Ageing and Episodic Memory: Combining Neuropsychological and Event-Related Potential Approaches to Investigate Strategic Retrieval

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Declaration

This thesis is submitted in fulfilment of the requirement for the degree of Doctor of Philosophy at the Universtiy of Stirling. I declare that the work contained in this thesis is my own apart from quotations and citations that have been stated in the text, and that this work has not been submitted, either in whole or in part, for any other degree or qualification.

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Next, I want to thank my Mum and Dad. If it was not for your belief that I could be anything I wanted to be and encouragement to do so, I do not think I would have achieved what I have to date.

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Abstract

This thesis investigates the effect of normal ageing on the strategies adopted during episodic memory retrieval, using a combination of neuropsychological profiling and neuroimaging data measured during performance on a source memory exclusion task. The exclusion task is a type of source memory task where participants distinguish between targets (studied items from one source e.g. female voice), non-targets (studied items from another source e.g. male voice) and new items. Unlike a source memory task where three separate buttons are pressed for each item at test, in the exclusion task one button is pressed for targets and a second for non-target and new items. As this task is more complex than a normal source memory paradigm and also allows participants to perform the task in more than one way, it places high emphasis on the use of strategies to facilitate retrieval and is therefore ideal for investigating strategic retrieval.

Previous source memory studies have shown that while older adults are reasonably good at recognising whether items are old or new, they show marked impairments at remembering the source in which items were presented at study. Dual process theories propose that the age-related decline in source memory occurs because recollection becomes impaired with ageing whereas familiarity remains relatively spared. The results reported in this thesis support dual process theory. Experiment 2a showed that, behaviourally, as expected, the young outperformed the elderly. Event-related potentials (ERPs), recorded while a source memory exclusion test was performed, revealed that both young and older adults showed bilateral frontal and left parietal old/new effects, thought to index familiarity and recollection respectively. Importantly, the magnitude of the left parietal effect was significantly reduced in the older adults.

The ERP findings also suggested that dual process theories represent an oversimplification of episodic memory decline with age. In Experiment 1a, three temporally and topographically distinct late frontal old/new effects were present in the younger adults: a bilateral anterior frontal effect (450-900ms post stimulus), a right prefrontal effect (900-1300ms) and a right frontal effect (1300-2000ms). Significant positive correlations between the magnitude of these effects and performance on neuropsychological tests of executive functioning in Experiment 1b, revealed that the bilateral anterior frontal effect was related to working memory, strategy use and planning; the right prefrontal effect was related to working memory and planning while the right frontal effect was related to planning. By contrast, the older adults in Experiment 2a only produced the right frontal effect, which correlated with planning across all three time windows in Experiment 2c. Post-retrieval monitoring in older adults therefore appeared to be qualitatively different than their younger counterparts. Performance on the neuropsychological tests in Experiment 2b, revealed that the older adults’ working memory and strategy use was impaired compared to the young, whereas planning was relatively intact, suggesting that age-related differences in post retrieval processing may be due to reduced executive functioning in older adults. Identifying distinct late frontal effects and demonstrating a relationship between these effects and specific executive functions is a novel finding.

The presence of a left parietal target greater than non-target difference in the young adults from Experiment 1a and 2a was interpreted as the young reducing recollection of irrelevant non-target information. The modulation did not differ in magnitude for targets and non-targets in the elderly adults from Experiment 2a, suggesting they were less able to reduce activation of goal irrelevant non-target information. The results in the young adults from Experiment 1a also highlight the importance of considering the context of source information on the processes engaged at retrieval. The bilateral frontal effect was significant for the retrieval of the intrinsic context (source information inherent to the studied item), but not the extrinsic context (source information not inherent to the studied item). This finding was interpreted within a unitisation framework, where the intrinsic context became unitised with the item and enhanced familiarity based remembering.

The findings also highlight that in order to fully understand post retrieval processing in both young and old adults, focus should move away from examining quantitative differences in the right frontal effect over long time periods and instead identify qualitatively distinct late frontal effects that may reflect the engagement of various executive functions over time.

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Chapter 1 Memory

Memory refers to an organism's ability to encode, store and subsequently retrieve information. From the cognitive psychologists' perspective, memory comprises a number of independent subsystems and therefore it is not a unitary phenomenon (Tulving, 1999). These subsystems include working memory, which is a temporary storage and manipulation system of limited capacity, and long-term memory, which supports the long-term storage of large amounts of information. Long-term memory is divided into declarative memory (memory that is consciously communicated or declared to others) and procedural memory (memory for skills etc. that are acted out without conscious thought about the procedure or prior learning experience e.g. driving a car). Declarative memory is further divided into two systems called episodic memory (memory for personally experienced events) and semantic memory (memory for facts). The research described in this thesis is concerned with understanding how information is retrieved from episodic memory. This chapter will begin by describing the organization of memory in greater detail. This description will be followed by a consideration of single and dual process theories, along with a discussion of source memory and strategic retrieval from episodic memory.

1.1 The Organization of Memory

Memory research has focussed on fractionating memory into a number of discrete subsystems in order to improve our understanding of how we remember information. A lot of our knowledge of the subsystems of memory comes from neuropsychological assessment of amnesic patients, who often have certain memory deficits while other memories are preserved. Neuropsychological evidence for distinct memory subsystems has been supplemented by results from experimental psychology and neuroimaging using healthy participants. Based on the converging evidence from neuropsychology, experimental psychology and neuroimaging, the unitary phenomenon of memory has been steadily divided; the first important distinction is between the working memory system and the long-term memory system.

1.2 Working Memory and Long-Term Memory

Baddeley and Hitch (1974) introduced a multicomponent working memory model, comprised of an attentional control system – the central executive – along with two limited capacity short-term memory storage systems – the phonological loop and the visuospatial sketchpad. The phonological loop holds speech and acoustic based information in temporary storage. The storage is dependent on a memory trace that fades in seconds unless there is rehearsal. Rehearsal is thought to depend on either covert or overt vocalization. The visuospatial sketchpad performs a similar function as the phonological loop but for visual and spatial information. Rehearsal is thought to occur, possibly involving eye movements. The central executive is not a storage system, but in fact controls the flow of information to and from the two short-term memory systems; it is important for the manipulation of information in short-term memory.

Baddeley (2000) included a fourth component in the model - the episodic buffer. This buffer is a short-term storage system, controlled by the central executive, linking information from the phonological loop and visuospatial sketchpad to form integrated units of visual, spatial, and verbal information with chronological ordering, such as the memory of a story or a movie scene. The episodic buffer is also assumed to link information from the two storage systems of the working memory model with information from episodic long-term memory. The system is accessible through conscious awareness and differs from episodic long-term memory in being temporary in nature. The main motivation for introducing the episodic buffer was the observation that some (in particular, highly intelligent) patients with amnesia, who presumably have no ability to encode new information in long-term memory, nevertheless have good short-term recall of visual, spatial, and verbal aspects of stories, recalling much more information than could be held in the phonological loop or visuospatial sketchpad (Baddeley and Wilson, 2002).

Biologically, working memory involves temporary electrical activity of neurons in the brain that can become long-term memory through the process of rehearsal. Rehearsal results in long term potentiation, which is the long term increase of electrical activity in the brain leading to more permanent neurochemical changes (Kandel, 2007).

Neuropsychological evidence strongly suggests that working memory and long-term memory are separate systems. One of the most famous cases in memory research is the case study of patient H.M., who had parts of his hippocampus, parahippocampal cortices, and surrounding tissue removed in an attempt to cure his epilepsy (Scoville and Milner, 1957). H.M’s resultant long-term memory deficit took the form of anterograde amnesia (an inability to form new memories) and partial retrograde amnesia (an inability to recall events that occurred before the onset of amnesia). Despite his gross reduction in long-term memory functioning, H.M. appeared to have spared working memory functioning: he performed well on tests of working memory such as the digit span task that requires the temporary storage and manipulation of information. H.M. therefore provides an example of a single dissociation between working memory and long-term memory, with damage to his long-term memory and spared functioning of his working memory (for other similar cases, see Baddeley and Warrington, 1970;

Cave and Squire, 1992). The case study of H.M. was groundbreaking because it demonstrated that specific memory functions are dissociable from one another.

The example of a single dissociation between working memory and long-term memory provided by patient H.M. does not provide conclusive evidence that the two systems are functionally independent. It may be the case that long-term memory retrieval is more difficult than working memory, with the two systems relying on the same cognitive processes. Consequently, to provide stronger evidence for distinct memory systems, demonstration of a double dissociation is necessary, where one factor affects performance on task A but not task B, while a second factor affects performance on task B but not task A. Process purity is an important issue to consider when demonstrating a double dissociation. A task is ‘process pure’ when it is supported by a single cognitive process. The rational behind double dissociations is that if each task is process pure and that each cognitive process is supported by discrete brain regions, then a double dissociation provides evidence that the processes supporting tasks A and B are separate. Shallice and Warrington (1970) described the case of patient K.F. who demonstrated the opposite pattern of memory impairment to H.M., namely a severe deficit on working memory tasks but intact performance on long-term memory tasks. Together the cases of H.M. and K.F. represent a double dissociation, providing strong evidence that working memory and long-term memory are functionally independent systems.

Although demonstrations of functional independence have been used to support the view of multiple distinct memory systems, the evidence they provide is not compelling. According to Dunn and Kirsner (2003), the interpretation of a double dissociation as evidence for separate systems depends on the selective influence assumption, which states that each variable must affect only one process, and that each process must contribute to only one task. As tasks are seldom process pure, this assumption is rarely met. Consequently, the distinction between working memory and long-term memory should not be viewed as being unbreakable (Estes, 1999; Ranganath and Blumenfeld, 2005). However, Baddeley (2003) noted that double dissociations still remain a useful tool in understanding complex cognitive systems because they place stronger constraints on identifying separate systems than the alternative stochastic independence approach. Stochastic independence is obtained when there is no significant correlation between two tasks. The rationale behind this is that if two tasks rely on the same system then the tasks should correlate, if they rely on different systems there should be no correlation between performance.

1.3 Declarative and Procedural Memory

Long-term memory has itself been fractionated into declarative and procedural memory systems (Tulving, 1983). Declarative memory allows previously experienced information to influence the present via consciousness, whereas procedural memory (comprising skill and habit learning, and priming) enables past experience to influence the present without realising that we are in fact remembering.

Explicit and implicit memory tasks are used to assess declarative and procedural memory, respectively. Explicit memory tasks require participants to remember previously encountered items, for example words studied in a list. Recognition memory is an example of an explicit memory task, where a list of items is studied followed by a test list containing studied and unstudied items. The task during the test phase is to indicate whether each item is old (was present in the study list) or new (presented for the first time in the test list). In contrast, implicit memory tasks do not require participants to retrieve previously encountered information. Instead, participants typically make non-mnemonic responses to a series of items, for example by assessing perceptual information. Priming is assessed by enhanced performance or speeded response times to repeated items compared to new items.

As discussed previously, two forms of memory can only be considered as distinct systems if they are shown to be functionally independent (Sherry and Schacter, 1987). Healthy adults have shown double dissociations between implicit and explicit memory tasks. For example, Jacoby and Dallas (1981) showed that deep processing (level of semantic meaning) compared to shallow processing (level of perceptual features) at study, improved performance on explicit memory tasks, leaving implicit memory task performance unaffected. In addition, Jacoby and Dallas (1981) noted that changes between study and test modalities or perceptual features reduced accuracy on implicit but not explicit tasks. Performance on explicit memory tasks is sensitive to depths of processing whereas implicit memory task performance is stimulus specific.

1.4 Episodic and Semantic Memory

Declarative memory has been divided into two distinct subsystems: episodic memory and semantic memory. The products of retrieval from both episodic and semantic memory are available to consciousness, with episodic memory providing a record of personally experienced events, and semantic memory forming the basis of facts and knowledge about the world. A typical example that distinguishes between the two systems is provided by considering the question ‘What is the capital of Italy?’ Information from semantic memory has been retrieved if the correct answer ‘Rome’ comes to mind as a fact. In contrast, information from episodic memory has been retrieved if a particular personal episode involving the fact that Rome is the capital of Italy comes to mind.

Although there is evidence that the semantic and episodic memory systems interact (Greve et al., 2007), neuropsychological evidence supports the contention that they are distinct subsystems of declarative memory. For example, evidence for a double dissociation is provided by patients L.P. (De Renzi et al., 1987) and K.C. (Tulving et al., 1991). L.P.'s inability to name objects or famous people, but ability to perform recognition memory tasks, demonstrated impaired semantic memory but spared episodic memory. In contrast, K.C.'s ability to learn new facts, but inability to perform recognition memory tasks, demonstrated spared semantic memory and impaired episodic memory. Further evidence of a dissociation between episodic and semantic memory comes from Vargha-Khadem et al. (1997) who demonstrated that amnesics with damage to the hippocampus but some spared parahippocampal cortex were able to demonstrate some degree of intact semantic memory despite severe anterograde amnesia. These findings led the authors to propose that episodic memory is dependent on the hippocampus whereas semantic memory depends on the parahippocampus.

This thesis is concerned with how information is retrieved from episodic memory. Consequently, the following sections will describe episodic memory in more detail, beginning with a discussion of the neuroanatomical basis of episodic memory, and followed by a description of several theoretical accounts of episodic memory.

