts display the amplitude of activity for hits and correct rejections in the unprimed, part primed and primed conditions at a representative electrode (error bars show S.E.M). Scalp maps show the distribution of effects for significant contrasts.

Figure 8.11 shows a summary of the data for the 500-1100ms time window at a representative electrode site, along with topographic maps of significant priming effects for hits and correct rejections. The next level of analysis on the data was designed to compare the magnitude and distribution of effects for primed compared to unprimed hits and correct rejections, as this contrast was significant in both cases. Analysis was performed on difference waveforms, using ANOVA with the factors of test status (old, new), location (F, FC, C, CP, P, PO), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed no main effect or interactions including the factor of test status, indicating that effects for the primed vs. unprimed contrast did not differ in magnitude or distribution across hits and correct rejections.

In summary, analysis of the priming data during the 500-1100ms time window revealed a different pattern of effects for hits and correct rejections at posterior locations. For hits primed words were more negative going than unprimed words, with no difference evident between primed and part primed words. By contrast, for correct rejections waveforms for primed words were more negative going than waveforms for part primed and unprimed words.

8.4.2 Summary

Between -100-150ms analysis of the data revealed a different pattern of results for primed hits and correct rejections. In the data for hits, primed words did not differ from unprimed words, while in the data for correct rejections both priming conditions were equally more negative going at superior centro-parietal locations than waveforms for the unprimed condition. Between 250-500ms, analysis of the data revealed a similar pattern of results for hits and correct rejections. Overall,

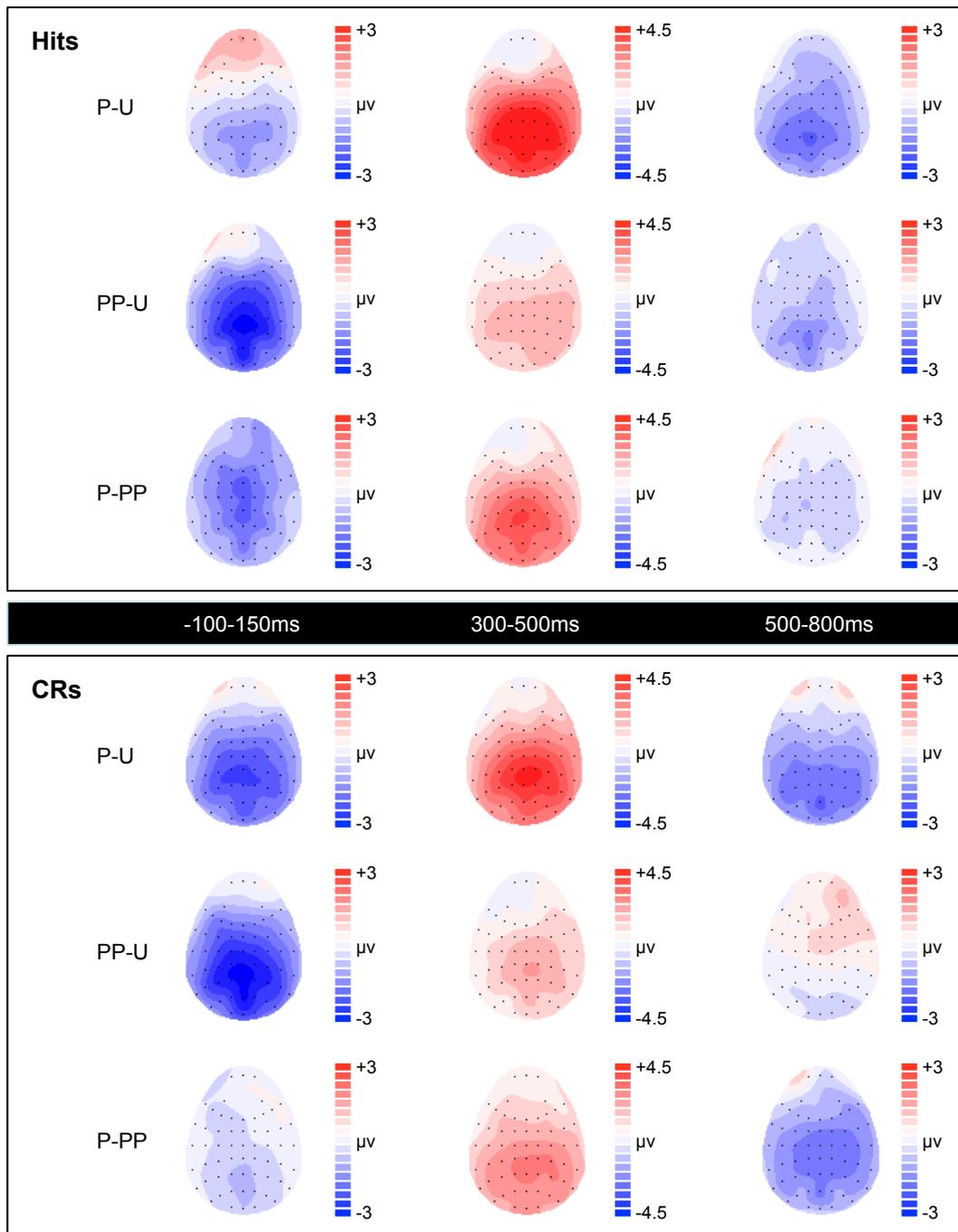


Figure 8.12: Priming topographic summary. Topographic maps summarise differences between hits and correct rejections for the unprimed part primed and primed conditions.

the data demonstrated a graded priming effect for hits and correct rejections over centro-parietal locations, with primed waveforms more positive going than part primed waveforms, which were in turn more positive going than unprimed waveforms. Magnitude comparisons for hits and correct rejections across contrasts revealed a larger difference between part primed and primed words for hits than for correct rejections, the size and distribution of all other effects were comparable for hits and correct rejections. Between 500-1100ms, analysis of the data revealed a different pattern of effects for hits and correct rejections at posterior locations. For hits primed words were more negative going than unprimed words, with no difference evident between primed and part primed words. By contrast, for correct rejections waveforms for primed words were more negative going than waveforms for part primed and unprimed words.

8.4.3 Memory contrasts

Grand average ERPs for correct responses to old and new words are displayed for the unprimed condition in Figure 8.13, for the part primed condition in Figure 8.14, and for the primed condition in Figure 8.15. From 150ms prior to target onset waveforms for primed words were more positive going for hits than for correct rejections at central locations, but this effect was not evident in waveforms for unprimed or part primed words. Between 300-500ms after onset of target words waveforms were more positive going for hits than for correct rejections in all three conditions, but appeared to differ in distribution. Old/new effects for the unprimed condition appeared frontally focused, while effects for the primed condition appeared to be focused over central and posterior locations. By contrast, differences for the part primed condition were widespread, covering frontal,

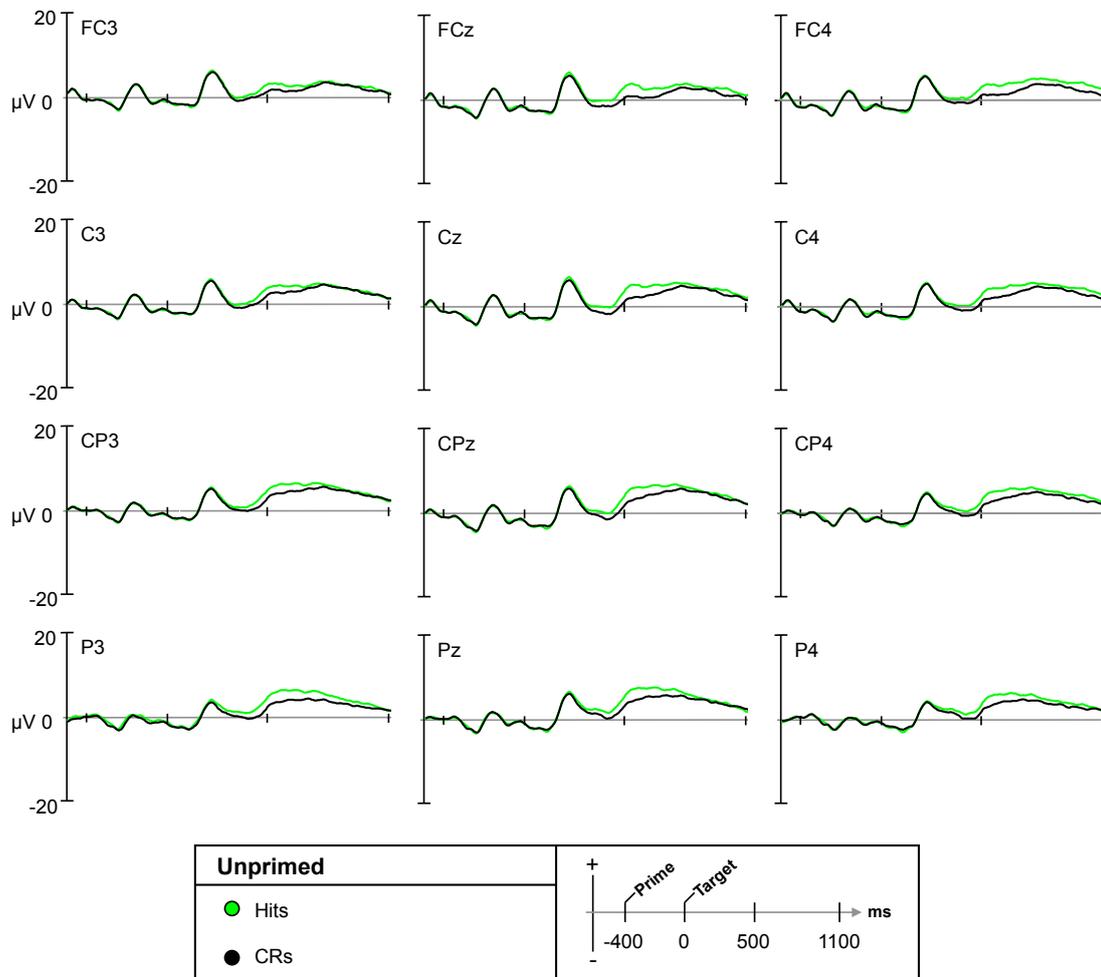


Figure 8.13: Memory effects for unprimed words. Grand average ERPs for hits and correct rejections in the unprimed condition. Waveforms were more positive going for hits than for correct rejections at mid-frontal locations between 300-500ms, and continued to be more positive going into the 500-800ms time window, but with a skew over right-frontal locations.