1.4.1 Neuroanatomical Model of Episodic Memory

Episodic memory involves the prefrontal cortex and the hippocampus and surrounding parahippocampus of the medial temporal lobe (MTL) formation (Tulving and

Markowitsch, 1998; Shimamura and Squire, 1987; Squire and Zola, 1996; 1998). Although Vargha-Khadem et al. (1997) implicated the parahippocampus in semantic memory only, this area of the MTL is also important for the encoding and retrieval of familiarity based information in episodic memory, whereas recollection is associated with the hippocampus (see section 1.4.2.2 for a description of familiarity and recollection). The aforementioned regions of the MTL form the ‘core’ memory system, while the prefrontal cortex acts in a supporting role. During episodic encoding, the prefrontal cortex appears to control the input of information into the MTL (Moscovitch, 1994), where it forms a memory trace (Schacter et al., 1998; Eichenbaum, 2000). Although the MTL is necessary for encoding, the memory trace itself is thought to be stored elsewhere, in the areas of the cortex that mediated the initial processing of the episode. During retrieval, in a process known as ecphory (Tulving, 1983), the memory trace is reactivated through an interaction with an external (or internally-generated) retrieval cue (Moscovitch, 1994). The prefrontal cortex mediates MTL output during retrieval through executive control or ‘working-with-memory’ processes, and activation of the prefrontal cortex occurs independently of retrieval success (Moscovitch, 1994).

The contribution of the MTL to episodic encoding and retrieval is rapid, allowing memory for personal events to occur in the absence of conscious effort (Buckner, 2003). In contrast, frontal lobe involvement in episodic retrieval is largely effortful and conscious (Wheeler et al., 1997). The importance of the frontal lobes in episodic memory is evident from studies of frontal lobe patients who exhibit behavioural impairments on a range of episodic tests, including source memory, recall and, to a lesser extent, recognition (Wheeler et al., 1995; 1997).

The prefrontal cortex is associated with our executive functions (Aron et al., 2004), which are a set of higher order cognitive processes (e.g. working memory, planning, flexibility of thinking and responding, and strategy use). As described earlier, working memory is a temporary storage and manipulation system of limited capacity (Baddeley and Hitch, 1974). Planning involves the identification and organisation of steps needed to carry out an intention or achieve a goal; in order to plan it is necessary to look ahead, conceive of alternatives and weigh and make choices (Lezak et al., 2004). Flexibility of thinking and responding is the ability to regulate behaviour by focussing on a thought or action and being able to shift to another thought or action according to the demands of the situation (Lezak et al., 2004). Finally, strategy use involves seeking out a range of solutions to solve problems and choosing the most appropriate for the situation (Baddeley, 2007). Neuroimaging studies have shown that different regions of the prefrontal cortex are associated with the aforementioned executive functions: PET scanning studies have shown that performance on working memory tasks activate dorsal and ventral prefrontal regions (Mehta et al., 2000; Owen et al., 1996; Robbins et al., 1998), performance on planning tasks activate the right dorsolateral prefrontal cortex (Baker, et al., 1996; Morris et al., 1993; Owen et al., 1996), while performance on tests assessing flexibility of thinking and responding activate regions within the anterior prefrontal lobe (Rogers et al., 2000).

Considering the range of executive processes that can coordinate episodic memory, by simply saying that the prefrontal cortex mediates MTL output during retrieval through executive control or ‘working-with-memory’ processes, the neuroanatomical model falls short in providing a clear account of the role of the prefrontal cortex in episodic memory. Neuroimaging studies provide considerable evidence that different regions of the prefrontal cortex are active during episodic memory retrieval, possibly reflecting the engagement of various executive functions. The recruitment of the anterior prefrontal cortex appears to be dependent on the retrieval task demands or the amount of cognitive effort required. For example, retrieval of source information (Nolde et al., 1998) or weakly encoded information (Wheeler and Buckner, 2003) has been linked to anterior prefrontal cortex activation. In contrast, activation of posterior prefrontal cortex regions appears to be linked to the retrieval of verbal information (Wagner et al., 1998; Buckner, 2003). Activation of the right prefrontal cortex generalises across verbal and non-verbal materials, and is typically long in duration during fMRI studies, indicating the involvement in monitoring of retrieval attempts (Buckner and Wheeler, 2001). The extended duration of the right prefrontal cortex activation can be compared with the extended duration of the late right frontal old/new effect reported in ERP studies of episodic memory (see ERPs, Recognition Memory and Ageing chapter). It follows, therefore, that establishing a relationship between the activation of different regions of the prefrontal cortex during episodic memory retrieval, and specific executive functions, will further our understanding of the role of the prefrontal cortex during episodic memory retrieval.

1.4.2 Theoretical Accounts of Episodic Memory

Episodic memory has been studied in the laboratory using a variety of tasks, including free-recall, cued-recall and recognition. As the research reported in this thesis employs a source memory recognition task, the remainder of this chapter will focus on recognition memory. Recognition memory tasks consist of a study phase, where participants study a list of items, followed by a test phase, where a list of studied and unstudied items are presented; the participant is required to make an old/new discrimination between studied (old) and unstudied (new) items. Two opposing theoretical accounts attempt to explain the contribution of episodic memory retrieval to performance on recognition memory tasks: single-process models and dual-process models. Single-process models assert that old/new decisions are based on one single retrieval process (e.g. Green and Swets, 1966; Banks, 1970; Donaldson, 1996; Dunn, 2004; Heathcote et al., 2006), whereas dual process models maintain that two dissociable retrieval processes support recognition memory (Atkinson and Juola, 1974; Jacoby and Dallas, 1981; Mandler, 1980; Tulving, 1985; Yonelinas, 1994). As the research in this thesis supports a dual-process theory perspective, the remainder of the chapter will mainly focus on dual-process theories of recognition memory. Firstly, however, although a wide range of evidence refutes the single-process perspective (see Yonelinas, 2002), a brief overview of single-process theories will be provided.

1.4.2.1 Single-Process Theories

Several single-process models of recognition memory (e.g. SAM, Gillund and Shiffrin, 1984; MINERVA 2, Hintzman, 1988; TODAM, Murdock, 1997; REM, Shiffrin and Steyvers, 1997; BCDMEM, Dennis and Humphreys, 2001) assert that old/new decisions are based on an assessment of memory strength. Most of these models are based on signal detection theory (Green and Swets, 1966; Macmillan and Creelman, 1991; Snodgrass and Corwin, 1988), where old and new items form partially overlapping Gaussian distributions along a continuum of familiarity or memory strength. The distribution of old items lie further along the continuum than the distribution of new items, due to the previous presentation of old items.

Participants set a decision criterion along the memory strength continuum (Figure 1). If an item’s memory strength is judged to be above the criterion then an ‘old’ response is made, whereas if the memory strength is judged to be below the criterion then a ‘new’ response is made. The old and new distributions overlap so that some new items have greater memory strength than some old items, and some old items have less memory strength than some new items.

Old items that have a memory strength falling above the decision criterion are correct responses and are classed as hits, whereas old items associated with a memory strength falling below the criterion are incorrect responses and are called misses. In addition, new items with a memory strength below the criterion are correct responses and are known as correct rejections, while new items associated with a memory strength above the criterion are incorrect responses, otherwise known as false alarms. Within signal detection theory, the signal refers to the hit rate and the noise refers to the false alarm rate.

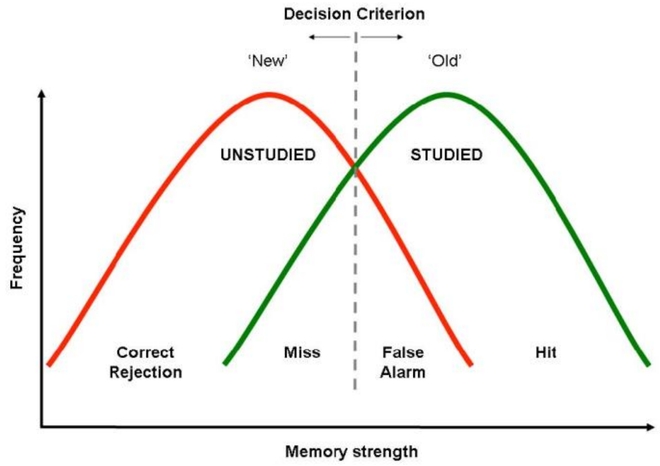

Figure 1. Signal detection model

The signal detection model of recognition memory incorporates two important measures of memory performance: discriminability (or sensitivity) and response bias. Discriminability refers to how well old items can be distinguished from new items, and is represented as the distance between the old and new distributions (Figure 2). When discriminability is high, the old and new items differ greatly in familiarity so the distributions are more spread apart. In contrast, when discriminability is low, the old and new items do not differ greatly in familiarity so the distributions are closer together. d’ (dee prime) is the measure of discriminability. d’ is the hit rate minus the false alarm rate, but the hits and false alarms are transformed first using a Gaussian z transformation:

$$d' = z(H) - z(FA)$$

The z transformation converts the hit and false alarm rates to a z score (i.e. to standard deviation units). A hit or false alarm rate of 0.5 is converted into a z score of zero; proportions larger than 0.5 are converted into positive z scores, whereas proportions lower than 0.5 are converted into negative z scores. If a participant cannot discriminate at all the hit rate equals the false alarm rate and d’ is zero. As long as the hit rate is greater than or equal to the false alarm rate d’ must be greater than or equal to zero. The larger the d’ value the greater the discriminability. Therefore, when assessing memory performance the hit rate itself is insufficient, the proportion of false alarms must also be taken into account. Dependent on the false alarm rate, smaller hit rates could indicate a better discrimination than larger hit rates. For example, a hit rate of 0.5 with 0.2 false alarms reflects better discrimination performance than a hit rate of 0.9 with 0.9 false alarms.

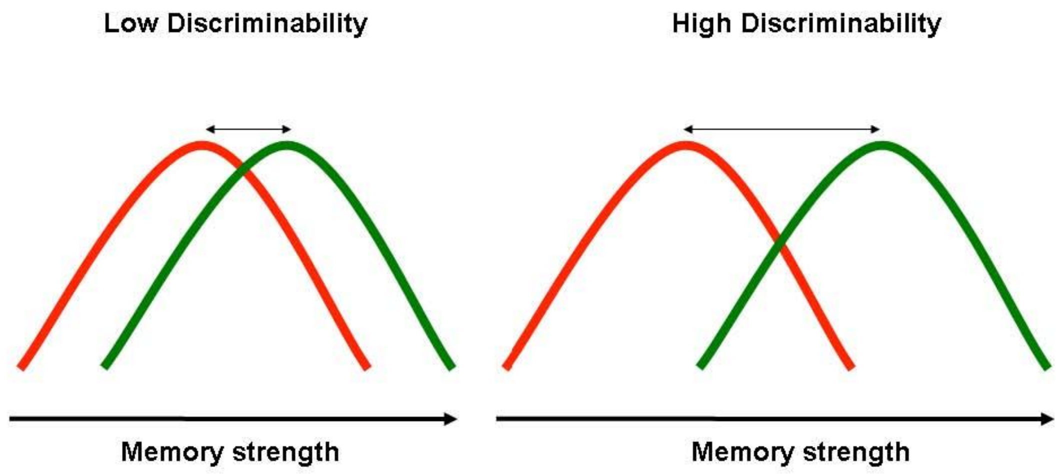

Figure 2. Discriminability in the signal detection model

Response bias refers to how liberal or conservative participants are in responding 'old' when uncertain. Response bias is reflected in the decision criteria placement (Figure 3). When the criterion is raised (moved to the right) both the hits and false alarm rates decrease, reflecting a conservative bias (i.e. predominantly new responses are made; old responses are only made when the participant is sure the item is old). When the criterion is lowered (moved to the left) both the hits and false alarm rates increase reflecting a liberal bias (i.e. predominantly old responses are made; new responses are only made when the participant is sure the item is new). The criterion adopted depends on whether the participant wants to minimise false alarms or misses: a conservative bias minimises false alarms whereas a liberal bias minimises misses. Criterion location c is the measure of response bias. c is the hit rate plus the false alarm rate, but again the hits and false alarms are transformed first using a Gaussian z transformation:

$$c = z(H) + z(FA)$$

If the sum of the hits and false alarms is equal to the sum of the correct rejections and misses then there is no bias. If the sum of the hits and false alarms is greater than the sum of the correct rejections and misses then there is a liberal bias, whereas if the sum of the hits and false alarms is less than the sum of the correct rejections and misses then there is a conservative bias.

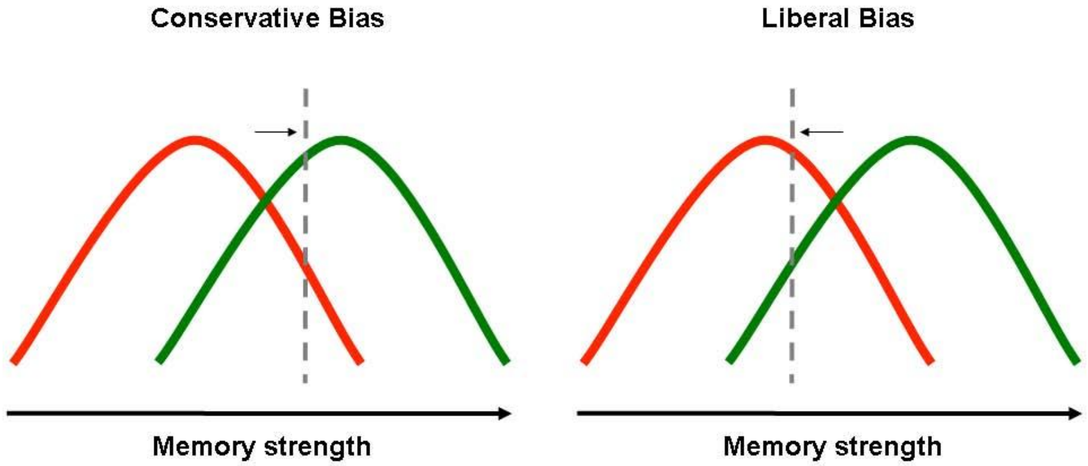

Figure 3. Response bias in the signal detection model

Discriminability indicates whether participants can perform the task, whereas bias indicates how they perform the task. Discriminability and bias are independent, therefore d’ and c are good measures of discriminability and bias because one remains constant when the other changes (Macmillan and Creelman, 1991). Single-process models of recognition memory are attractive because they provide parsimonious accounts for the contribution of episodic memory to performance on recognition memory tasks. However, the models are open to criticism (see section 1.4.2.2.1 – evidence for two retrieval processes also provides evidence against single process theories) and consequently, many cognitive psychologists accept that dual-process theories provide a better account for performance on episodic memory tasks.

1.4.2.2 Dual-Process Theories

A number of dual-process models (Atkinson and Juola Model, 1974; Mandler Model, 1980; Jacoby Model, 1981; Tulving Model, 1985; Yonelinas Model, 1994) maintain that two dissociable retrieval processes support recognition memory: familiarity and recollection. All dual-process models are similar in that they propose that familiarity and recollection are dissociable retrieval processes. Familiarity is recognition of an item without retrieval of any contextual information, and resembles the memory strength based retrieval process described by single-process models. In contrast, recollection involves the recognition of an item along with the retrieval of contextual information, such as when and where the item was encoded. The models are often treated as slight variations of the same basic theory.

The models differ, however, in the predictions they make about whether familiarity and recollection operate in parallel or serially, and how they conceptualise the relationship between familiarity and recollection. Three different views of the relationship between familiarity and recollection have been suggested: independence, exclusivity and redundancy (Joordens and Merikle, 1993; Knowlton, 1998). According to the independence view, familiarity can occur alone, recollection can occur alone, or familiarity and recollection can co-occur. The exclusivity view, in contrast, proposes that familiarity or recollection can happen alone but the two processes do not co-occur. Finally, the redundancy view states that familiarity can occur alone, or familiarity and recollection co-occur; recollection does not happen without familiarity. Prior to describing the dominant dual-process models, along with their predictions about how the processes operate and the proposed relationships between familiarity and recollection, the following section will review evidence in support of the involvement of two processes in recognition memory.

1.4.2.2.1 Evidence for Two Recognition Processes

A wide range of evidence attests to the dual-process theory view that two dissociable retrieval processes support recognition memory. Behavioural experiments of normal healthy adults have shown that short delays between test stimulus presentation and response result in higher false alarms than longer delays (Reed, 1973; Dosher, 1984; Gronlund and Ratcliff, 1989; Hintzman and Curren, 1994; McElree et al., 1999). False alarms are assumed to result from familiarity, therefore with longer delays a second process could be engaged that over-rides familiarity, resulting in fewer false alarms; this data suggests that more than one process supports recognition memory. In addition, item recognition is preserved at short delays while context recognition is impaired (Hintzman and Caulton, 1997; Gronlund et al., 1997;.Hintzman et al., 1998).

Dual process theories also draw on evidence from neurological patients. For example, amnesic patients have relatively spared item recognition but impaired memory for associative recognition, indicating that the regions damaged in amnesia are more important for the latter than the former type of recognition judgement (Huppert and Piercy, 1976; 1978; Hurst and Volpe, 1982; Mayes, 1992; Aggleton et al., 2000).

Animal research has provided another strand of evidence supporting dual process theories. Investigations using rats and non-human primates have shown that parahippocampal lesions disrupt the discrimination of familiar and novel items, whereas hippocampal lesions result in a specific deficit for memory for associations between studied items (Eichenbaum et al., 1994; Fortin et al., 2004). These studies suggest that the parahippocampal region supports familiarity, while the hippocampus supports recollection. Furthermore, Aggleton and Brown (1999) stated that familiarity, and in particular recollection, interact with the prefrontal cortex.

Finally, evidence in support of dual process theories comes from fMRI data. Yonelinas et al. (2005) used confidence ratings during a recognition memory task to separate the contributions of familiarity and recollection in normal human adults. High confidence responses, assumed to reflect recollection based remembering, were associated with increased hippocampal activation, whereas low confidence familiarity based responses were associated with increased parahippocampal activation. In addition to the aforementioned studies, event-related potential studies have debatably provided the strongest evidence in support of dual-process theory (see ERPs, Recognition Memory and Ageing Chapter).

1.4.2.2.2 The Atkinson and Juola Model - Conditional Search

Atkinson and Juola (1974) proposed the conditional search model, which states that familiarity is a fast process assessing perceptual information, whereas recollection is slower and assesses semantic information. According to the model, recognition judgements are modelled on a modified version of signal detection theory. The participant sets a high criterion and accepts test items with familiarity ratings exceeding this criterion as being old (studied), and test items with familiarity ratings falling below a lower criterion as new (correct rejections). For items falling between these criteria, which would require guessing if only familiarity was available, the participant engages in an extended recollection process. This process is a slower method than the fast acting familiarity judgement, and assesses semantic information rather than perceptual information, allowing more detailed contextual material to be retrieved. Therefore, Atkinson and Juola propose that familiarity is the primary basis for recognition and recollection is only used when familiarity information is uncertain. The relationship between familiarity and recollection proposed by the conditional search model is conditional, with recollection being conditional upon the failure of familiarity, and redundant, where recollected items are familiar but their familiarity level is not useful for distinguishing them from new items.

1.4.2.2.3 The Mandler Model - Independence

Mandler's Independence Model (1980) separates recognition memory in terms of a fast acting assessment of item familiarity that is based on signal detection theory, or recollection, which is a slower extended memory search process. For example, we may see someone on the bus that is familiar to us, but it may require considerable time and deliberation to recognise who they are. Central to The Independence Model is the view that familiarity reflects intra-item integration of the perceptual aspects of the item in memory. The item itself is focused on, and recognition occurs without the retrieval of any contextual information. By contrast, recollection involves a search/retrieval process where elaborative (conceptual or semantic) or inter-item information is retrieved. The context surrounding the encoding of the event is focused on, rather than simply the event itself.

Mandler (1980) proposed the independence view. Atkinson and Juola's model and Mandler's model essentially differ only on the questions of whether the two processes begin in parallel or serially, and the relationship between familiarity and recollection. Mandler rejected Atkinson and Juola's view that failure of familiarity is followed by a search process. Instead Mandler proposed that familiarity and recollection are independent and operate in parallel.

1.4.2.2.4 The Jacoby Model – Automatic vs. Consciously-Controlled Processing

Jacoby and Dallas (1981) also proposed that familiarity and recollection are independent, parallel processes. In their model, familiarity is based on an automatic assessment of perceptual fluency, i.e. the easier/more fluent the processing is at encoding (e.g., items presented more clearly) the more familiar the item will become at retrieval. In contrast, recollection represents the intentional, controlled process that recovers contextual information about the encoding episode. While the conditional search and independence models view familiarity as the activation of a general perceptual, or semantic, representation, Jacoby's model views familiarity as reflecting memory for a particular presentation of an item: stimuli that have been processed more fluently are more familiar. Consequently, Jacoby's model considers both familiarity and recollection to reflect detailed episodic information for prior episodes.

1.4.2.2.5 The Tulving Model – Knowing and Remembering

Tulving (1985) argued that familiarity and recollection map onto the conscious experience of knowing that a retrieval cue has been encountered previously, and the conscious experience of remembering specific episodic information, respectively. Furthermore, familiarity is controlled by the semantic memory system, whereas recollection is controlled by the episodic memory system. The two systems are believed to operate independently and in parallel at retrieval, and have a trade-off relationship: impoverished semantic memory traces can be compensated for by the episodic memory system, and impoverished episodic memory traces can be compensated for by the semantic memory system.

1.4.2.2.6 The Yonelinas Model – A Signal Detection/Threshold Model

The Yonelinas Model (1994) argues that familiarity and recollection differ in the type of information (quantitative vs. qualitative, respectively) they provide about the stimulus at retrieval. Familiarity is based on the signal detection model, and reflects the assessment of quantitative memory strength. In contrast, recollection is viewed as a threshold process, whereby qualitative information about the previous episode is retrieved on an all-or-none basis. Recollection and familiarity are assumed to be independent, with both processes initiating in parallel, but with familiarity information becoming available more rapidly than recollection information.

Threshold Theory (Krantz, 1969; Luce, 1963) assumes that the decision space is characterised by a few discrete states, rather than the continuous assessment of memory strength proposed by signal detection theory. While signal detection theory asserts that every item has a varying level of familiarity, threshold theory is all-or-nothing (i.e. items are either recognised or they are not).

In two-high threshold theory there are two memory thresholds, one for old items and one for new items (Figure 4). The theory is termed high threshold because new items can never cross the old item threshold and old items can never cross the new item threshold.

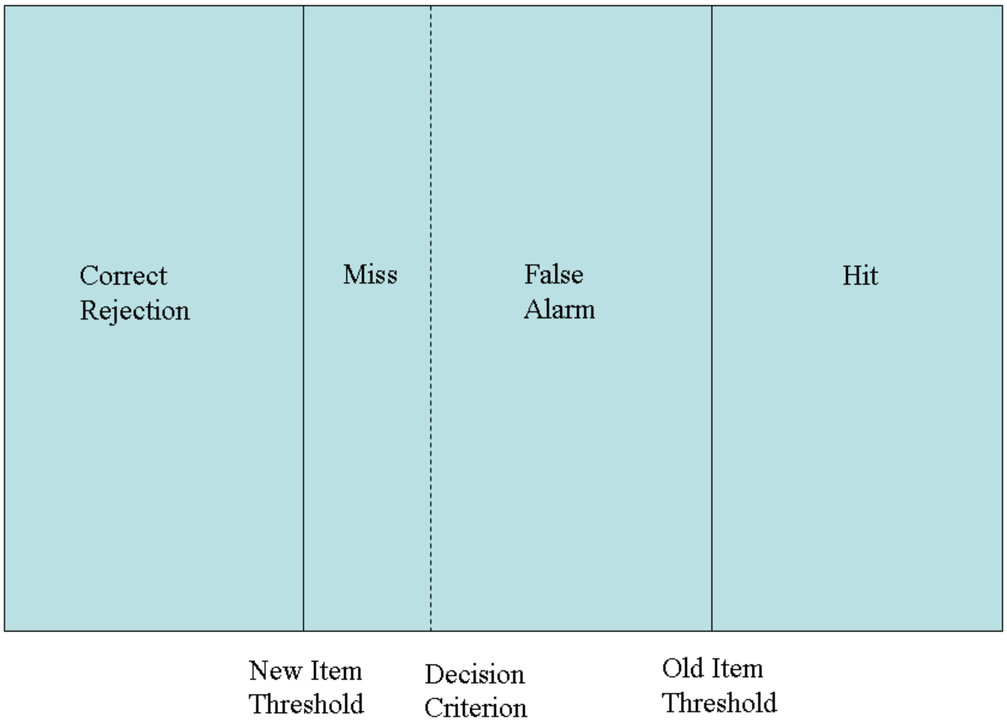

Figure 4. Two-high threshold theory

The two thresholds define three possible memory states: old recognition, new recognition and uncertainty. Old items crossing the old recognition threshold will be identified as old; new items crossing the new recognition threshold will be identified as new; items in the uncertain state will be classed as old or new depending on the participant's response bias. The bias criterion is located in the uncertain state. In Figure 4 the decision criterion is placed to the left, reflecting a liberal bias that results in increased false alarms. A criterion placed to the right would result in a conservative bias and increased misses. False alarms and misses always occur from the uncertain state.

As for the signal detection model, two-high threshold theory also incorporates measures of discriminability and response bias. Pr is the measure of discriminability and is the hit rate minus the false alarm rate:

$$Pr = H - FA$$

The hit rate is composed of a certain proportion of true recognition plus lucky guesses from the uncertain state. Because false alarms are only generated from the uncertain state, the false alarm rate is said to be a direct estimate of the probability of saying ‘yes’ when uncertain. Therefore, the discriminability measure Pr is thought to be a correction for guessing.

Br is the measure of response bias, and is calculated by dividing the false alarm rate by 1 minus Pr:

$$Br = FA / (1 – Pr)$$

A value of Br equal to 0.5 indicates a neutral bias, a value greater than 0.5 indicates a liberal bias, and a value less than 0.5 indicates a conservative bias.

Signal detection theory and two-high threshold theory differ in their underlying assumptions about how participants perform recognition memory tasks: signal detection theory assumes a memory strength continuum, whereas threshold theory proposes a few discrete memory states. Despite these differences, their measures of discriminability and bias do not differ greatly (Snodgrass and Corwin, 1988); however, these authors do suggest that two-high threshold theory is slightly more sensitive than signal detection theory. Consequently, and in accordance with the majority of recognition memory studies, the research reported in this thesis adopts discriminability and bias measures from the two-high threshold theory.

Although the aforementioned dual process models have identified recollection and familiarity as two dissociable retrieval processes supporting recognition memory, a fundamental question is how to determine whether familiarity and/or recollection are contributing to performance. Task dissociation methods (e.g., recall/recognition comparisons and item/associative recognition comparisons) provide one answer to this question by aiming to identify a task or test condition that isolates the two processes. A tight experimental design should in theory lead to ‘pure insertion’ or ‘process purity’, which means that the contrast of the two conditions will reveal the operation of a single process (familiarity or recollection). However, according to Jacoby (1991) task dissociation methods do not measure the contributions of familiarity and recollection in a pure and uncontaminated way. For example, although familiarity and recollection are viewed as dissociable processes, explicit recognition tests frequently reflect a blend of both. Consequently, the Tulving, Jacoby and Yonelinas dual process models have developed process estimation methods to estimate the separate contribution of recollection and familiarity to overall performance on a task. These procedures are introduced in the following sections.