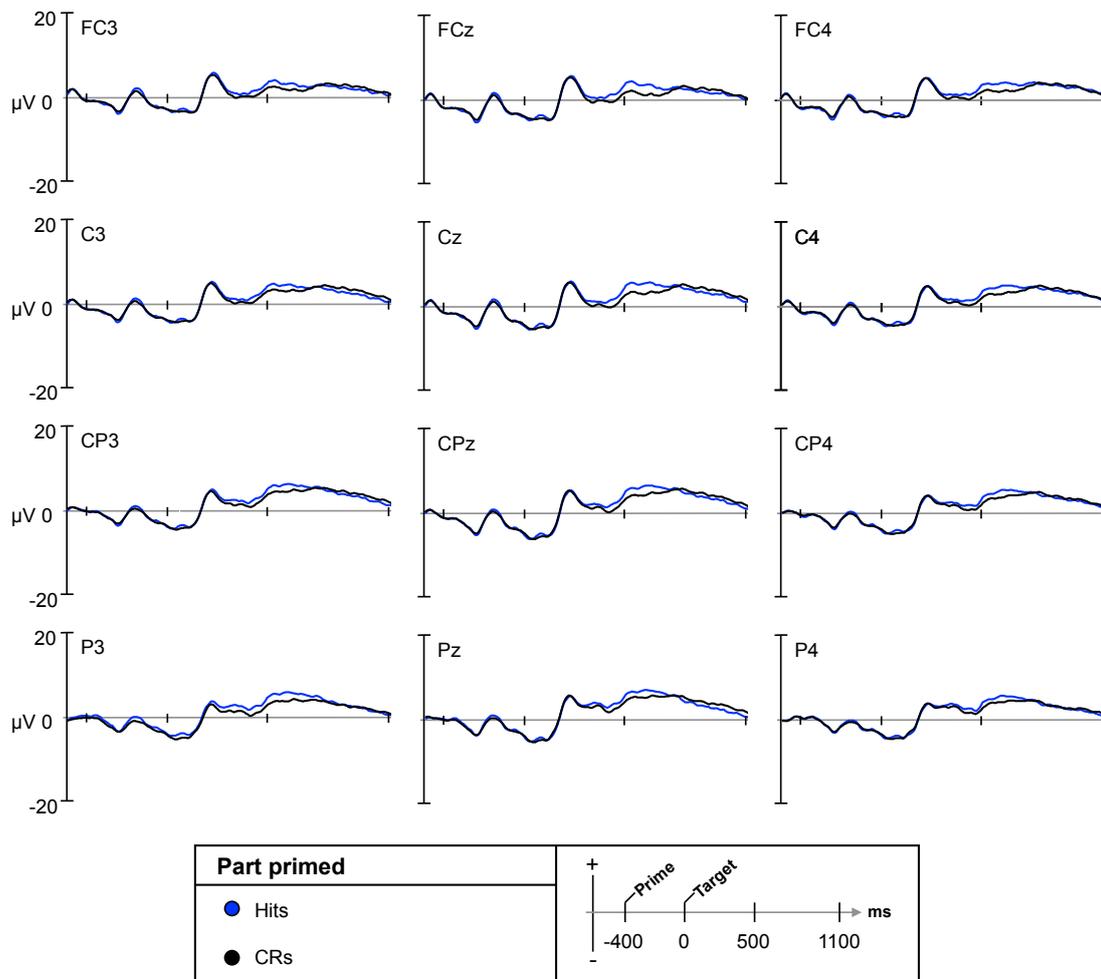


Figure 8.14: Memory effects for part primed words. Grand average ERPs for hits and correct rejections in the part primed condition. Waveforms were more positive going for hits than for correct rejections across locations between 300-500ms, and continued to be more positive going into the 500-800ms time window, but with a skew towards frontal locations.

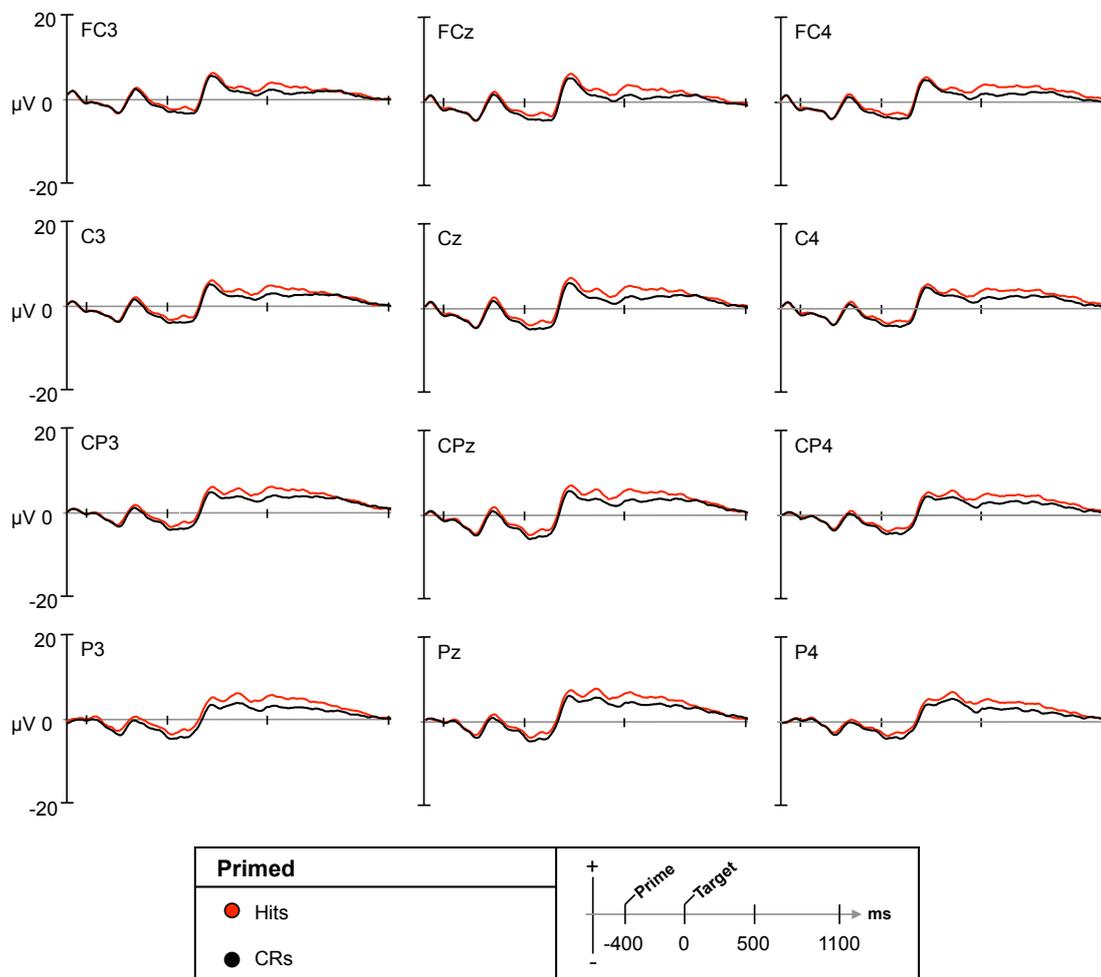


Figure 8.15: Memory effects for primed words. Grand average ERPs for hits and correct rejections in the primed condition. Waveforms were slightly more positive going for hits than for correct rejections from 150ms prior to target at superior sites over central locations. Between 300-500ms, waveforms were again more positive going for hits over central locations, and this positivity continued into the 500-800ms time window, but exhibited a right-frontal focus in the later window.

central and posterior locations. Between 500-800ms, waveforms continued to be more positive going for hits than for correct rejections in all three conditions, with an apparent focus over right-frontal locations.