1.4.2.3 Separating Recollection and Familiarity – The Remember/Know Procedure

In Tulving’s (1985) remember/know procedure, in addition to endorsing recognised items as old, participants also make subjective remember/know judgements. Remembering is defined as the retrieval of both item and contextual information, whereas knowing is characterised by the feeling that an item has been presented previously, without the retrieval of contextual information. Remember responses are thought to result from recollection, while know responses are the consequence of familiarity. Two potential problems with this procedure are: first the procedure is based on the assumption that familiarity and recollection are exclusive; second with all subjective measures it is possible that different response patterns may be the result of different interpretations of the same remember/know instructions (Gardiner et al., 2002). Although the results of the remember/know paradigm are often in accordance with other process estimation methods (Yonelinas 2002), Gardiner (2001) suggested that subjectivity might explain why some studies show agreement between remember/know data, while others show disagreement.

1.4.2.4 Separating Recollection and Familiarity – The Process Dissociation Procedure

Jacoby's (1991) process dissociation procedure (PDP) overcomes the potential limitation of subjectivity in the remember/know procedure by providing an objective measure of recollection and familiarity. Participants are required to perform two similar recognition tasks (inclusion and exclusion tasks) under different instructions. Two sets of study items are presented, e.g. words spoken in a male or female voice. In the inclusion task, participants are required to respond old to all study items, regardless of how they were encountered at study. In the exclusion task, participants are told to respond old only to one set of study items, responding new to study items from the other set. Making separate responses for each set of study items in the exclusion task therefore requires the retrieval of the study item and contextual information; the exclusion task is thus designed to promote recollection, and familiarity will undermine performance. In contrast, producing the same response for the two sets of study item in the inclusion task can be on the basis of familiarity or recollection, therefore familiarity aids performance. Estimates of the contribution of familiarity and recollection are obtained by entering the results of both tasks into two equations (for details of the equations, see Jacoby, 1991).

The PDP is based on the assumption that familiarity and recollection are independent. In support of this assumption studies have shown dissociations between the estimates of familiarity versus recollection. Factors that produce changes in recollection but do not change familiarity have been shown in ageing studies (Jacoby, 1999; Jennings and Jacoby, 1997) and divided attention (Jacoby and Kelly, 1992). In addition, an increase in both familiarity and recollection occurs for semantic compared to shallow processing (Toth, 1996), and when solving an anagram rather than reading a word only (Jacoby, 1991). Finally, changes in familiarity but not recollection have been observed for the revelation effect, where better recognition of studied items occurs if they only become gradually revealed at test (Lecompte, 1995).

The Independence assumption has been controversial. For example, Curran and Hintzman (1995) found a correlation between familiarity and recollection and concluded that this was a violation of the independence assumption. However, it is not entirely clear what impact these violations have on the estimates of familiarity and recollection (McBride, Dosher and Gage, 2001). According to Jacoby (1998) in the majority of experimental conditions familiarity and recollection operate independently. Experiments showing agreement between the estimates obtained from the PDP and other methods supports the validity of the PDP (Yonelinas, 2001).

1.4.2.5 Separating Recollection and Familiarity – The ROC Procedure

The receiver operating characteristic (ROC) method (Yonelinas, 1994) uses one recognition task to examine the effect of different confidence values on hits and false alarms. The confidence values are obtained by asking participants to rate on a scale how confident they are that a test item is old or new. The hits and false alarms are then plotted at the various confidence values. ROC curves for familiarity are relatively symmetrical compared to the curves for recollection, due to recollection responses being made with high confidence. The precise contributions of recollection and familiarity to the recognition task are gauged by fitting dual process equations to the ROC curves and solving them for each data point (for details of the ROC equations, see Yonelinas et al., 1998). The ROC method is based on the assumption that familiarity and recollection are independent, and that familiarity is a signal detection process whereas recollection is a threshold process.

As the validity of the process estimation methods described above depends on the accuracy of their assumptions regarding the relationship between familiarity and recollection, it is advisable to look for converging evidence across a variety of procedures. Therefore the research reported in this thesis uses event-related potentials (ERPs) to measure the putative neural correlates of familiarity and recollection. ERP data has demonstrated qualitatively distinct patterns of scalp-recorded activity that are considered to reflect the operation of familiarity and recollection. In fact, Donaldson and Curran (2007) have argued that the findings from ERP studies have provided the strongest evidence for dual process theories. In addition to the ERP data, a version of the PDP is also used to measure familiarity and recollection – the source memory exclusion task. In addition to providing an estimate of familiarity and recollection, this task has been widely used to investigate strategic retrieval in episodic memory – the aim of the research reported in this thesis. As the previous studies using the source memory exclusion task have employed ERP methodology, they will be reviewed in the ‘ERPs, Memory and Ageing’ chapter. However, an appreciation of source memory and strategic retrieval is necessary to understand the more complicated exclusion task; the following section will therefore provide a description of source memory and strategic retrieval.

1.4.3 Source Memory and Strategic Retrieval

Source memory tasks are designed to investigate episodic memory (Johnson, 2008). During source memory tasks, participants study items in two different sources (e.g. words spoken in a male or female voice); at test they are required to not only identify if the item is old or new, but to also remember the source in which the item was presented at study. Because these tasks require the retrieval of contextual information they promote recollection. Neuroimaging studies have frequently shown increased activity in the hippocampus during the retrieval of items for which the source is subsequently recollected, compared to recognised items for which the source is not remembered (Davachi et al., 2003; Ranganath et al., 2003; Kesinger and Schacter, 2006). In contrast, increased activity in the parahippocampus, another MTL region, has been associated with familiarity based item recognition but not with successful source memory (Davachi et al., 2003; Ranganath et al., 2003; Weis et al., 2004; Kensinger and Schachter, 2006; Uncapher at al., 2006). These findings are in accordance with proposals that the hippocampal MTL region is important for recollection based remembering, whereas the parahippocampal MTL region is critical for familiarity based remembering (Aggleton and Brown, 2005, 2006; Diana et al., 2007; Eichenbaum et al., 2007).

Due to their greater complexity than old/new item recognition tasks, source memory tasks are used to investigate strategic retrieval. Strategic retrieval is the retrieval of episodic information by implementing a self-initiated process (Dzulkifli and Wilding, 2005); the more difficult the task is the greater the need for strategic retrieval to maximise performance. An example of strategic retrieval would be reflecting back on retrieved information to ensure accuracy. Studies of patients with frontal lobe damage suggest a role for the frontal cortex in strategic retrieval (Buckner, 2002).

1.5 Conclusion

A variety of evidence has been presented suggesting that memory comprises a number of distinct subsystems and is therefore not a unitary phenomenon. Converging evidence from neuropsychology, experimental psychology and neuroimaging have demonstrated that: working memory and long-term memory are separate systems; long-term memory is divided into declarative and procedural memory systems; declarative memory is further divided into two systems called episodic and semantic memory; finally, the retrieval of information from episodic memory may involve two dissociable processes called familiarity and recollection, and is supported by the prefrontal cortex.

Prior to describing the experimental work, Chapter 3 will discuss ERP methodology, while Chapter 4 will describe studies using ERPs to investigate recognition memory in young and older adults. First, however, Chapter 2 will discuss episodic memory in relation to ageing.

Chapter 2 Memory and Ageing

One of the key concerns of older adults is the experience of memory loss. Subjective reports of age-related memory loss have been corroborated with objective experimental data showing that memory does indeed decline with age. Studies comparing the effects of ageing on episodic memory, procedural memory, working memory and semantic memory find that episodic memory is especially impaired in normal ageing (Nilsson, 2003); whereas procedural memory is relatively spared with age (Fleischman et al., 2004), working memory shows some decline (Verhaeghen and Salthouse, 1997) and semantic knowledge, such as vocabulary, actually improves somewhat with age (Verhaeghen, 2003).

As the research in this thesis is concerned with retrieval from episodic memory, the scope of this chapter is to provide an overview of the effects of normal, healthy ageing on episodic memory. Because working memory performance will also be assessed, the working memory ageing literature will be considered too. However, prior to reviewing the patterns of age-related episodic and working memory impairment that are generally observed, the following section will provide a brief overview of the possible influence of common health problems experienced by older people on memory.

2.1 Ageing, Memory and Health

Ageing is often associated with health problems (Fozard et al., 1990) that can have a deleterious effect on memory (Nolan and Blass, 2002). For example, memory loss is one of the hallmark symptoms of Alzheimer’s disease and other forms of dementia. However other health problems may also be associated with memory deficits in the elderly (Backman et al., 2000a). Incidences of untreated hypertension in midlife, for instance, appear to contribute towards changes in brain morphology in old age. These changes include increases in cerebral white matter, which are related to memory decline (Soderlund et al., 2003; Van Petten et al., 2004). Furthermore, depression in older adults has also been widely associated with increased subjective memory complaints (Albert, 1981; Feehan et al., 1991; Williams et al., 1987), and objective depression-related memory deficits (King et al., 1991; Van Boxtel et al., 2004; for meta-analyses, see Burt et al., 1995; Kindermann and Brown, 1997).

This thesis investigates the effect of normal healthy ageing on the retrieval strategies adopted in episodic memory. Consequently, to ensure that all participants were free from any major health problems that may have contributed to their memory performance, they were asked to provide a self-reported rating of their current health status, a brief medical history, and were screened for depression and dementia. Subjective health reports were used due to the complexity and expense of obtaining objective measures. Although objective measures may be more reliable, Bazargan and Barbre (1994) noted a positive correlation between self-rated health and objective health measures.

2.2 Memory Changes with Ageing

2.2.1 Working Memory

As discussed in the Memory chapter, working memory consists of short-term memory subsystems for the temporary storage of information, and a central executive that is important for the manipulation of information in short-term memory. Studies using digit span tasks to investigate short-term memory and ageing suggest a small, but reliable, advantage for young participants (see Verhaeghen et al., 1993 for a meta-analysis). Age-related decrements on working memory tasks, however, are larger than those found in short-term memory tasks (Daneman and Carpenter, 1980; Salthouse and Babcock, 1991; Salthouse, 1993). The distinction between short-term memory and working memory is that the former involves temporarily storing information whereas the latter entails manipulating or ‘working with’ the temporarily stored information. Studies using the CANTAB battery to assess changes in working memory with normal ageing have consistently found positive correlations between ageing and working memory decline (Robbins et al., 1994; Robbins et al., 1998; De Luca et al., 2003). Ageing studies have also suggested a close relationship between working memory and episodic memory. For example, Frieske and Park (1993) showed that working memory performance mediated ageing differences in the recognition of complex scenes. As working memory involves the temporary storage and manipulation of information, it is important for monitoring the retrieval of information from episodic memory; a clear example of strategic retrieval (Verhaeghen and Salthouse, 1997).

2.2.2 Episodic Memory

The age-related decline in performance on episodic memory tasks is often moderate to large. While in recall tasks, older adults frequently produce more exclusions (failures to recall) and intrusions (recall of never-presented items) and repeat more previously recalled items than young adults, in recognition tasks they often show increased false alarms (Zacks et al., 2000). The elderly are typically more impaired in recall than recognition, most likely because recall is usually more difficult than recognition (Moscovitch and Winocur, 1995).

In addition to exhibiting impaired episodic memory retrieval, the elderly also have poorer episodic encoding compared to young adults (Luo et al., 2007); research shows that older adults tend to use inadequate encoding strategies (Perfect and Dasgupta, 1997; Naveh-Benjamin, 2000). Consequently, ageing differences at retrieval may be due to impaired retrieval and/or encoding. As the research reported in this thesis focuses on age-related changes in episodic memory retrieval, encoding tasks were held constant between age groups in an attempt to ensure the young and old were using the same encoding strategy. Any observed age-related differences at retrieval were therefore more likely to be due to retrieval than encoding.

2.2.2.1 Recollection and Familiarity

Studies investigating memory and ageing using source memory recognition tasks have revealed a clear pattern of results. While the elderly are reasonably good at recognising whether an item is old or new, they show marked impairments in remembering the source in which the items were presented at study. For example, McIntyre and Craik (1987) and Schacter et al. (1991) presented fictitious facts by two different voices to young and older adults, and found that although the elderly were relatively fine at remembering the facts themselves, they showed a significant decline in recollecting the voice in which the facts were presented. In addition, a meta-analysis of research comparing memory for items themselves (including the recognition or recall of words or pictures) with memory for context (including different colours, modalities or voices) confirmed that age-related memory decline is moderate for the items, but large for their context (Spencer and Raz, 1995).

Dual process theory proposes that the age-related decline in source memory occurs because recollection is required for the accurate retrieval of context; recollection becomes impaired with ageing whereas familiarity remains relatively spared. The ‘false fame’ paradigm provides support for this proposition (Dywan and Jacoby, 1990; Jennings and Jacoby, 1993). In this paradigm, participants are required to read a series of non-famous names, and are then presented with a list including the previously presented non-famous names along with famous names, and have to decide whether the people are famous or not. Compared to young adults, older adults more often than not identify the previously presented non-famous names as famous. Using the process dissociation procedure, Jennings and Jacoby (1993) established that the age difference occurred because, compared with young adults, the elderly relied more on familiarity and less on recollection. The process dissociation procedure has also been used with verbal stimuli to demonstrate that recollection becomes impaired with ageing, while familiarity remains mostly unaffected (Jacoby et al., 1996; Hay and Jacoby, 1996; Jennings and Jacoby, 1997; Jacoby, 1999; Benjamin and Craik, 2001).

Dual process theory provides one account for the effects of ageing on episodic memory, however other influential theories do exist. These theories address cognitive ageing in general, and in doing so provide additional accounts for age-related changes in episodic memory. The following section describes the other four main theories of cognitive ageing: speed of processing, reduced inhibition, reduced processing resources and the frontal lobe theory.