For memory contrasts time windows submitted to analysis were -150-150ms, 300-500ms, 500-800ms. The first window was chosen to capture the pre-target central old/new effect evident in the data for the primed condition, and the later two windows were chosen to capture the neural correlates of familiarity and recollection reported in the literature. The first level of analysis on the data was designed to identify variations in old/new effects across conditions and time windows, employing ANOVA with the factors of test status (old, new), condition (unprimed, part primed, primed), location (F, FC, C, CP, P PO), laterality (left, midline, right) and time window (-150-150ms, 300-500ms, 500-800ms). Results revealed a significant five-way interaction between test status, condition, location, laterality and time window [$F(9.1,264.4)=3.63$, $p<0.001$], and the presence of this interaction provides strong evidence of variation in the pattern of old/new effects over the three time windows chosen for analysis.

Table 8.10: Memory ANOVAs by time window. Results of ANOVAs contrasting midline sites with the factors of condition, test status, location and laterality for the three time windows chosen for analysis of old/new effects.

	-150-150ms	300-500ms	500-800ms
Test status	-	$F(1,29)=24.71$, $p<0.001$	$F(1,29)=17.66$, $p<0.001$
Test status*Cond	$F(2,58)=3.80$, $p=0.028$	-	-
Test*Cond*Loc*Lat	-	$F(5.9,171.5)=4.47$, $p<0.001$	$F(6.2,180.1)=6.46$, $p<0.001$

To further elucidate the pattern of memory related activity, a second level of analysis was performed separately on the data from each time window, using ANOVA with the factors of test status (old, new), condition (unprimed, part

primed, primed), and location (Fz, FCz, Cz, CPz, Pz, POz). The results of this analysis are summarised in Table 8.10 and demonstrate that old/new differences were present in all three time windows; varying as a function of condition in the first time window, and as a function of condition, location and laterality in the later two time windows. Subsidiary analyses to characterize old/new effects were performed on average activity over three electrodes sites for four regions of interest: left-frontal (LF: F1, F3, F5), right-frontal (RF: F2, F4, F6), left-parietal (LP: P1, P3, P5) and right-parietal (RP: P2, P4, P6). The analysis took the form of contrasts between hits and correct rejections performed separately for each condition, using ANOVA with the factors of test status (old, new), location (frontal, parietal), hemisphere (left, right) and electrode (inferior, mid, superior); the results for each time window are reported separately in the following sections.

8.4.3.1 Time window -150 to 150ms

From 150ms prior to the onset of the target words, waveforms for primed words were more positive going for hits than for correct rejections at central locations, but this effect was not evident in waveforms for unprimed and part primed words (see Figure 8.16 for data from CPz). Importantly, initial analysis for the unprimed and part primed conditions confirmed the absence of pre-target old/new differences, revealing no main effects or interactions including the factor of test status. Analysis for the primed condition revealed a significant main effect of test status [$F(1,29)=8.25$, $p=0.008$], but no significant interactions including the factor of test status, reflecting the presence of a slight positivity for hits over frontal and parietal locations. Inspection of the data suggests that this early old/new effect is larger over central sites, which were excluded from initial analysis. Analysis was

repeated including two additional regions of interest, left-central (LC: C1, C3, C5) and right-central (RC: C2, C4, C6); to better capture the locus of this early effect. Results revealed a significant main effect of test status [$F(1,29)=8.91$, $p=0.006$], and an interaction between test status, location and electrode [$F(1.8,52.9)=3.55$, $p=0.04$]. As can be seen in Figure 8.16, this result reflects the presence of a positivity for primed hits over central locations at superior electrode sites.

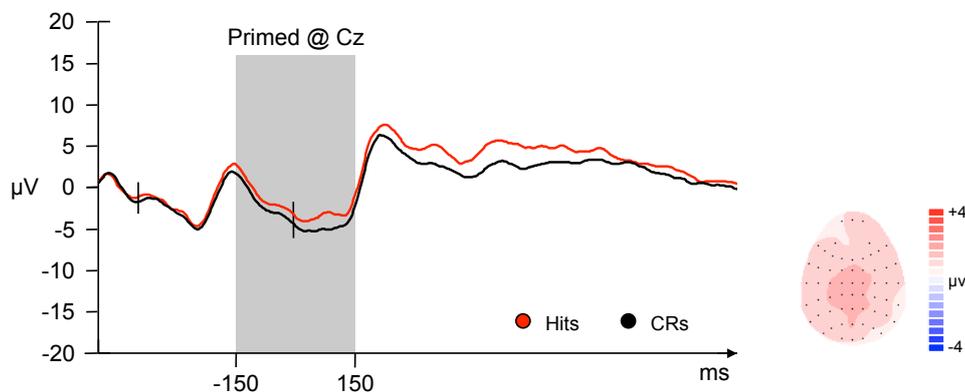


Figure 8.16: Memory @ Cz (-150-150ms). Grand average ERPs for hits and correct rejections in the primed condition at electrode Cz. Topographic maps show the difference between the hits and correct rejections. Waveforms were more positive going for hits than for correct rejections across central and posterior locations at superior electrode sites.

Subsidiary analysis at frontal locations revealed no main effect or interactions including the factor of test status, demonstrating the absence of old/new differences. Analysis at central locations revealed a significant main effect of test status [$F(1,29)=9.77$, $p=0.004$], and a significant interaction between test status and electrode [$F(1.1,33.2)=6.06$, $p=0.016$]. Analysis at parietal locations also produced a significant main effect of test status [$F(1,29)=11.53$, $p=0.002$], and a significant interaction between test status and electrode [$F(1.1,31.3)=6.84$, $p=0.012$]. Consistent with this pattern of results, further examination of the data for the primed condition confirmed that old/new differences for the primed condition were maximal at electrode CPz ($t(29)=3.53$, $p=0.001$). In summary,

the data for the primed condition demonstrated the presence of a centrally distributed old/new effect that was not present in the data for the unprimed or part primed conditions.

8.4.3.2 Time window 300 to 500ms

From 300-500ms after the onset of target words, waveforms were more positive going for hits than for correct rejections in all three conditions but appeared to differ in distribution, with the largest difference between hits and correct rejections for the primed condition over central and posterior locations (see Figure 8.17 for data from Cz). As some of the old/new effects in the current time window appeared more centrally distributed, initial analysis was again adapted to employ six regions of interest, including central sites. Initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,29)=9.30$, $p=0.005$], along with significant interactions between test status and electrode [$F(1.1,31.4)=15.47$, $p<0.001$], and test status, location and hemisphere [$F(1,29)=5.99$, $p=0.009$], reflecting the presence of a positivity for unprimed hits over superior electrode sites, with a slight skew over the right hemisphere at frontal sites. Subsidiary analysis revealed significant main effects and significant interactions between test status and electrode at frontal [$F(1.1,31.1)=6.10$, $p=0.017$], central [$F(1.2,34.4)=12.09$, $p=0.001$], and parietal locations [$F(1.1,31.7)=11.08$, $p=0.002$], confirming the presence of a positivity for unprimed hits at superior sites extending from frontal to parietal locations. Further examination of the data for the unprimed condition confirmed that old/new differences were maximal at electrode FCz ($t(29)=3.85$, $p=0.001$).

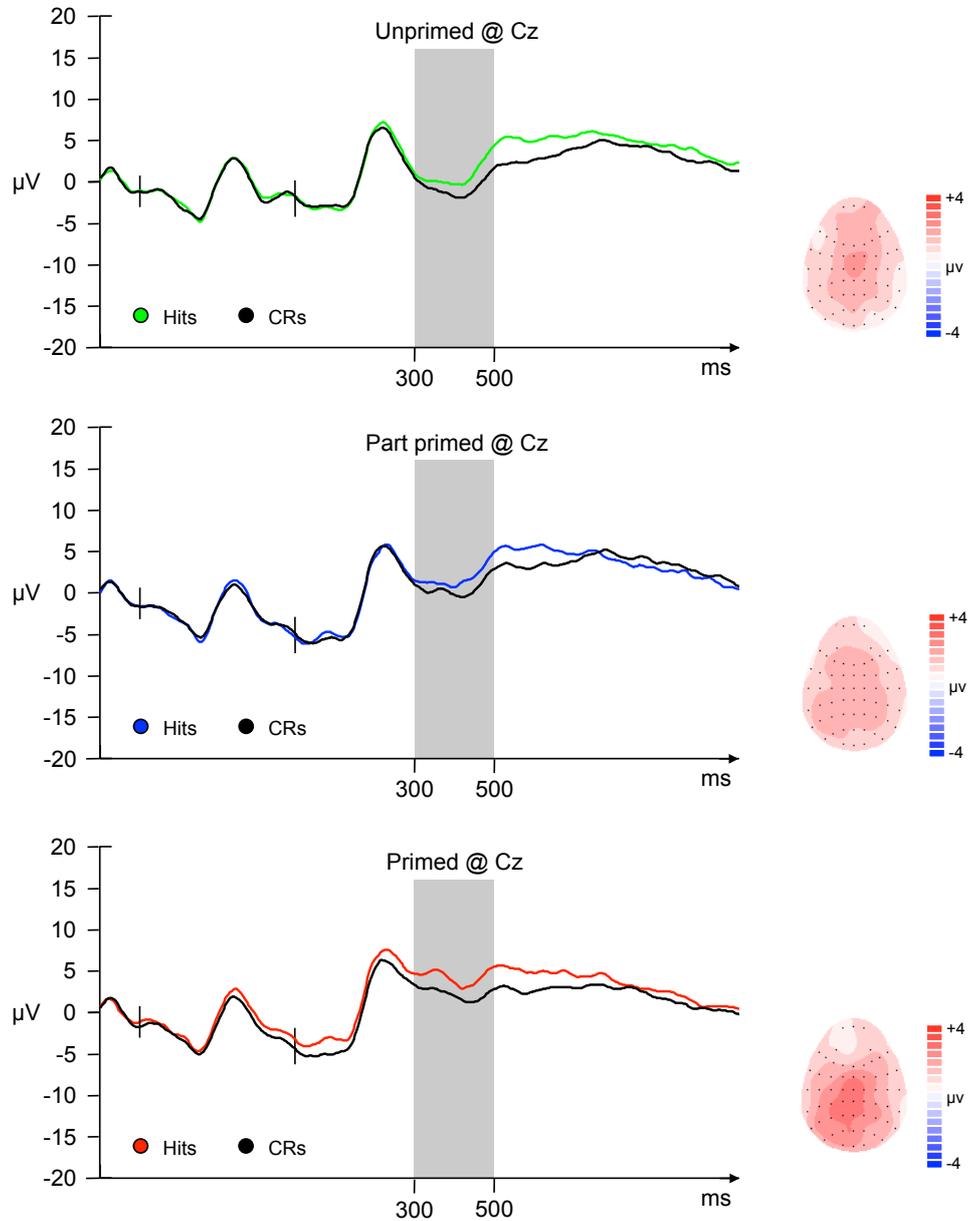


Figure 8.17: Memory @ Cz (300-500ms). Grand average ERPs for hits and correct rejections for the unprimed, part primed and primed conditions at electrode Cz. Topographic maps show the difference between the hits and correct rejections for each condition. Waveforms were more positive going for hits than for correct rejections in all three conditions, but appeared to differ slightly in distribution.

Initial analysis for the part primed condition revealed a significant main effect of test status [$F(1,29)=12.89$, $p=0.001$], but no interactions including the factor of test status, indicating the presence of a slight but widespread positivity for part primed hits across locations and electrode sites. Further examination of the data for the part primed condition confirmed that old/new differences were maximal at electrode Cz ($t(29)=3.01$, $p=0.005$). Initial analysis for the primed condition revealed a significant main effect of test status [$F(1,29)=12.58$, $p=0.001$], and a significant interaction between test status, location and electrode [$F(2.1,59.8)=5.30$, $p=0.007$], reflecting the presence of a positivity for primed hits at superior sites over central and posterior locations. Subsidiary analysis at frontal locations only revealed a marginally significant main effect of test status [$F(1,29)=4.15$, $p=0.051$], but no interactions including the factor of test status. Analysis at central locations revealed a significant main effect of test status [$F(1,29)=12.93$, $p=0.001$], and a significant interaction between test status and electrode [$F(1.1,31.3)=10.81$, $p=0.002$]. Subsidiary analysis at parietal locations also revealed a significant main effect of test status [$F(1,29)=18.10$, $p<0.001$], and a significant interaction between test status and electrode [$F(1.1,30.7)=6.90$, $p=0.012$]. Consistent with this pattern of results, further examination of the data for the primed condition confirmed that old/new differences were maximal at electrode Cz ($t(29)=3.89$, $p=0.001$).

The next level of analysis was designed to contrast the magnitude of old/new effects across conditions and was performed on difference waveforms, using ANOVA with the factors of condition (unprimed, part primed, primed), location (frontal, central, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed a significant interaction between condition, location and electrode [$F(4,117.2)=2.53$, $p=0.044$]. Subsidiary analysis contrasting the magnitude

of effects for the primed and unprimed condition confirmed the presence of an interaction between condition, location and electrode [$F(1.9, 55.3)=3.37, p=0.043$]. Analysis contrasting the primed and part primed conditions also revealed a significant interaction between condition, location and electrode [$F(2.5,75.2)=4.37, p=0.01$]. As can be seen in Figure 8.17 these results reflect the presence of larger effects for the primed compared to the unprimed and part primed conditions at superior sites over posterior locations. Follow up analysis contrasting the magnitude of effects at electrode Pz confirmed this interpretation, demonstrating the presence of significantly larger effects for the primed compared to the unprimed ($t(29)=2.55, p=0.016$), and part primed ($t(29)=3.33, p=0.002$), conditions.

To investigate whether these differences reflected genuine changes in topography, follow up analysis was performed on rescaled data for each contrast. Analysis contrasting effects for the unprimed and primed conditions revealed a significant interaction between condition, location and electrode [$F(2.4,72.2)=3.56, p=0.024$], confirming that the difference in magnitude reflected a genuine change in distribution, with a more posterior focus for the primed compared to the unprimed condition. All other contrasts were non-significant, indicating the absence of differences in distribution. Inspection of the data also suggested that old/new differences onset earlier for the primed compared to the unprimed and part primed conditions, diverging from around 200ms after target onset. To investigate, the data for the primed condition during the 200-300ms time window was submitted to ANOVA with the factors of test status (old, new), location (frontal, central, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed a significant main effect of test status [$F(1,29)=5.56, p=0.019$], and a significant interaction between condition, location and electrode [$F(2.4, 58.2)=3.37, p=0.036$]. These results matched the pattern of results reported above for the

primed condition during the 300-500ms time window and confirm that old/new effect at central locations onset earlier in the primed condition.

In summary, during the 300-500ms time window significant old/new differences were present for all three conditions and were maximal over superior locations. Analysis of the data demonstrated that old/new effects were larger in magnitude over posterior locations for the primed compared to the unprimed and part primed conditions. Topographic analysis confirmed that old/new effects for the unprimed and primed conditions differed in distribution, with a more posterior focus for the primed condition. In addition, old/new effects for the primed condition onset 100ms earlier than effects for the unprimed and part primed conditions.

8.4.3.3 Time window 500 to 800ms

From 500-800ms after target onset, waveforms for hits were more positive going than waveforms for correct rejections in all three conditions, with a focus over right-frontal and locations (see Figure 8.18 for data). Initial analysis for the unprimed condition revealed a significant main effect of test status [$F(1,29)=32.79$, $p<0.001$], and a significant interaction between test status, location, hemisphere and electrode [$F(1.6,47.6)=5.84$, $p=0.008$]. Subsidiary analysis at frontal locations revealed a significant main effect of test status [$F(1,29)=20.63$, $p<0.001$], and a significant interaction between test status, hemisphere and electrode [$F(1.8,51.7)=6.98$, $p=0.003$]. Analysis at parietal locations revealed a significant main effect of test status [$F(1,29)=29.41$, $p<0.001$], and a significant interaction between test status and electrode [$F(1.2,35.1)=15.27$, $p<0.001$]. As can be seen in Figure 8.17, these results demonstrate the presence of a positivity at right-frontal sites, with a spread over superior sites at parietal locations.