2.3 Theories of Ageing and Memory

2.3.1 Speed of Processing

Older adults frequently require increased time compared to young adults to complete cognitive tasks (e.g. Salthouse, 1996; Verghaeghen and Salthouse, 1997). Speed of processing theory proposes that this increased time reflects a reduction in the speed at which many cognitive processes operate in the elderly, therefore reduced processing speed is a major contributing factor to age-related memory decline. Salthouse (1996) proposed that two general mechanisms underlie the relationship between speed of processing and memory performance. The first mechanism – the limited time mechanism – states that the time to perform a later operation may be limited if most of the available time is occupied by the execution of earlier operations. The second mechanism – the simultaneity mechanism – proposes that information from different sources may not be available as fast as in the young, resulting in earlier information being lost by the time later processing is completed. Either of these mechanisms can result in slower performance on memory tasks, which can either be accurate or inaccurate. Earlier stages of processing may be slowed but accurate, but can result in poor performance if this slowing results in a failure to reach later stages.

Evidence in support of the speed of processing theory comes from a variety of sources that have found evidence that performance on perceptual speed tasks is an excellent indicator of age-related performance on episodic memory tasks. Perceptual speed tasks require rapid perceptual same-difference judgements about pairs of digits or letter strings. Speed of processing is measured by the number of correct judgements made within a certain time limit. Bunce and Macready (2005), for example, found that measures of perceptual processing speed accounted for older adults producing less remember responses and more know responses. In addition, correlations between processing speed and accuracy on episodic memory tasks revealed that up to 70% of the age-related variance in accuracy may be related to variance in processing speed (Salthouse, 1996; Verhaeghen and Salthouse, 1997; Park and Hedden, 2001).

2.3.2 Inhibition Deficit Hypothesis

The inhibition deficit hypothesis (Hasher and Zacks, 1988; see also Zacks and Hasher, 1994; Zacks et al., 1996; Hasher et al., 1999) proposes that we perform cognitive tasks through two mechanisms of selective attention: activation and inhibition. Inhibition suppresses the activation of goal irrelevant information so it is less likely to enter working memory, freeing space for goal relevant information; irrelevant information that does enter working memory is quickly removed. Attentional inhibition may also prevent the return of attention to a previously rejected item, such as an external stimulus or an internal thought. The inhibition deficit hypothesis states that the inhibitory mechanism becomes deficient with ageing, resulting in older adults being slower, less able to focus on goal relevant information, and worse at remembering details than young adults.

Support for the inhibition deficit hypothesis comes from the negative priming effect. When the brain is required to inhibit a response to a stimuli, having it uninhibit that response takes some time. The delay is called the Negative Priming Effect. The brain has been prepared to take extra time in producing a response, because that response was previously suppressed. Negative priming is frequently assessed using a variation of the Stroop Test, where the participant is presented with the name of a colour printed in a different colour font. The participant is told to ignore what the word says, and to instead say the colour of the font. On an immediately subsequent trial, the participant is presented with the name of a colour printed in the previously suppressed font, and is again told to say the colour of the font: for example on the first trial the word GREEN is printed in blue font and the participant is required to say ‘blue’. In the subsequent trial, the word RED is printed in green font and the participant is required to say ‘green’. Several studies have demonstrated that, in comparison to young people, older adults have a reduced Negative Priming Effect, indicating that their attentional inhibition to previous stimuli is poorer (Hasher et al., 1991; Kane et al., 1994; Stoltzfus et al., 1993). In addition, the elderly show a range of effects consistent with the notion of reduced inhibition. These effects include increased susceptibility to concurrent environmental distracters (Connelly et al., 1991), and from concurrently activated goal irrelevant thoughts (Gerrard et al., 1991).

2.3.3 Reduced Processing Resources

While the inhibition deficit hypothesis proposed that attentional inhibition is deficient in the elderly, the reduced processing resources theory states that the attentional resources available to older adults for conscious processing are less than that available to the young (Craik and Simon, 1980; Craik and Byrd, 1982; Craik, 1983). Therefore, retrieval tasks that require a great deal of self-initiated processing, or strategic retrieval, should be most susceptible to ageing because strategies are effortful and demand attentional resources (Light, 1991).

Examining the consequences of divided attention on memory performance has provided evidence in support of the reduced processing resources theory. Dividing attention between a primary task and a simultaneously performed secondary task is more demanding than performing the primary task alone, therefore requires increased attentional resources. For example, dividing attention at encoding produces age-related recognition memory deficits during retrieval, indicating that the attentional resources of the elderly were reduced compared to the young (Craik and McDowd, 1987; Anderson et al., 1998). In addition, Whiting and Smith (1997) found that dividing attention at retrieval reduced recognition memory performance more so for older than for younger adults.

The three general resource theories outlined above are not in competition. Reduced speed of processing, reduced inhibitory control and reduced processing resources are likely to operate together to produce the age-related memory impairment seen in many studies (Luo and Craik, 2008). These three theories provided the predominant theoretical explanations of adult age differences in cognition in the 1980s and 1990s (Phillips and Henry, 2005). However, one major criticism of these theories is their lack of specification, i.e. their precise anatomical substrates are yet to be identified (Salthouse, 1996). In the 1990s, attention shifted away from general resource theories to the frontal lobe hypothesis of cognitive ageing, which combined neuroanatomical and neuropsychological evidence to relate cognitive changes to neural changes in the frontal lobes.

2.3.4 The Frontal Lobe Hypothesis

Neuroanatomical research has consistently shown that decreases in brain volume and increases in cerebrospinal fluid occur with ageing (Stafford et al., 1988; Raz, 2000). However, there are greater age-related changes in both the neuroanatomy and neurochemistry of the frontal lobes than other cortical regions. The PFC shows a 10-17% reduction in volume compared to 1-8% reduction elsewhere (West, 1996). In addition to decreases in frontal lobe volume with ageing, alterations in glucose metabolism and cerebral blood flow have been observed in the region (Madden and

Hoffman, 1997; Raz, 2000), along with declines in neuronal synaptic density and dendritic arborisation (Esiri, 1994), and increases in white matter (Kawamura et al., 1993; Pantoni and Garcia, 1997).

The frontal lobes sub-serve our executive functions. Neuropsychological studies have revealed that patients with frontal lobe damage show a range of executive impairments and, as executive functions play an important role in controlling memory retrieval, these studies have also indicated that memory disruption is a key characteristic of frontal damage (Stuss and Benson, 1987). Essentially, the range of executive related deficits seen with normal ageing is highly similar to that found in frontal lobe patients (Moscovitch and Winocur, 1995; but see Phillips and Henry, 2005 for discrepant findings). Consistent with frontal lobe patients, healthy adults demonstrate an age-related decline on tasks such as the Wisconsin Card Sorting Test, which is considered to tap executive functioning, including inhibition (Cohn et al., 1984; Daigneault et al., 1992; Shilling et al., 2002) and cognitive switching (Hughes and Bryan, 2002; Isingrini and Vazou, 1997; Parkin and Java, 1999).

While the aforementioned results convincingly substantiate the frontal lobe hypothesis of ageing, several important limitations must be highlighted: Firstly, just as the lack of uniformity of frontal lesions introduces a high degree of variability into patient data, the age-related changes in the neuroanatomy and neurochemistry of the frontal lobes will also show a high degree of variability from person to person, making a precise characterisation of the frontal lobe hypothesis of ageing difficult. Secondly, neuropsychological tests of frontal functioning only provide an indirect indication of age-related changes in the frontal lobes and, as it is impossible to measure executive functions without tapping other cognitive functions such as attention or perception (Phillips and Henry, 2005), performance on these tests may also reflect a combination of impairment on the three general resource theories outlined previously (reduced speed of processing, reduced inhibitory control and reduced processing resources). Nonetheless, over the last decade, neuroimaging techniques have provided a tool to directly investigate the relationship between the brain and cognitive ageing; combining the findings from neuroimaging and neuropsychology can provide a more complete picture of the brain regions affected by ageing and the consequences on cognition. The following section presents evidence from functional haemodynamic neuroimaging studies, showing the age-related changes in the frontal cortex that are involved in episodic retrieval.

2.3.4.1 Neuroimaging: Changes in Frontal Lobe Activation with Age

Neuroimaging studies have shown that age-related anatomical changes in the frontal lobes are associated with lower frontal activation in older adults during episodic retrieval (Grady, 2002). The more common finding, however, from neuroimaging studies is that age-related anatomical changes in the frontal lobes are related to more widespread and often equivalent levels of activation in frontal lobe regions than young adults, especially during episodic retrieval (Nyberg et al., 1996; Cabeza, 2002).

The pattern of frontal activity observed in the elderly, whether epitomized by lower frontal activation or more widespread and equivalent levels of activation, could reflect the neuroanatomical or neurochemical changes in the ageing frontal lobes that are associated with older adults being less effective at using retrieval strategies (Madden et al., 2002). Alternatively the age-related differences could reflect compensatory processes to help counteract the cognitive decline related to changes in the frontal lobes. Support for the compensation account comes from a variety of sources. For example, an event-related fMRI study showed that when episodic memory performance was equated between young and older adults, older adults exhibited increased bilaterality (Morcom et al., 2003). In addition, younger adults also show increased bilateral frontal activation when the working memory load of a task increases (e.g. Jonides et al., 1997). Furthermore, a PET study showed that older adults who performed well on a source memory task exhibited bilateral prefrontal activation, whereas those who performed less well produced only right-sided activation (Cabeza et al., 2002).

It seems unlikely that the effects of neuroanatomical and neurochemical changes in the ageing brain on cognition are restricted to the frontal lobes (Greenwood, 2000; Band et al., 2002). The following section therefore reviews evidence implicating structural and neurochemical changes in the hippocampus in the age-related decline in episodic memory.

2.4 The Hippocampus/Parahippocampus and Ageing

The hippocampus and parahippocampus are part of the larger medial temporal lobe (MTL) memory system that is involved in declarative memory formation (semantic and episodic memory). Given the critical role of the MTL area in the creation of new episodic memories, this brain region is a clear contender to be involved in certain age-related episodic memory deficits.

While the MTL region is anatomically less susceptible to ageing than the frontal lobes, age-related volume decreases have also been noted in this area (for a review, see Van Petten et al., 2004). Significantly, evidence has indicated that this volume decrease is associated with episodic memory impairment. Golomb et al. (1994) and Raz (2000) reported significant positive correlations between hippocampal volume loss and memory decline in the elderly, and longitudinal studies have shown hippocampal reduction to be an indicator of memory impairment (De Leon et al., 1997; Golomb et al., 1996). However, other research has reported negative correlations between hippocampal volume loss and memory decline in ageing (Sullivan et al., 1995; for a meta analysis see Van Petten, 2004), showing that the evidence regarding the role of hippocampal reduction on episodic memory is not consistent.

Importantly, neuropsychological findings indicate that the contributions of the MTL and the frontal lobes to age-related memory impairment are distinct. Glisky et al., (1995) clustered older adults into high and low groups depending on their scores on tests of MTL and frontal functioning. The low MTL functioning group performed poorly on a simple item recognition test, whereas the low frontal group were unimpaired. In contrast, the low MTL group performed well on a source memory task, while the low frontal group showed a significant deficit. The dual process theory interpretation of these findings is that the MTL formation is principally involved in familiarity, whereas the frontal lobes are involved in recollection. The familiarity view of the MTL contribution to memory decline is corroborated by an account that older adults with high MTL functioning were better than their low MTL counterparts at discriminating between lures showing differing levels of similarity to target stimuli (Rubin et al., 1999). However, reduced MTL functioning may also be related to impaired recollection: positive correlations have been noted between MTL test scores and performance on cued-recall tasks (Winocur et al., 1996) and memory for context (Henkel et al., 1998).

A main drawback of neuropsychological testing is that it can only provide indirect evidence of the association between the MTL formation and age-related memory changes. In contrast, haemodynamic neuroimaging has permitted direct observations of alterations in MTL activity during episodic retrieval tasks, and the weight of evidence suggests that the elderly rely more on familiarity. For example, in an fMRI study of memory and ageing, Springer et al. (2005) construed a link between an increased MTL BOLD response in the elderly and weak recognition performance as reflecting a greater reliance on familiarity (for comparable results from a PET study of cued-recall, see Backman et al., 1997). In addition, in a remember/know recognition test, the elderly produced a reduced hippocampal BOLD signal to correctly identified old words, along with an increase in parahippocampal activity (Cabeza et al., 2004). Because, in comparison to the young group, the elderly also produced more know responses (even though overall accuracy was age equivalent), the authors concluded that the pattern of activation reflected the older adults' increased reliance on familiarity.

2.4.1 Regional Account vs. Network Account of Age-Related Episodic Memory Decline

The aforementioned research, implicating age-related changes in the frontal lobes and the MTL system in episodic memory decline, assumes a regional account. According to this account, cognitive ageing is limited to separate brain areas. For example, a reduction in right PFC activation during episodic memory retrieval in older adults only reflects an ageing change in the right PFC (Cabeza, 2002). The alternative network account proposes that a network of inter-connected brain areas mediates cognitive performance, with ageing influencing not only the function of separate brain regions, but also the myelinated connections between them (Greenwood, 2000). According to this account, therefore, a reduction in PFC activation during episodic memory retrieval in older adults could reflect an ageing change in the right PFC alone, or it could reflect changes in the connection between brain areas.

Evidence for the network account comes from reports of collaborative MTL and frontal activations during the encoding and retrieval of object identity and location only in younger adults (Schiavetto et al., 2002). The older group appeared unable to recruit these encoding and retrieval networks, and alternatively showed decreased MTL activations, along with increased PFC activations. In addition, using structural equation modelling during episodic encoding and retrieval tasks, Cabeza et al. (1997) showed age-related changes in connectivity both within the PFC and between the PFC and other brain areas.