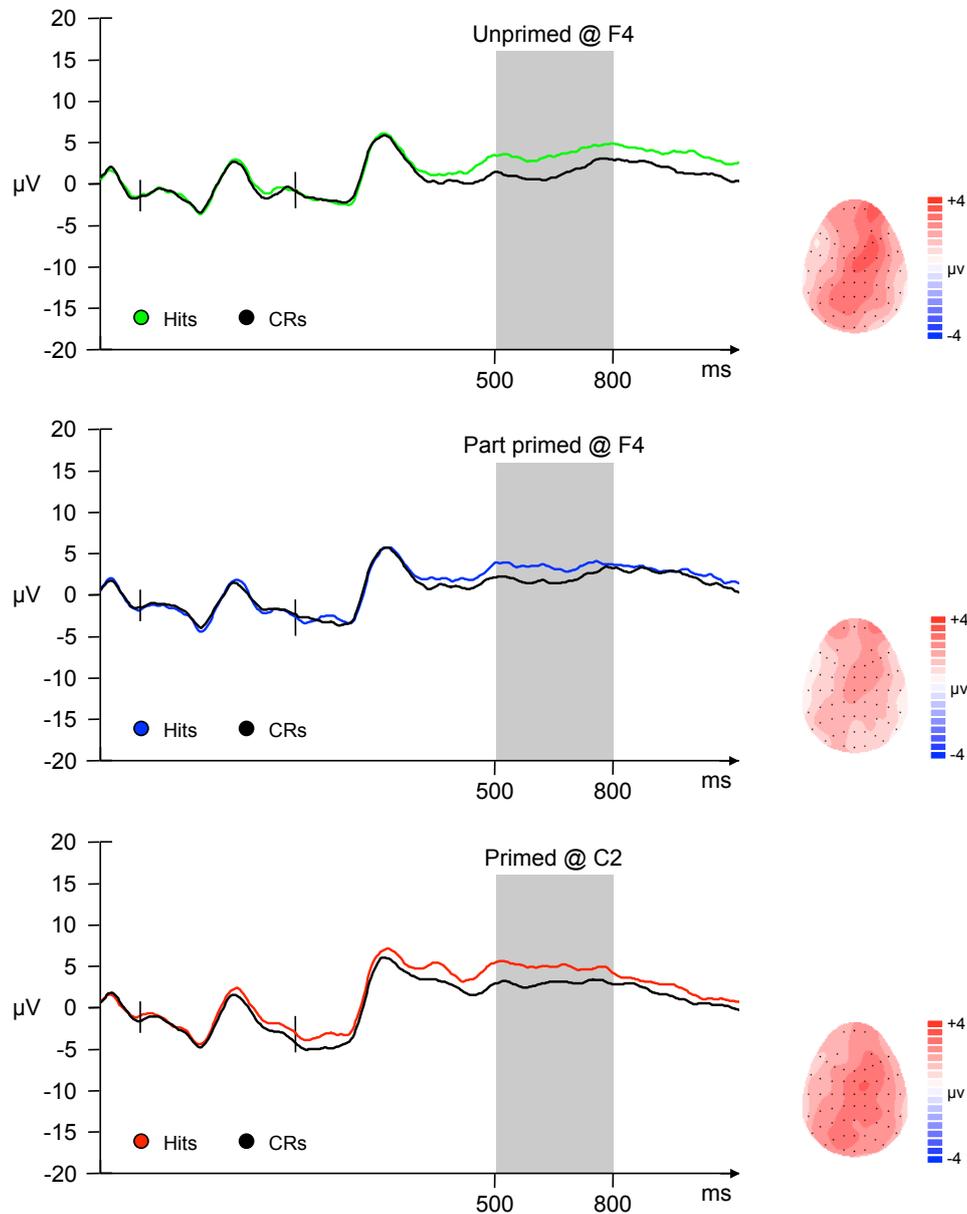


Figure 8.18: Memory (500-800ms). Grand average ERPs for hits and correct rejections in the unprimed, part primed and primed conditions at representative electrodes. Topographic maps show the difference between the hits and correct rejections for each condition. Waveforms were more positive going for hits than for correct rejections in all three conditions with a right-frontal focus.

Consistent with this pattern of results, further examination of the data for the unprimed condition confirmed that old/new differences were maximal at electrode F4 ($t(29)=5.46$, $p<0.001$).

Initial analysis for the part primed condition revealed a significant main effect of test status [$F(1,29)=4.92$, $p=0.034$], and a significant interaction between test status, location, hemisphere and electrode [$F(1.9,54.3)=5.92$, $p=0.006$], again reflecting the presence of a positivity for part primed hits at right-frontal locations. Subsidiary analysis at separate locations confirmed this pattern of results, demonstrating a significant main effect of test status [$F(1,29)=4.62$, $p=0.040$], and a significant interaction between test status and hemisphere [$F(1,29)=7.47$, $p=0.011$] at frontal locations, but no main effect or interactions including the factor of test status at parietal locations. Further examination of the data for the part primed condition confirmed that old/new differences were also maximal at electrode F4 ($t(29)=2.76$, $p=0.016$). Initial analysis for the primed condition revealed a significant main effect of test status [$F(1,29)=11.32$, $p=0.002$], and a significant interaction between test status, location and hemisphere [$F(1,29)=4.80$, $p=0.037$]. As can be seen in Figure 8.17, this interaction again suggests the presence of right-frontal old/new differences in the primed condition. Subsidiary analysis at separate locations confirmed this pattern of results, demonstrating a significant main effect of test status [$F(1,29)=9.15$, $p=0.005$], and a significant interaction between test status and hemisphere [$F(1,29)=4.50$, $p=0.043$] at frontal locations, but only a significant main effect of test status at parietal locations [$F(1,29)=10.15$, $p=0.003$]. Further examination of the data for the primed condition confirmed that old/new differences were maximal at electrode C2 ($t(29)=3.11$, $p=0.004$).

The next level of analysis was designed to contrast the magnitude of old/new effects across conditions and was performed on difference waveforms, using ANOVA with the factors of condition (unprimed, part primed, primed), location (frontal, central, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). Results revealed no main effect or interactions including the factor of test status, confirming that old/new effects did not differ in magnitude or distribution across conditions. In summary, between 500-800ms the data evidenced the presence of old/new differences with a largely right-frontal distribution across conditions, that did not differ substantially in magnitude or distribution.

8.4.3.4 Topographic analysis

The next level of analysis was designed to compare the distribution of old/new effects across time windows. Analysis was performed separately for each condition, using ANOVA with the factors of time window (300-500ms, 500-800ms), location (frontal, central, parietal), hemisphere (left, right) and electrode (inferior, mid, superior). Results for the unprimed condition revealed a significant interaction between time window, location and hemisphere [$F(2,58)=6.17$, $p=0.004$], and results for the part primed condition also revealed a significant interaction between time window, location and hemisphere [$F(2,58)=3.71$, $p=0.03$]. These results confirm a change in distribution for the unprimed and part primed condition over time from central to right-frontal locations. Analysis contrasting effects across time windows for the primed condition revealed a significant interaction between time window and hemisphere [$F(1,29)=5.16$, $p=0.031$], indicating a shift from a more left sided distribution between 300-500ms to a more right sided distribution during the 500-800ms time window. Contrasting the early onset old/new effect evident between -150-150ms with the later effect between 300-500ms failed

to reveal significant interactions including the factor of time window, indicating that these effects did not differ in distribution over time.

8.4.4 Summary

Between -150-150ms, data for the primed condition demonstrated the presence of a centrally distributed old/new effect that was not present in the data for the unprimed or part primed conditions. During the 300-500ms time window significant old/new differences were present for all three conditions and were maximal over superior locations. Analysis of the data demonstrated that old/new effects were larger in magnitude over posterior locations for the primed compared to the unprimed and part primed conditions.

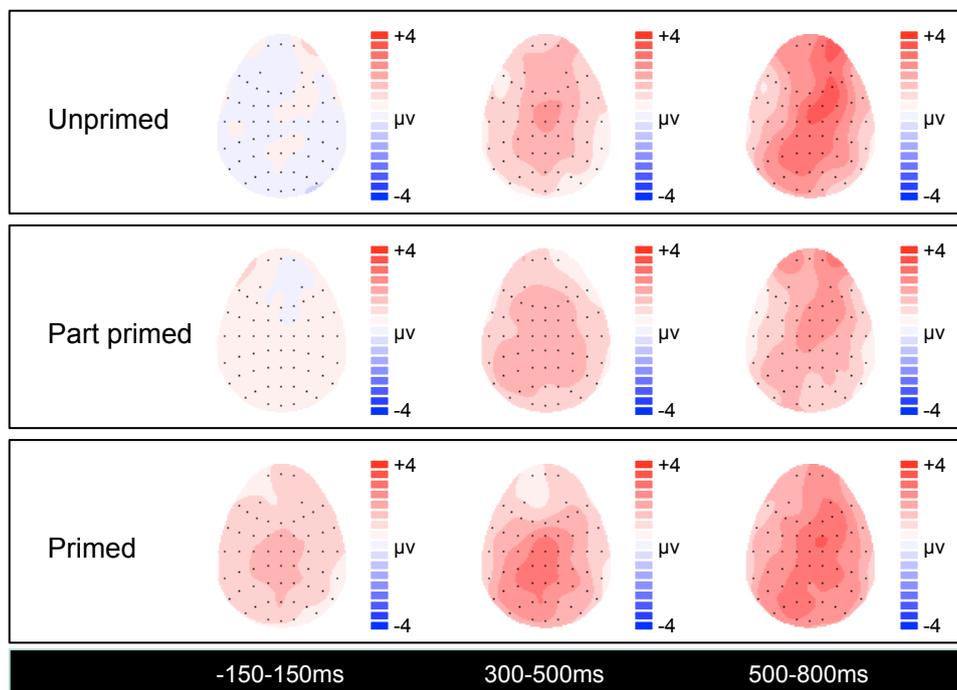


Figure 8.19: Memory topographic summary. Topographic maps summarise differences between hits and correct rejections for the unprimed part primed and primed conditions.

Topographic analysis confirmed that old/new effects for the unprimed and primed conditions differed in distribution, with a more posterior focus for the primed condition. In addition, old/new effects for the primed condition onset 100ms earlier than effects for the unprimed and part primed conditions. Between 500-800ms the data evidenced the presence of old/new differences with a largely right-frontal distribution across conditions, that did not differ substantially in magnitude or distribution.

8.5 Discussion

The main aim of the current study was to query the relationship between N400 priming effects and FN400 effects associated with familiarity. Specifically, manipulating the ease of semantic integration between prime and target pairings was intended to reduce the magnitude of N400 and investigate the consequences of this reduction for FN400 potentials. We made two predictions of the relationship between N400 and FN400 potentials. Firstly, we reasoned that if N400 and FN400 potentials are functionally equivalent, reductions in the N400 would be expected to be matched by reductions in FN400 potentials. Secondly, we reasoned that if N400 and FN400 potentials are functionally independent, then manipulating the ease of semantic integration between prime and target pairings should modulate N400 potentials, but leave FN400 potentials largely unaffected. In contrast to the previous experiment the behavioural data demonstrated a slight increase in mean accuracy for the primed compared to the unprimed and part primed conditions, along with an increase in corrected estimates of familiarity for the primed compared to the part primed condition. Response time data demonstrated a graded reduction in response times for part primed and primed words compared

to unprimed words, with the fastest responses evident for the primed condition. Consistent with the pattern of response times the ERP data clearly evidence the presence of changes in priming effects.

The pattern of effects for hits and correct rejections differed for the early and late negativities. During the early time window waveforms for part primed hits were more negative going than for unprimed hits at centro-parietal locations, but waveforms for primed hits did not differ substantially from activity from unprimed hits. By contrast, for correct rejections waveforms were equally more negative going for primed and part primed compared to unprimed correct rejections at centro-parietal locations. Taken together, these findings appear to suggest that prior exposure at study changed processing related to anticipation of the target in the current study. However, the presence of an early onsetting memory effect in the primed condition warns against this conclusion, suggesting instead that the lack of difference between primed and unprimed hits was driven by a memory related increase in activity for primed hits. The late negativity between 500-1100ms over posterior locations also exhibited a different pattern between conditions for hits and correct rejections. For hits, waveforms for primed and part primed words were equally more negative going than waveforms for unprimed words. By contrast, for correct rejections waveforms for primed words were more negative going than waveforms for part primed and unprimed words. On this basis, it appears that the negativity for part primed words is modulated by whether or not it can be related to a recently accessed post-lexical representation, with fluency at this stage only apparent when prior exposure at study facilitates completion of the partial prime.

In contrast to differences evident between hits and correct rejections for the early and late negativities, the data for hits and correct rejections during the time win-

dow for the N400 displayed a similar pattern of results. Replicating the findings of Holcomb & Grainger (2006), the data demonstrated the presence of graded N400 effects over centro-parietal locations, where primed waveforms were more positive going than part primed waveforms, which were in turn were more positive going than unprimed waveforms. While the priming data clearly demonstrated that inclusion of the partial prime modulated N400 potentials, the memory effects apparent in the data failed to directly confirm either of our predictions, as clear mid-frontal old/new differences were only apparent in the data for the unprimed condition between 300-500ms. Comparison of memory effects across conditions confirmed that old/new effects onset earlier and were larger in magnitude over posterior locations for the primed compared to the unprimed and part primed conditions. In addition, topographic analysis confirmed that old/new effects for the unprimed and primed conditions differed in distribution, with a more posterior focus for the primed condition. There are two potentially plausible interpretations of the current data. Firstly, it could be argued that old/new effects across conditions reflect the operation of conceptual priming, with the distribution across the scalp varying with the degree of semantic overlap. Alternatively, it could be argued that effects for the part primed and primed conditions consist of partially overlapping FN400 and N400 effects.

On the basis of the current data, it is difficult to rule out either of these interpretations. Previous research has demonstrated that the distribution of N400 effects can be dependent upon the exact nature of the eliciting stimuli. For example, N400 effects have been found to exhibit a more frontal distribution for pictures than for words (Kounios & Holcomb, 1994), and for concrete compared to abstract words (Ganis, Kutas & Sereno, 1996). However, the eliciting stimuli in the current experiment were consistent across conditions, so the difference in distri-

bution between the primed and unprimed conditions cannot be accounted for by differences in stimulus properties, but may be accounted for by differences in the underlying representations supporting retrieval. Data for the primed condition also evidenced the presence of an early onsetting pre-target old/new difference over central locations that did not differ in distribution from the old/new difference present during the 300-500ms time window. Based on the assumption that exposure to the prime facilitated semantic access pre-target, it could be argued that successful retrieval was supported by reactivating the same post-lexical entry after target onset. By contrast, it could be argued that retrieval for the unprimed condition required access to an episodic trace, causing the observed difference in distribution, and tentatively suggesting that neural correlates of conceptual priming and familiarity should be dissociable.

8.5.1 Summary

The main aim of the current study was to query the relationship between the N400 and FN400 effects previously associated with familiarity. We made two predictions concerning the potential relationship between N400 and FN400 potentials. Firstly, we reasoned that if N400 and FN400 potentials are functionally equivalent, reductions in the N400 would be expected to be matched by reductions in FN400 potentials. Secondly, we reasoned that if N400 and FN400 potentials are functionally independent, then manipulating the ease of semantic integration between prime and target pairings should modulate N400 potentials, but leave FN400 potentials largely unaffected. While the priming data clearly demonstrated that inclusion of the partial prime modulated N400 potentials, the memory effects apparent in the data failed to confirm either of our predictions.

It remains possible that the current data for the primed and part primed conditions may reflect overlapping N400 and FN400 potentials, making it impossible to assess whether they are functionally equivalent or independent. Nonetheless, differences in the distribution of old/new effects for the primed and unprimed conditions tentatively suggest that neural correlates of conceptual priming and familiarity can be differentiated.

Chapter 9

General discussion

This thesis reported a series of studies designed to investigate interactions between implicit priming and explicit recognition. These investigations attempted to answer two broad questions. Firstly, do implicit priming and explicit recognition interact at retrieval, and secondly, what is the nature of the relationship between priming, familiarity and recollection. These broad questions were addressed by employing masked repetition priming within the confines of a standard recognition test, to directly investigate how the degree of priming influenced neural correlates of familiarity and recollection. This final chapter will provide a brief overview of the main findings from each experiment, and will discuss these findings in relation to the wider literature. As the findings for each experiment have already been discussed in detail in the relevant chapters, the current chapter will focus on discussion of the pattern of findings across experiments. The research questions outlined in Chapter 3 (Section 3.3) will also be addressed, before directions for future research are outlined, and conclusions that can be drawn on the basis of the data reported in this thesis are presented.

9.1 Summary of results

Experiments 1 and 2 were designed to explore interactions between repetition priming and neural correlates of familiarity and recollection, by manipulating the degree of priming via masked repetition at test, within the confines of a standard recognition task. Experiment 1 employed a shallow encoding task and responses at test were speeded to encourage reliance on familiarity based recognition. Experiment 2 was identical in design, but in contrast to experiment 1, employed a deep encoding task to promote recollection. Experiments 3 and 4 represented a departure from this initial strategy and were designed to manipulate the degree of priming more directly. Experiment 3 manipulated the SOA between prime and target pairings, seeking to identify factors determining whether retrieval will be implicit or explicit, and investigate the nature of N400 effects. Experiment 4 manipulated the degree of priming via the addition of a partial prime condition and was specifically designed to investigate the relationship between the N400 and FN400 effects. The following sections will provide a brief overview of the electrophysiological results for priming and memory contrasts across experiments.

9.1.1 Priming effects

Priming contrasts for Experiments 1 and 2 both revealed the presence of three priming related modulations, an early (-50-150ms) posterior negativity, followed by a widespread centro-parietal positivity (250-500ms), and a later (500-1100ms) posterior negativity for primed compared to unprimed words. In both experiments the magnitude and distribution of the early negativity did not differ for hits and correct rejections, while the late negativity was modulated by exposure to words at study, being larger in magnitude for hits than for correct rejections.

Crucially, N400 effects evident between 250-500ms in both experiments did differ as a function of the encoding task. Under shallow encoding conditions in Experiment 1, N400 effects were equivalent in magnitude for hits and correct rejections. By contrast, under deep encoding conditions in Experiment 2, N400 effects were larger in magnitude for hits than for correct rejections, mapping onto the response time data, and providing clear evidence of additional priming carried over from the encoding phase.

The pattern of priming effects in Experiment 3 for the standard SOA largely replicated the findings reported above for experiment 1, with the exception that the early negativity was not apparent in the data for hits. For the longer SOA the data again evidenced the presence of an early central negativity (-350 to 150ms) that was only significant for correct rejections, and a later posterior negativity (500-1100ms), that was larger for hits than correct rejections. The most notable difference in priming effects across SOAs was the apparent modulation of the N400, which onset earlier and was longer in duration (-100-500ms) for the 698ms SOA. In addition, comparison of the late negativity across SOAs demonstrated larger effects for hits and correct rejections at the longer SOA. In Experiment 4, the data again revealed the presence of three priming related modulations, an early posterior negativity (-100-150ms), followed by a centro-parietal positivity (250-500ms), and a later posterior negativity (500-1100ms). Importantly, N400 effects evident between 250-500ms were modulated by the priming manipulation, with primed waveforms more positive going than part primed waveforms, which were in turn were more positive going than unprimed waveforms.

The early negativity found for hits and correct rejections in experiments 1, 2 and 4, and for correct rejections in experiment 3 has not been observed in previous research employing masked priming. As noted earlier, previous research has iden-

tified a number of early onsetting components that are modulated by immediate masked priming (Holcomb & Grainger, 2006), but the early effect found here across experiments does not map directly onto any of these early visual components. It is common practice in priming research to use unrelated words as an unprimed baseline, but the current series of experiments employed repetition of the word “blank” to act as a more neutral baseline, based on research suggesting that repetition over a large number of trials leads to habituation (Dien et al., 2006). On this basis, it is plausible that the effect onsetting pre-target in the current series of experiments reflects an artifact of differences in processing created by habituation, rather than being directly related to priming *per se*. The presence of the early effect for unstudied words across experiments supports this interpretation. In essence, studied words could legitimately produce pre-target priming effects at test, due to the match between the study words and masked primes, but this is not the case for unstudied words.