2.5 Conclusion

The detrimental effect of ageing on working memory and, in particular, episodic memory has been well reported. As working memory is important for monitoring the retrieval of information from episodic memory, ageing studies have suggested a close relationship between working memory and episodic memory. However, the effect of normal, healthy ageing on memory can be influenced by common health problems that occur with ageing, such as depression. These health problems must therefore be controlled for where possible before investigating the effects of normal ageing on memory.

The episodic memory literature shows that while the elderly are reasonably good at simple item recognition tasks, they show marked impairments in source or context memory tasks. The dual process theory proposes that the age-related decline in source memory occurs because recollection becomes impaired with ageing, resulting in an increased reliance on familiarity. The speed of processing theory, reduced inhibition theory, reduced processing resources theory and the frontal lobe theory provide additional accounts, suggesting that age-related changes in episodic memory occur due to a reduction in the speed at which many cognitive processes operate, a reduced ability to suppress goal-irrelevant information, a reduction in the availability of attentional resources and changes in both the neuroanatomy and neurochemistry of the frontal lobes, respectively. Importantly, these theories are not in competition, and are likely to operate together to produce age-related memory impairments. The frontal lobe theory has proved particularly influential due to combined neuroanatomical and neuropsychological evidence that relate cognitive changes to neural changes in the frontal lobes. Despite the importance of the frontal lobes to episodic memory (Wheeler et al., 1995; 1997), and in particular to the retrieval of source information, the MTL system is nonetheless widely considered to be fundamentally involved in episodic memory (Eichenbaum et al., 1994; Aggleton and Brown, 1999; Fortin et al., 2004).

While some neuroimaging studies have suggested that the age-related anatomical changes in the frontal lobes are associated with lower frontal activation in older adults during episodic retrieval, the more common finding is more widespread and often equivalent levels of activation. In particular, PFC activation may be more bilateral in elderly adults compared to young adults, and although the involvement of the hippocampus in recognition memory may show an age-related decrease, parahippocampal activation seems to increase with age.

Chapter 3 Event-Related Potentials

In 1929, Hans Berger discovered that the electrical activity of the human brain could be recorded by placing two electrodes on the scalp and connecting them to a differential amplifier. This record of electrical activity is known as the electroencephalogram, or EEG, and is plotted as changes in voltage over time. The frequency (number of waves per second) of normal EEG ranges from 0.01 Hz to 40 Hz or more (i.e. between 0.01 and 40 or more waveforms per second), and the amplitude (height) ranges from approximately –100 to +100 μV (Rugg and Coles, 1995). The EEG contains all scalp detectable activity, however the neural activity related to the cognitive process of interest (the signal), is in the order of 5-10 μV (Kutas and Dale, 1997) so it must therefore be extracted from the background brain activity (the noise). To extract the signal from the noise, ‘epochs’ of the EEG are identified, which are temporal segments that are time locked to an event (e.g. the presentation of a stimulus). Averaging these epochs across trials for each participant, and subsequently across participants, attenuates the noise, revealing the signal: the event-related potential (ERP). The ERP represents the voltage changes that are related to the brain’s response to the stimulus.

ERPs are either exogenous or endogenous. Exogenous ERPs are the early sensory responses dependent on the physical properties of the stimuli, and occur within approximately 250ms of stimulus presentation. Endogenous ERPs are the later cognitive responses dependent on the participant’s interaction with the stimulus; they are of primary interest to cognitive psychologists because they provide a non-invasive method of investigating cognitive processes.

Due to their excellent temporal resolution, ERPs have an advantage over haemodynamic imaging techniques (fMRI and PET) that have poor temporal resolution. The speed of electrical transmission in the brain allows the time course of cognitive operations to be traced in ‘real time’ with near millisecond precision, whereas haemodynamic techniques are constrained by their measurement of blood flow occurring over several seconds. The haemodynamic techniques provide accurate spatial resolution (within a few millimetres) of the brain regions associated with cognitive functions. In contrast, the major disadvantage of the ERP technique is its poor spatial resolution (tens of millimetres). The poor spatial resolution of ERPs is due to smearing of electrical activity as it travels through the skull. In addition, only the firing of neurons organised into open fields can be detected by scalp electrodes, therefore activity from certain regions of the brain cannot be recorded at the scalp.

Prior to considering in detail how the ERP signal is recorded and extracted from the background noise, and the inferences that can be made about cognitive processes on the basis of ERP data, the relationship between the electrical activity generated by neurons in the brain and scalp recorded electrical activity will be considered. A discussion of neuronal electrogenesis is important as it provides constraints on the inferences that can be drawn from ERP data.

3.1 Neuronal Electrogenesis

3.1.1 Individual Neurons

The voltages recorded at the scalp result from electrical activity within neurons (Figure 5) in the brain. There are two main types of electrical activity associated with neurons: postsynaptic potentials and action potentials. Postsynaptic potentials determine whether or not a neuron fires, producing an action potential.

Neurons communicate via the release of neurotransmitters from the terminal buttons of the presynaptic neuron into the synapse (the extra cellular fluid-filled space between the terminal buttons of the presynaptic neuron and the dendrites of the postsynaptic neuron). The neurotransmitters diffuse across the synapse and attach to the dendrites of the postsynaptic neuron. The extra cellular space is positively charged, whereas the inside of the neuron is negatively charged. The neurotransmitters cause ion channels to open on the dendrites of the postsynaptic neuron, permitting ions to enter or leave the neuron, producing a postsynaptic potential. A postsynaptic potential is either excitatory (decreasing the negativity inside the neuron and increasing the likelihood that the neuron will fire) or inhibitory (increasing the negativity inside the neuron and decreasing the likelihood that the neuron will fire). The ion channels that open on the dendrites determine whether the postsynaptic potential is excitatory or inhibitory, not the neurotransmitter itself.

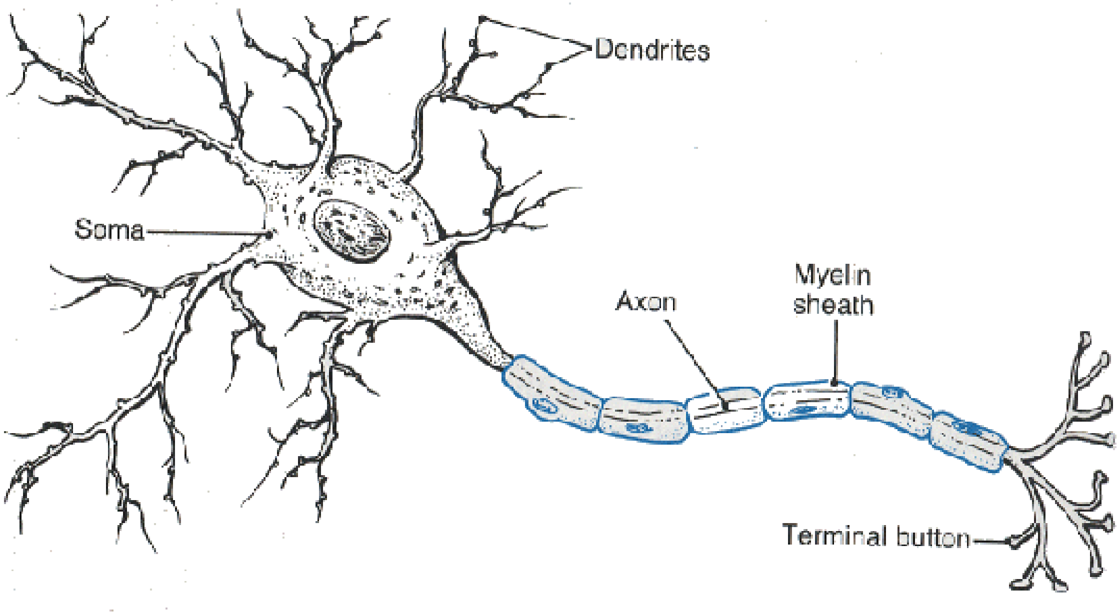

Figure 5. Structure of a Neuron

Excitatory postsynaptic potentials (EPSPs) occur when sodium channels open causing positive sodium ions to enter the neuron making the inside of the dendrites more positive and the outside of the dendrites more negative. In turn, positive current flows out of the cell body (soma), making the inside of the cell body more negative and creating a greater positivity in the extra cellular space surrounding the cell body. Together, the negativity at the extra cellular space surrounding the dendrites and the positivity at the extra cellular space surrounding the cell body create a tiny dipole (a pair of positive and negative electrical charges separated by a small distance).

Inhibitory post-synaptic potentials (IPSPs) occur when potassium or calcium channels open causing either positive potassium ions to leave the neuron or negative calcium ions to enter the neuron. The opening of either of these channels makes the inside of the dendrites more negative and the outside of the dendrites more positive. In turn, negative current flows out of the cell body, making the inside of the cell body more positive and creating a greater negativity in the extra cellular space surrounding the cell body. Together, the positivity at the extra cellular space surrounding the dendrites and the negativity at the extra cellular space surrounding the cell body create a tiny dipole in the opposite direction to the EPSP.

The EPSPs and IPSPs travel through the cell body to the axon. If the sum of EPSPs and IPSPs reaching the axon at any time decreases the negative voltage inside the axon to its threshold of excitation, the neuron fires producing an action potential. An action potential is a change in current flow across the membrane creating a voltage reversal, from a negative voltage inside the axon and a positive voltage outside the axon, to a positive voltage inside the axon and a negative voltage outside the axon. This voltage spike travels down the axon to the terminal buttons causing neurotransmitters to be released into the synapse. The neurotransmitters diffuse across the synapse and attach to the dendrites of the next neuron producing postsynaptic potentials, continuing the cycle.

ERPs predominantly reflect the dipoles created by postsynaptic potentials rather than action potentials (Allison et al., 1986; Wood, 1987). In the vast majority of cases, scalp electrodes cannot detect action potentials due to their timing. Neurons rarely fire at precisely the same time; therefore the negative/positive voltage reversal that occurs during the action potential does not occur at the same time in all neurons. Consequently, current will be flowing into one axon at the same time it is flowing out of another axon, so they cancel each other and produce a smaller signal at the nearby electrode (Luck, 2005). Scalp recordings only reflect action potentials if they occur in cortical structures close to the scalp or if multiple neurons fire in synchronization, then the voltages from the neurons summate producing a large enough voltage to be detected at the scalp.

The polarity recorded at any given scalp electrode depends on the electrode's location with regard to both the neural generator of the electrical activity and the reference electrode (Kutas and Dale, 1997). Accordingly, the observed polarity is a function of the spatial relationship between the recording electrode and the neural generator, and therefore does not convey any meaningful information about underlying cognitive processes (Allison et al., 1986; Wood and Allison, 1981).

3.1.2 Populations of Neurons

A dipole created by a postsynaptic potential of a single neuron is so small that it would be impossible to record it from a distant scalp electrode (Luck, 2005). However, when the postsynaptic potentials of many neurons occur in synchronization, the dipoles can summate, making it possible to measure the resulting voltage at the scalp. Whether the dipoles created by the postsynaptic potentials (and in rare circumstances, action potentials) can be detected at the scalp depends on the configuration of the neurons (Wood, 1987).

Populations of neurons are organised into open or closed fields. An open field configuration is where neurons are aligned in parallel. If the postsynaptic potentials in an open field occur in synchronisation, the dipoles from each individual neuron sum together to form a dipole that can be detected at some distance from the neural source (Lorente de No, 1947). Changes in the synchrony of postsynaptic potentials can reduce the ability to detect the activity of the dipoles and therefore alter the scalp recorded ERPs (Cooper et al., 1969). The majority of the pyramidal neurons in the cortex are organised into open field configurations, and these populations of neurons are thought to be the primary source of electrical activity detected at the scalp (Kutas and Dale, 1997).

A closed field configuration is where the cell bodies are assembled at the centre and the dendrites extend radially away from the cell bodies. This random orientation means that the positivity of one neuron may be adjacent to the negativity from the next neuron resulting in the individual dipoles cancelling each other out, and the activity of closed fields cannot be detected at the scalp. Closed field configurations are common in subcortical structures. The inability to detect the electrical activity of closed fields at the scalp highlights an important limitation of the ERP technique: failure to discover a difference in scalp recorded activity between two experimental conditions does not necessarily imply that the mental operations engaged by the conditions are identical. Functional differences between the conditions may exist, but may be located in closed fields. Null results may also arise because the magnitude of the effect is small and requires increased power to be detected. Consequently, any null findings should be treated with extreme caution (Rugg and Coles, 1995; Kutas and Dale, 1997; Otten and Rugg, 2005).

3.1.3 Volume Conduction

Scalp recorded ERPs therefore reflect the summed activity of populations of neurons somewhere in the brain where the requirements of synchronicity and open field configurations are met. The electrical activity of the dipoles is conducted to the scalp because the brain and its coverings (the meninges, skull and scalp) are volume conductors. Whether the positive or negative end of the dipole is present at any given point on the surface of the scalp depends on the position and orientation of the generator dipole and also the resistance and shape of the brain, skull and scalp.

It is difficult to identify the neural generators of scalp recorded ERPs for two reasons. Firstly, the skull is less conductive than brain tissue and causes smearing of the dipole across the scalp (Koles, 1998). Therefore an ERP generated in one part of the brain can lead to voltages at very distant parts of the scalp. Secondly, the size and shape of individual heads vary therefore averaging individual ERPs to produce grand average ERPs will unlikely produce an ERP that is a true representation of the individual ERPs.

3.2 Recording the ERP signal

3.2.1 Active Electrodes

Voltage is the potential for current to flow from one place to another, consequently there is no such thing as a voltage at a single point (Luck, 2005). Therefore an ERP waveform reflects the voltage difference over time between an active and a reference electrode (the reference electrode is discussed in the next section). However, directly measuring the voltage difference between two electrodes would reveal any surplus electrical charges that had built up in the participant and would obscure any neural signals. To solve this problem a differential amplifier is used. A differential amplifier uses three electrodes to record activity: an active electrode placed at the chosen site on the scalp, a reference electrode placed elsewhere on the scalp, and a ground electrode placed at a location on the scalp or body. The voltage from the ground electrode is subtracted from the active and reference electrodes and the amplifier then amplifies the difference between the active and reference electrodes [(active minus ground) minus (reference minus ground)]. Any electrical charges picked up by the ground electrode will be the same for the active minus ground and reference minus ground calculations and will therefore be eliminated by the subtraction.

In practice, one active electrode is rarely used in isolation. Simultaneous recording from a montage of active electrodes covering multiple scalp locations is necessary to quantify distinct ERP components that may be maximal at different scalp sites. The use of multiple recording sites allows ERPs to be differentiated on the basis of their distribution (topography), and has the additional benefit that eye movement artefacts are also more readily observed (Picton et al., 2000).

The placement of electrodes in the montage is typically based on the International 10-20 system (Jasper, 1958). This system uses features of the skull (the nasion, inion etc.) to position the electrodes on the scalp and assumes that the skull is symmetrical. However, although this assumption is rarely met, variability in electrode placement due to skull asymmetry does not appear to be large enough to result in alignment with different underlying cortical structures across participants (Binnie et al., 1982; Homan et al., 1987). The 10-20 system accommodates up to 75 electrodes. The larger the montage the greater the spatial resolution and hence greater accuracy in detecting topographic differences. However, there appears to be little difference in spatial resolution between montages of 64 electrodes and 128 electrodes (Tucker, 1993; Srinivasan et al., 1998) consequently due to the increased time to apply a montage of 128 electrodes, a montage of 64 electrodes was used in the research reported in this thesis.

3.2.2 Reference Electrode

If the reference electrode were to pick up the brain activity recorded by the active electrode, this activity would be cancelled out when the difference between the electrodes was calculated. Thus, although no site is truly neutral, it is essential to use the most neutral possible reference site. Previous ERP studies of recognition memory have generally used the bony prominences (mastoids) behind each ear. The mastoid references are easy to apply and are not distracting for the participant. To avoid a hemisphere bias, electrodes are placed at both the left and right mastoid and the wires are physically linked to create an average of the two mastoid electrodes as a reference (Miller et al., 1991). In practice, the EEG is often recorded using a left mastoid reference, allowing the quality of the right mastoid to be observed on-line. The left and right mastoids are then algebraically reconstructed off-line to create a linked mastoid reference, circumventing two potential problems associated with recording using a linked reference. First, linking the wires creates a zero-resistance electrical bridge between the hemispheres, which distorts the distribution of voltage over the scalp (Katznelson, 1981). Second, if the reference electrodes had different impedances (electrical resistance), then the linked mastoid reference would move toward the electrode with the lowest impedance and produce hemispheric bias (Miller et al., 1991).

The position of the reference electrode determines the morphology of the EEG waveform recorded at each active site. Amplitudes at active electrodes proximal to the reference electrode are attenuated more than amplitudes at more distal active electrodes. The research in this thesis uses the linked mastoid reference to facilitate comparison with previous episodic memory research.

3.2.3 Analogue-digital (A/D) conversion

The voltage difference between each active electrode and the reference electrode is recorded as an analogue signal therefore, as computers require digital signals, it must be converted into digital form. To do this, the analogue signal is firstly amplified (this is necessary because the voltage detected at the scalp is small) and then passed through high-pass and low-pass filters that remove activity that is not within the range of normal EEG (0.01 – 40 Hz). The high-pass filter passes high frequencies but attenuates low frequencies [e.g. electrogalvanic (skin) signals], whereas the low-pass filter passes low frequencies and reduces the amplitude of high frequencies [e.g. electromyographic (muscle) signals].

The analogue signal is then converted to a digital signal using an analogue-to-digital converter. The converter samples the analogue signal at discrete time points. The sampling period is the amount of time between consecutive samples (e.g. 8 ms) and the sampling rate is the number of samples taken per second (e.g. 125 Hz). The Nyquist Theorem is needed to decide the sampling rate to use. This theorem states that all of the information in an analogue signal can be obtained digitally as long as the sampling rate is at least twice the highest frequency present in the analogue signal. If the signal is sampled at a rate lower than this, information will not only be lost but artifactual low frequencies will be induced in the digitised data (this is known as aliasing; Picton et al., 1994).

3.3 Extracting the ERP Signal from the Noise

As stated in the previous section, the high and low pass filtering of the analogue signal prior to digitisation reduces contamination from electrical activity that lies beyond the range of normal EEG. However, the digitised signal still contains activity from background brain activity and artifacts (e.g. muscle tension, movement and eye blinks) that occur within the range of normal EEG. The ERP signal must therefore be extracted from the background noise before any information about the cognitive processes under investigation can be obtained. The following section examines the techniques used in this thesis to extract the signal from the noise, and discusses alternative methods where appropriate.

3.3.1 Ocular Artifact Reduction

Blinking and eye movements are the major sources of electrical contamination in the EEG, and are most pronounced at the front of the head. Within each eye there is a voltage gradient (i.e. a dipole), with positive at the front of the eye and negative at the back of the eye. When the eyes are stationary, this dipole creates a constant DC voltage across the scalp, which the high-pass filter of the amplifier removes. However, blinks modulate the conduction of the dipole to the surrounding regions causing a deflection in the EEG of 50-100 μV with a typical duration of 200-400ms. Eye movements result in the positive end of the dipole moving to the site the eyes have moved towards. For example, a rightward eye movement causes a positive-going voltage deflection on the right side of the scalp and a negative-going voltage on the left side of the scalp. Ocular artifacts are measured with the electro-oculogram or EOG. The EOG records differences in electric potential between electrodes placed above and below one of the eyes (vertical EOG, or VEOG) and the left of the left eye and the right of the right eye (horizontal EOG, HEOG).

One way of minimizing contamination of the EEG with blinks and eye movements is to ask participants to blink only when instructed, and to fixate on one point throughout the experiment. Trials containing EOG artifact are then rejected prior to the averaging process that creates ERPs. The artifact rejection method is not preferred for four main reasons: First, in some cases, discarding trials with eye blinks and eye movements might lead to an unrepresentative sample of trials (Gratton, 1998). Second, some groups of subjects (e.g. children, older adults or clinical populations) cannot easily control their blinking and eye movements, making it difficult to obtain a sufficient number of artifact free trials. Third, residual EOG activity may contaminate the accepted trials. Finally, instructing participants to refrain from blinking introduces a secondary task that may reduce concentration, increase tension and interfere with brain activity (Verleger, 1991).

The previous considerations have led to the development of artifact correction, which subtracts away the voltages due to ocular artifacts from the EEG, rather than rejecting trials with these artifacts. A linear relationship between EEG and EOG is assumed and regression techniques are used to compare EEG with EOG, and to compute correction weightings for each active electrode. The regression coefficients are then used to subtract a proportion of EOG from each active electrode channel. The research reported in this thesis uses a regression technique to correct blinks, and the voltages due to ocular artifacts are subtracted from the EEG.

3.3.2 Averaging

The ocular artifact corrected EEG still contains background electrical noise from ongoing mental processes, in addition to the ERP signal of interest. The ERP signal is smaller than the noise, and therefore cannot readily be distinguished in the EEG. Averaging is used to extract the signal from the noise. This technique involves averaging together epochs that are time-locked to an event (usually a stimulus presentation). The logic behind this procedure is as follows (Spencer, 2005). The EEG data on a single epoch is thought to consist of an ERP waveform (signal) plus random noise. The signal is assumed to be identical on each epoch, whereas the noise is assumed to be completely random and unrelated to the time locked event. Consequently, when a large number of epochs are averaged together the noise reduces to a flat line (at zero microvolts), revealing the ERP waveform. The noise becomes smaller and smaller as the number of trials averaged together increases, making the signal more visible. In fact, the noise decreases, and the signal increases, as a function of the square root of the number of trials (Perry, 1966). Therefore doubling the signal to noise ratio requires four times as many trials and quadrupling the signal to noise ratio requires sixteen times as many trials. Sixteen epochs is generally accepted in ERP research (including the research reported in this thesis) as providing a sufficient signal to noise ratio to view the ERP waveform.

In practice, the signal will rarely be identical on each epoch. Fatigue, boredom etc. may produce fluctuations in the amplitude of the signal as the recording progresses (Ruchkin, 1988), and correct guesses may result in the signal being absent in some epochs. However, in these circumstances the averaged waveform will still reflect the signal of interest, albeit slightly attenuated, and epoch-to-epoch signal variability is not considered to be problematic (Luck, 2005).

Although epoch-to-epoch variability in the ERP amplitude is not generally problematic, epoch-to-epoch variability in latency is sometimes a significant problem. This latency jitter distorts the averaged waveform by reducing its amplitude and causing it to spread out in time. Woody filtering is a technique used to correct latency jitter (Woody, 1967). This technique uses a template that approximates the shape of the signal, and uses cross-correlations to find the segment of the EEG waveform on each epoch that most closely matches the waveshape of the template. The EEG epochs are then aligned with respect to the estimated peak of the signal and averaged together. Woody filtering should be used with caution, however. The section of the waveform on any epoch that most closely matches the template may not always be the signal of interest, resulting in an averaged waveform that does not accurately reflect the amplitude and latency of the component of interest (Wastell, 1977).

3.3.3 Component Selection

When the ERP signal has been extracted from the background noise, the component of interest must be identified in order to draw inferences about underlying cognitive processes. A component is defined in terms of its polarity, amplitude, latency and scalp distribution. The polarity is a function of the spatial relationship between the recording electrode and the neural generator and therefore does not convey any meaningful information about underlying cognitive processes. The amplitude provides an index of the extent to which a cognitive process is engaged, whereas latency reveals the timing of the process, and scalp distribution provides an overall pattern of brain activation.

The subtraction method is the most commonly used technique in memory research to isolate the component of interest (Rugg and Coles, 1995). This method involves taking the difference in activity between two experimental conditions (e.g. the difference in activity to an old and new waveform). Cognitive neuroscience is predicated on the assumption that there is a direct mapping between neural activity and cognitive processes. Consequently, the component identified using the subtraction method should reflect the cognitive process that differs between the two conditions. Chapter 4 reviews the central ERP components regarding memory and discusses the evidence for their associated functional interpretation.

Principle component analysis (PCA), is an alternative to the subtraction method (Van Boxtel, 1998; Dien and Frishkoff, 2005). PCA uses patterns of covariance between experimental conditions to reflect differences in cognitive processes, and patterns of variance between electrodes to reflect differences in the source dipoles. This procedure has attracted criticism, however, for its inability to differentiate temporally overlapping components.

To facilitate comparisons with other ERP memory studies, the research reported in this thesis adopts the subtraction method to extract ERP components of interest. Each component is quantified by averaging the amplitude of the difference between two waveforms at a particular electrode (or group of electrodes) over a particular latency period. This area measure is less sensitive to noise than simply assessing the maximum deflection of a component (Handy, 2005). The following section details how inferences can be drawn from the components identified during experimental conditions.

3.4 Making Inferences from ERPs

When components have been identified, their reliability has to be assessed with statistical analyses. The optimal statistical test depends on the experimental design (e.g. within or between participants design), however the most commonly used test is the repeated measures analysis of variance (ANOVA). The research reported in this thesis used a repeated measures ANOVA for the within age comparison, and a mixed ANOVA for the between age comparison. The ANOVA calculates individual p-values for all factors and the likelihood that one reaches significance by chance increases with the number of factors. Therefore it is sensible to not include factors that are not necessary. To characterise the amplitude and scalp distribution of the ERP component, electrodes are divided into separate factors that correspond to different spatial locations: anterior and posterior location, left and right hemisphere, and superior, mid and inferior sites.

3.4.1 Making Inferences from Quantitative Differences

Significant quantitative (or magnitude) differences between two ERP waveforms suggest that the component underlying the difference is reliable. The first point in time at which the waveforms diverge, however, only provides an upper-bound estimate of the onset time of the component. Earlier differences may have been present in brain regions where the signal cannot propagate to the scalp (Rugg and Coles, 1995; Otten and Rugg, 2005). When reliable components are identified, it is important to assess whether the distributions of the components are equivalent, because qualitative differences in the distribution of components are assumed to reflect the operation of different cognitive processes across conditions.

3.4.2 Making Inferences from Qualitative Differences

Significant qualitative (or topographic) differences between two ERP difference waveforms refer to changes in scalp distribution across conditions. The inverse problem states that a dipole detected at the scalp is compatible with an infinite number of underlying generators, therefore firm conclusions cannot be drawn about the actual neural sources of scalp recorded activity. However, a qualitative difference between two difference waveforms generally indicates that at least partially non-overlapping neural populations are engaged and therefore different components are present.

As with quantitative differences, inferential statistics are used to assess the reliability of apparent qualitative differences. However, the ANOVA model assumes that ERP data is additive (i.e. a twofold increase in the strength of a neural generator adds a constant voltage to each electrode), whereas in reality ERP data is multiplicative (i.e. a twofold increase in source strength produces a twofold increase in voltage at each electrode). The ANOVA model interprets the multiplicative voltage increase as a qualitative difference rather than a quantitative difference, resulting in spurious topographic differences. To circumvent this issue, ERP data are normalised prior to topographic analyses (McCarthy and Wood, 1985). Normalisation eliminates amplitude differences that reflect changes in source strength between conditions but preserves the topographic differences across electrodes.