In summary, the pattern of priming effects across experiments was reasonably consistent, with differences between experiments directly related to the intended manipulations. Of specific interest in the current context are the reported modulations of N400 potentials. Contrasting shallow and deep encoding tasks across Experiments 1 and 2 evidenced larger N400 effects for hits under deep encoding conditions. Increasing the SOA between prime and target pairings in Experiment 3 produced N400 effects that onset earlier and were longer in duration. Finally, manipulating the degree of match between prime and target pairings in Experiment 4, by including a partial prime condition, produced graded N400 effects for hits and correct rejections. As the results for priming contrasts have already been discussed in detail in the relevant chapters, further reference to priming effects

in the current chapter will be limited to discussion of the relationship between priming and memory effects where necessary.

9.1.2 Memory effects

In contrast to priming effects, the pattern of memory effects was highly variable across experiments and between conditions. In Experiment 1, data for the unprimed condition demonstrated the presence of mid-frontal old/new effects, that were consistent with the distribution and latency of FN400 old/new effects previously reported in the literature. Surprisingly, given recent links in the literature between priming induced fluency and familiarity, mid-frontal old/new effects were not evident in the data for the primed condition. In Experiment 2, data for both conditions evidenced the presence of left-parietal old/new effects, but the conditions differed in the onset time of these effects. Unprimed ERPs were consistent with previous identifications of recollection (500-800ms), but in primed ERPs the left-parietal old/new effect was evident earlier during the 300-500ms time window, which is normally associated with the onset of familiarity as indexed by the FN400. Further analysis demonstrated that left-parietal effects for the primed condition onset around 200ms after target onset, with effects for the unprimed not evident until around 400ms after target onset.

In Experiment 3, data for the unprimed condition displayed a similar pattern across SOAs, with mid-frontal old/new effects evident for both SOAs during the 300-500ms time window and continuing into the 500-800ms time window. By contrast data for the primed condition varied as a function of SOA during the 300-500ms time window, with left-parietal old/new effects evident for the short SOA and mid-frontal old/new effects evident for the longer SOA. In addition, fur-

ther examination of the data demonstrated that significant old/new differences were present at left-parietal sites from target onset for the short SOA and continued into the 300-500ms time window. Comparing the distribution of memory effects across SOAs for the primed condition between 300-500ms confirmed that differences apparent in the data reflected a genuine difference in process engagement, with left-parietal effects previously associated with recollection evident for the short SOA, and mid-frontal effects previously linked to familiarity evident for the long SOA. Right-frontal old/new differences were present in the primed condition for both SOAs between 500-800ms, and did not differ substantially in magnitude or distribution. In addition to old/new effects in the time windows associated with familiarity and recollection, the data for the primed condition also revealed the presence of a pre-target old/new difference over fronto-polar sites that continued into the post-target period for the long SOA.

In Experiment 4, data for the primed condition evidenced the presence of a centrally distributed pre-target old/new effect that continued into the post-target period, and was not present in the data for the unprimed or part primed conditions. During the 300-500ms time window significant old/new differences were present for all three conditions and were maximal over superior locations, but appeared to differ in distribution. Old/new effects with a clear mid-frontal distribution were only evident for the unprimed condition. Data for the part primed condition displayed the presence of a widespread positivity across locations, while data for the primed condition exhibited a focus over central and posterior locations. Analysis of the data demonstrated that old/new effects were larger in magnitude over posterior locations for the primed compared to the unprimed and part primed conditions. Comparing the distribution of memory effects across conditions confirmed that old/new effects for the unprimed and primed conditions

differed in distribution, with a more posterior focus for the primed condition. In addition, old/new effects for the primed condition onset 100ms earlier than effects for the unprimed and part primed conditions. Right-frontal old/new differences were present in all three conditions between 500-800ms, and did not differ substantially in magnitude or distribution.

In summary, across experiments clear mid-frontal old/new effects were only evident for the primed condition in Experiment 3 at the longer SOA. Left-parietal old/new effects were present for the primed condition in Experiment 2 and in Experiment 3 for the short SOA. In both cases, left-parietal effects were evident during the 300-500ms time window normally associated with the onset of familiarity. In Experiment 2, left-parietal effects became evident from 200ms after target onset, while in Experiment 3 old/new differences at left-parietal sites were present from target onset. In addition, Experiments 3 & 4 both elicited pre-target old/new effects for the primed condition, but these early memory effects differed in distribution across experiments, with a focus over fronto-polar sites for the long SOA in experiment 3, and a focus over central sites in Experiment 4. Right-frontal old/new effects were present for the primed condition between 500-800ms in Experiment 3 for both SOAs and in Experiment 4 across conditions. The previous sections have provided a brief overview of the main findings from all of the experiments reported in this thesis, the following sections will discuss these findings in relation to the research questions and within the context of the wider literature.

9.2 Theoretical implications

Despite a wealth of research employing ERPs to dissociate multiple potential contributions to recognition, less attention has been paid to potential interactions between priming and recognition, and as such the relationship between these implicit and explicit forms of memory has remained unclear. Importantly, it has recently been claimed that the operation of implicit memory during explicit memory tests presents a significant confound for ERP investigations of recognition, limiting theoretical progress by “contaminating” neural correlates of explicit retrieval (Voss & Paller, 2007). The main aim of this thesis was to explore the nature of potential interactions between priming and episodic memory, in the hope of gaining a better understanding of the respective contributions of implicit and explicit processing to recognition. The findings of the studies reported in this thesis generally support the view that priming, familiarity and recollection are independent memory processes with distinct neural correlates, but that interactions between implicit and explicit retrieval processes do occur during recognition tests. Moreover, across experiments priming appears to act as a gating mechanism, with the engagement of familiarity or recollection being dependent on the outcome of implicit processing.

The bulk of behavioural research to date supports the view that priming selectively influences recognition based on familiarity (e.g., Rajaram & Geraci, 2000; Miller et al., 2008; Woollams et al., 2008). As noted earlier, the majority of ERP research in this area has focused on investigating conceptual priming, based on the proposal that differences between old and new items in recognition tests can potentially be driven by repeated access to semantic information, calling into question links between mid-frontal old/new effects and familiarity (Paller

et al., 2007). A number of studies have demonstrated that mid-frontal old/new effects are absent in conditions that do not support access to conceptual information (e.g., Voss & Paller, 2006; Yovel & Paller, 2004), but others have shown that mid-frontal effects are present for stimuli that are not inherently meaningful (e.g., see Curran, 1999; Curran et al., 2002; Groh-Bordin et al., 2006). More generally, a number of authors have commented on the possibility that the qualitative experience of familiarity may be supported by more than one source of evidence, and that both perceptual and conceptual priming may serve as pre-cursors to explicit recognition (e.g., Groh-Bordin et al., 2006; Rugg & Curran, 2007).

The current series of experiments did not set out to separate perceptual and conceptual contributions to priming. As noted earlier, repetition from study to test and between prime-target pairings means that priming could be perceptual or conceptual in nature. While initially repetition primes were thought to provide a measure of the degree of perceptual priming (e.g., Tulving & Schacter, 1990), more recently it has been appreciated that repetition can also produce conceptual priming, particularly when the stimuli involved are words (Voss et al., 2010b). The current findings are consistent with this view, demonstrating the presence of reliable N400 effects across experiments, and with prior work demonstrating that masked words can be processed for meaning in the absence of awareness (Dehaene et al., 1998). Despite evidence that masked primes were processed for meaning in the current series of experiments, the data do not support the view that FN400 effects are merely driven by repeated access to semantic information. The absence of mid-frontal old/new effects for primed words in the first experiment is not consistent with prior research demonstrating the absence of mid-frontal old/new effects, because the stimuli employed here were meaningful (e.g., Yovel & Paller,

2004), demonstrating that the presence or absence of FN400 effects is not entirely driven by the properties of the eliciting stimulus.

In fact, only one experiment reported in this thesis evidenced the presence of clear mid-frontal old/new effects for primed words, when the SOA between prime and target pairings was increased (Experiment 3). It was reasoned that increasing the distance between prime and target words would engender a greater degree of fluency by allowing extra time for semantic information from the prime to be processed, and that this higher degree of fluency may promote reliance on familiarity. In addition to eliciting FN400 effects as we expected, increasing the duration of the SOA between prime and target pairings modulated N400 effects, which onset earlier and were longer in overall duration. On the basis of the data from experiment 3 it appears that an increase in post-lexical semantic processing may engender reliance on familiarity based retrieval under certain circumstances. Taken together, the findings of the first and third experiments appear to suggest that it is not the availability of conceptual information that determines the presence or absence of FN400 effects, but the extent of semantic elaboration. However, another potentially critical difference between these experiments was whether retrieval was automatic or strategic.

As noted earlier, Badgaiyan & Posner (1997) contrasted implicit and explicit retrieval instructions during word stem completion, finding that activity at frontal sites was only present under explicit instructions, when priming alone was not a sufficient basis for making a response. The absence of mid-frontal effects for primed words in the first experiment is consistent with this evidence, and the matched memory performance across conditions clearly demonstrates that priming can be sufficient to drive accurate recognition. Recently, De Chastelaine et al. (2009) suggested that FN400 potentials may reflect a control process that is re-

quired to support retrieval only when memory traces are weak. Interpreting the presence of mid-frontal effects when increasing the SOA between prime and target on this basis suggests that a greater degree of semantic elaboration, as indexed by more sustained N400 effects, creates interference and forces reliance upon familiarity. Contrasting memory performance across the series of experiments reported in this thesis also supports the view that differences in the engagement of retrieval processes were potentially driven by changes in retrieval strategy.

Previous research has indicated that fluency induced by priming impacts memory performance (e.g., Cleary, 2004; Jacoby & Whitehouse, 1989; Westerman et al., 2002, 2003; Whittlesea et al., 1990; Parkin et al., 2001). In essence, priming is thought to encourage a more liberal response bias (Ratcliff & McKoon, 1996; Thapar & Rouder, 2001), increasing the probability that a primed item will be classified as studied at test. As noted earlier, one undesirable aspect of this view is that it is difficult to see how priming can be classified as an implicit memory phenomenon *per se*, given that fluency manipulations also tend to increase illusory recognition. Voss et al. (2008) were the first to demonstrate the possibility of accurate implicit recognition, and the data reported in the current thesis provide support for this view, demonstrating that priming does not necessitate changes in memory performance. Interestingly, across experiments the presence of right-frontal old/new effects appeared to be predictive of changes in memory performance for primed words, suggesting that decision monitoring processes play a critical role in determining performance outcomes.

In the first two experiments right-frontal old/new effects were not apparent in the data and memory performance was matched for the primed and unprimed conditions. In the the third experiment right-frontal effects were apparent in the data for the primed condition between 500-800ms across SOAs, and the behavioural

data demonstrated an increase in false alarm rates for the primed compared to the unprimed condition. In the final experiment, right-frontal effects were present across all three conditions, and the behavioural data demonstrated an increase in the hit rate for the primed compared to the unprimed and part primed conditions. As such, findings from the later experiments are consistent with previous research demonstrating that fluency induced by priming can increase the probability that a primed item will be classified as studied at test (e.g., Jacoby & Whitehouse, 1989; Whittlesea et al., 1990). Interestingly, across experiments the magnitude of right-frontal effects was not modulated by priming, supporting the view that right-frontal old/new effects are not directly related to evaluating the products of retrieval, but instead reflect a generic marker of decision making processes (Hayama, Johnson & Rugg, 2008). More importantly, the data suggest that changes in performance are not directly related to the operation of familiarity or recollection, as right-frontal effects were found following both forms of retrieval.

Recently, it has been demonstrated that fluency manipulations can also influence recollection (e.g., Brown & Bodner, 2011; Kurilla & Westerman, 2008; Taylor & Henson, 2012). As noted earlier, one line of evidence supporting the idea of potential interactions between priming and recollection comes from studies demonstrating that under certain circumstances recollection can operate faster than familiarity (Dewhurst & Conway, 1994; Gardiner et al., 1999; Henson et al., 1999). The current findings are consistent with this evidence and go further by demonstrating that these findings are not merely an artifact of behavioural methods applied to dissociate familiarity and recollection (Yonelinas, 2002), but reflect a genuine change in the timing of underlying neural processing related to recollection, consistent with the findings of Woollams et al. (2008). Across exper-

iments the onset time of left-parietal effects varied. Under deep encoding conditions differences became apparent between 200-300ms after target onset (Exp.2), while under shallow encoding conditions differences were apparent within 100ms of target onset (Exp.3). Taken together, this difference in onset times across experiments suggests that temporal characteristics of recollection can be highly variable, but it is clear that priming can elicit left-parietal effects that occur early and can potentially overlap into the time window normally associated with the FN400 and N400 effects.

As noted earlier, based on the literature there are a number of possible interpretations of the early onsetting left-parietal effects found here and its functional significance remains an open question. One potential objection to the current data would be to argue that masked priming merely facilitates processing of item information, allowing a retrieval attempt to be initiated earlier in the processing stream. However, the difference in onset times across experiments, and the fact that onset times are not proportional to the distance between prime and target pairings, suggests that this view of the current data is not appropriate. Our preferred interpretation is that the early onsetting left-parietal old/new effects reported here reflect a more automatic form of recollection divorced from subjective experience, supported by studies demonstrating hippocampal contributions during implicit memory tests in the absence of explicit retrieval (e.g., Daselaar et al., 2006; Hannula & Ranganath, 2009; Schacter et al., 2004). On this view, the presence of the repetition primes acted as a proximal retrieval cue, engaging the first stage of recollection described by Moscovitch (2008).

So far, the current section has focused on discussion of the differences in findings across experiments in relation to the literature, the remainder of this section

will relate these findings to the broad research questions that this thesis set out address shown below.

Research questions:

1. Do implicit priming and explicit recognition interact?
2. What is the relationship between priming, familiarity and recollection?

The findings of the studies reported in this thesis generally support the view that priming, familiarity and recollection are independent memory processes with distinct neural correlates. Interestingly, across the entire series of experiments reported in this thesis, neural correlates of familiarity and recollection were never present together within a single condition, supporting the view that they operate entirely independently, and that either process can result in retrieval. Moreover, the current findings demonstrate that the engagement of explicit recognition signals can be determined or influenced by the outcome of implicit processing, suggesting that interactions between priming and explicit retrieval processes do occur during recognition testing. Crucially, priming appears to influence when, or even if, neural signals previously associated with explicit recognition will be observed.

As noted earlier, some dual-process theories suggest that common processes may underlie both familiarity in recognition memory and priming on implicit memory tests (Jacoby & Dallas, 1981; Mandler, 1980), and it has also been claimed that familiarity is closely related to conceptual priming (Paller et al., 2007). The current data suggests instead that priming acts as a gating mechanism determining whether or not familiarity will be observed, with only a high degree of semantic

elaboration engaging neural correlates of familiarity. Moreover, the data clearly demonstrate that priming is sufficient to support recognition in the absence of neural signals associated with explicit recognition. In addition, and in contrast to the bulk of prior evidence, the current findings also demonstrate an interaction between priming and neural correlates of recollection, with priming reducing the latency of left-parietal effects.

9.3 Future directions

Although the research reported in this thesis clearly demonstrates interactions between priming and neural correlates of recollection, the exact nature of this early onsetting recollection effect remains unclear on the basis of the current data. While early onsetting left-parietal old/new effects have been reported previously (e.g., De Chastelaine et al., 2009; Vilberg et al., 2006; Woollams et al., 2008), it is open to debate whether these effects reflect superior recollection of contextual information, or whether recollection should be considered a two-stage process (Moscovitch, 2008), with earlier onsetting left-parietal effects indexing a more automatic non-strategic form of recollection. Future research should query this early onsetting left-parietal effect further to establish if it differs in nature from later onsetting left-parietal effects previously associated with recollection. Specifically, the addition of an incidental source task to the current design would help to differentiate between these options.

In addition, future work should attempt to identify factors involved in whether or not priming will impact memory accuracy. The findings reported here suggest that changes in the comparative degree of fluency between conditions, due to manipulating prime-target SOA and including the partial primes in the later ex-

periments, resulted in changes in performance for primed words. Moreover, the presence of right-frontal old/new effects was implicated in these changes, suggesting that right-frontal effects may reflect the attribution of fluency to prior exposure. Right-frontal old/new effects have been reported in a number of recognition memory experiments, but it remains a matter of debate whether they are related to accuracy (e.g., Hayama et al., 2008; Trott et al., 1999; Wilding & Rugg, 1996). Right-frontal effects were not modulated by priming in the experiments reported in this thesis, making it difficult to assess on the basis of the current data exactly how right-frontal activity drives changes in performance.

The data reported in this thesis suggest that N400 priming effects and FN400 old/new effects make independent contributions to recognition. However, Experiment 4 set out to directly test whether FN400 and N400 potentials were independent or functionally equivalent, but the results were less than clear as a result of potential of component overlap between N400 and FN400 potentials. Relatively few studies to date have directly contrasted N400 and FN400 effects (although see Voss & Federmeier, 2011). In order to address claims that FN400 potentials are equivalent to N400 potentials, more research in this area is warranted. However, the outcome of attempting to contrast these effects in the current thesis suggests that a novel approach will be required to avoid component overlap, and that convergent evidence from functional imaging is necessary.

9.4 Conclusion

The aim of this thesis was to explore interactions between priming and episodic memory using ERPs to investigate the respective contributions of priming, familiarity and recollection to retrieval. The findings from the series of experiments

reported in this thesis have provided new insights into interactions between priming and recognition. Importantly, in contrast to the majority of findings in the literature, the current findings demonstrate the presence of interactions between priming and recollection, and that mid-frontal old/new effects indexing familiarity are not merely driven by repeated access to semantic information. In addition, the current series of experiments have also demonstrated that under certain circumstances, priming is sufficient to support accurate recognition, and does not necessitate changes in memory performance. Moreover, the data suggest that priming can act as a gating mechanism, with the engagement of familiarity or recollection being dependant on the outcome of implicit processing. Overall, the current data clearly demonstrate that there are multiple potentially interacting routes to recognition. Investigating the nature of these complex interactions between implicit priming and explicit recognition will undoubtedly continue to be a fascinating topic of research for years to come.

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