There is debate as to whether normalisation is necessary. For example, Haig et al. (1997) and Urbach and Kutas (2002) argue that the procedure fails to consider differences in variance between conditions, and normalisation can therefore obscure, or produce misleading distributional differences. Other authors (Ruchkin et al., 1999; Wilding, 2006), however, promote that normalisation should be performed prior to topographic analyses, but that significant results should only be interpreted as confirming the presence of distributional differences between conditions. The nature of these differences should then be inferred from the pattern observed in the unscaled data. While aware that normalisation may produce conservative results, the topographic analyses reported in this thesis employ the maximum/minimum method recommended by McCarthy and Wood (1985). This method finds the maximum and minimum values in each condition, subtracts the minimum from every data point, and divides the data point by the difference between the maximum and minimum.

The ANOVAs assessing quantitative and qualitative differences employ the Greenhouse-Geisser correction for non-sphericity of data (Greenhouse and Geisser, 1959), and corrected df values and associated F ratios are reported where appropriate. A data set is spherical if the variances within all levels of any repeated-measures factor are equal and the covariance between the levels is the same. However, EEG data is often non-spherical because the degree of shared variance between any two EEG electrodes depends on their relative locations, therefore as the distance between the electrodes increases, so shared variance and homogeneity of covariance decreases. As the ANOVA model assumes that the data set is spherical, and the probability of a Type-1 error increases if this assumption is violated, the Greenhouse-Geisser correction is necessary prior to analyses.

3.5 Conclusion

This chapter commenced with a discussion of the neural origin of ERPs. The ERP reflects the dipole of the summed post-synaptic potentials of populations of neurons somewhere in the brain, when the requirements of synchronicity and open field configurations are met. This electrical activity is conducted to the scalp and is recorded from a montage of electrodes, which are linked to a suitable reference site. Once the signal is recorded, amplified, filtered and digitised, the small ERP signal must be extracted from the background EEG noise using artefact reduction and averaging techniques. Once the ERP signal is extracted, the subtraction method is used to isolate the ERP component that reflects the underlying cognitive process of interest between two experimental conditions. The reliability of the ERP components has to be confirmed with statistical analyses. Significant quantitative (or magnitude) differences between two ERP waveforms suggest that the component underlying the difference is reliable. In contrast, significant qualitative (or topographic) differences between two ERP difference waveforms suggests that different components are present across conditions.

Chapter 4 ERPs, Memory and Ageing

The previous chapters have predominantly reviewed the behavioural literature regarding recognition memory and ageing. Based on differences in accuracy or RT for example, behavioural investigations can provide an indication of how episodic memory changes with age. It is difficult, however, to make substantial inferences about these memory changes from behavioural data alone (e.g. the timing/order of cognitive processes and in particular how strategies changes with age). Consequently, over the last two decades experimental psychologists and neuroscientists have used the event-related potential (ERP) methodology to investigate the information processing that underlies episodic memory.

Recall and recognition paradigms have been used to examine the neural correlates of episodic memory encoding, focussing on ‘difference in subsequent memory’ (Dm) effects. Dm effects are the difference between the waveforms of studied items that were remembered at retrieval and studied items that were forgotten at retrieval. Also, after the manipulation of either encoding or retrieval tasks, the waveforms of new items have been compared to investigate the neural correlates of retrieval attempts. Finally, by employing the recognition memory paradigm, studies have used the ERP old/new effect (difference between correctly recognised previously seen or ‘old’ items and correctly rejected unseen or ‘new’ items) to investigate the neural correlates of successful retrieval. As the focus of the research in this thesis is on the neural correlates of successful episodic retrieval, the remainder of the chapter will review literature on the effects of ageing in this area, along with considerations of strategic retrieval. First, however, the ERP old/new effects will be examined in detail.

4.1 ERP Old/New Effects

In study-test paradigms, successful recognition is generally associated with old waveforms becoming more positive in amplitude than new waveforms from approximately 200ms post-stimulus onset. The significant difference between the amplitudes of old and new waveforms (as stated previously the difference is called the ERP old/new effect) can persist until the end of a 2000ms recording epoch, and has been divided into a family of old/new effects based on their polarity, latency and scalp distribution. Four of the old/new effects that are associated with recognition memory tasks and are relevant for the research presented in this thesis will be described in detail: the left parietal old/new effect, the bilateral frontal old/new effect, the right frontal old/new effect and the late posterior negativity.

4.1.1 The Left Parietal Old/New Effect

The left parietal old/new effect is a positivity from around 400-900ms post stimulus that is maximal over the left parietal scalp. Item recognition, associative recognition, source memory and cued recall paradigms have all been shown to elicit the modulation (Rugg, 1995; Friedman and Johnson, 2000; Mecklinger, 2000; Donaldson et al., 2002) and it has been observed for verbal and pictorial stimuli (e.g. Schloerscheidt and Rugg, 1997; 2004; Ranganath and Paller, 2000; Duarte et al., 2004). However, the effect is not always left sided and can demonstrate different posterior patterns for other types of material (e.g. abstract objects and spatial locations, Mecklinger, 2000; abstract patterns, Van Petten and Senkfor, 1996; faces, Yovel and Paller, 2004; MacKenzie and Donaldson, 2007).

Because the amplitude of the left parietal effect positively correlates with the hit rate and therefore does not simply reflect the repetition of stimuli (Johnson et al., 1985;

1998a), and is absent from ERPs evoked by false alarms and misses and so is not only related to making a response (Sanquist et al., 1980; Rugg and Doyle, 1992), it is widely considered to index recollection (Allan et al., 1998; Rugg and Curran, 2007). In particular, the following sources of evidence support a recollection interpretation of the left parietal effect. Firstly, ERP studies using the remember/know procedure have often found larger left parietal effects for remember responses than for know responses (e.g. Smith, 1993; Duzel et al., 1997; Mark and Rugg, 1998; Duarte et al., 2004; Vilberg et al., 2006). Secondly, the left parietal effect has been observed for items studied under deep encoding conditions but not shallow encoding conditions (Paller and Kutas, 1992; Rugg et al., 1998a); deep encoding promotes recollection whereas shallow encoding promotes familiarity. Thirdly, the effect has been found to be reduced in magnitude following divided attention (Curran, 2004); dividing attention reduces recollection based remembering, encouraging recognition based on familiarity. Finally, in source memory studies, the left parietal effect tends to be larger for correct source judgements compared to incorrect source judgements (Wilding et al., 1995; 1996; Trott et al., 1997; Mark and Rugg, 1998; Senkfor and Van Petten, 1998).

4.1.1.1 Neural Substrates of the Left Parietal Effect

While ERPs have excellent temporal resolution, their limited spatial resolution makes deducing their neural origins very difficult. Source localization procedures have failed to overcome this problem. However, the available evidence does suggest that the hippocampus is responsible for the generation of the left parietal effect. Patients with hippocampal damage exhibit attenuated or non-existent left parietal effects (Rugg et al., 1991; Mecklinger et al., 1998; Duzel et al., 2001). However, a review of event-related fMRI studies of episodic retrieval has shown that BOLD activation in the left inferior parietal lobe positively correlates with the magnitude of the left parietal effect, suggesting that the neural generators of the effect may be located in this area (Wagner et al., 2005). As noted in the 'Event-Related Potentials' chapter, only activity from neurons organised into an open field configuration can be detected at the scalp. These open field configurations are predominantly located in the cortex, therefore scalp recorded activity is believed to originate in areas of the cortex close to the skull. By contrast, the hippocampus is a sub-cortical structure whose activity is unlikely to be detectable at the scalp. Consequently, it is proposed that the hippocampus projects activity to the left inferior parietal lobe, and the left parietal effect reflects activity from this area.

4.1.2 The Bilateral Frontal Old/New Effect

The bilateral frontal old/new effect (also known as the FN400, see e.g. Curran, 1999; 2000; Curran and Cleary, 2003) is a brief positivity from approximately 300-500ms post stimulus over bilateral frontal electrodes for correctly recognised old items compared to a correct rejection baseline. While the left parietal effect is generally accepted as being a neural correlate of recollection, the functional significance of the bilateral frontal effect has remained questionable. Following the dual process view that familiarity is fast acting and occurs more rapidly than recollection, the most influential interpretation proposes that the effect represents familiarity (Rugg and Curran, 2007). Rugg et al., (1998) formalized the link between the modulation and familiarity following the discovery that during a levels of processing manipulation, the left parietal effect was significant after a deep encoding condition but not a shallow encoding condition, whereas the bilateral frontal effect was significant for both encoding manipulations. Based on the view that memory after both shallow and deep encoding is supported by familiarity but only deep encoding promotes recollection, the authors provided strong evidence in favour of a familiarity interpretation of the bilateral frontal effect.

Other evidence consistent with a familiarity account comes from the finding that the magnitude of the bilateral frontal effect was equivalent for studied words (e.g. cookie) and plurality-reversed lures (e.g. cookies) that were given an ‘old’ response, whereas the left parietal effect was only significant for studied words given an ‘old’ response (Curran, 2000). Curran reasoned that recollection was required to recall the specific plurality of words, therefore plurality-reversed lures were only miss-identified as old on the basis of familiarity. Consequently, the author concluded that the bilateral frontal effect represented familiarity. Curran and Cleary (2003) conducted a similar study with mirror-reversed pictures as lures, which were intended to be analogous to the plurality-reversed lures of Curran (2000). Again, the magnitude of the bilateral frontal effect was equivalent for studied pictures and mirror-reversed lures that were given an ‘old’ response, while only studied pictures given an ‘old’ response were associated with a reliable left parietal effect. This finding is important not only for supporting a familiarity account of the bilateral frontal effect, but also in showing that because the effect was significant for words and pictures it is not material specific. Nessler and Mecklinger (2003) and Geng et al. (2007) also found similar findings using studied words and semantically-related lure words.

The aforementioned studies indicate that the bilateral frontal effect is sensitive to conceptual fluency as opposed to perceptual fluency. Perceptual fluency involves the processing of physical features, such as modality (e.g. visual verses auditory verses pictorial) and shape (Jacoby and Dallas, 1981). In contrast, conceptual fluency involves the processing of meanings (Hamann, 1990). If the bilateral frontal effect was related to perceptual fluency, then mirror-reversed pictures would have produced a smaller bilateral frontal effect compared to studied pictures. In contrast, if the effect was related to conceptual fluency then, as was found, equivalent bilateral frontal effects would be expected for studied pictures and mirror-reversed lures.

Despite the compelling evidence for a familiarity interpretation, data has been presented that is consistent with alternative accounts of the bilateral frontal effect. Tsivilis et al. (2001) proposed a novelty hypothesis following the results from an object/background task. Participants were required to study pairings of everyday objects against background scenes, and at test to discriminate between old and new objects regardless of background. The bilateral frontal effect was similar for same pairings (old objects against the studied background) and rearranged pairings (old objects against a different studied background) but was absent for old/new pairings (old object against a new background). Consequently, according to the novelty hypothesis, because the bilateral frontal effect was significant for old objects paired with either same or rearranged backgrounds but not for old objects paired with new backgrounds, the effect indexes a process that involves the union of components of a prior episode (for a further discussion of the novelty hypothesis, see Schloerscheidt and Rugg, 2004)

An alternative view, that is currently under great debate, is that the bilateral frontal effect reflects conceptual implicit memory (Yovel and Paller, 2004; Voss and Paller, 2006; Woodruff et al., 2006). According to this account, the presentation of lures at test that are conceptually similar to studied items (e.g. semantically related) leads to a facilitation of processing of the studied and lure item due to two presentations of conceptually similar items. The bilateral frontal effect therefore reflects this conceptual implicit memory. Evidence in support of this view comes from Yovell and Paller (2004). Using faces as stimuli because purportedly, unlike words, they have never been encountered prior to the experiment and should therefore induce ‘pure’ familiarity, the

ERPs associated with familiarity and recollection both showed a parietal maxima, differing only quantitavely with familiarity being associated with a lower amplitude and shorter duration. The findings were related to a single process view of recognition, where familiarity is supported by a subset of the neural generators that support recollection. In addition, the authors proposed that because no bilateral frontal effect was observed for facial stimuli that are not conceptually related, the functional significance of the effect is related to conceptual memory rather than familiarity. Further support for this view comes from a study by Voss and Paller (2006) who demonstrated that the repetition of famous faces, which induced conceptual implicit memory, led to activity over bilateral frontal electrodes.

4.1.2.1 Neural Substrates of the Bilateral Frontal Effect

Evidence implicates the parahippocampus, but not the hippocampus, in the generation of the bilateral frontal effect. Mecklinger et al. (1998) investigated memory function in a group of amnesic patients with damage to the parahippocampus as a result of hypoxia due to myocardial infarction. ERPs were recorded during an object versus spatial memory task for the amnesic patients, along with an age-matched control group. Only the control group showed the bilateral frontal effect. Duzel et al. (2001) reported the case of a patient with localized hippocampal damage who showed a bilateral frontal effect, and Tendolkar et al. (1999) also reported a bilateral frontal effect in a group of Alzheimer’s disease patients who had reduced hippocampal volumes compared to age-matched controls.

4.1.3 The Right Frontal Old/New Effect

The right frontal old/new effect is a positivity for old items compared to new items that is maximal over the right frontal scalp, typically onsets around the same time as the left parietal effect (approximately 400ms post stimulus) and often continues until the end of a two second epoch. While the bilateral frontal effect and the left parietal effect seem to be associated with ecphory (episodic retrieval), the timing of the right frontal old/new effect has resulted in its interpretation as a neural correlate of post-retrieval processes.

Consistent with the bilateral frontal effect, the functional significance of the right frontal effect has also remained questionable. The modulation was first reported during source memory studies (Wilding and Rugg, 1996; 1997a), where as a result of it being larger for correct source judgements than incorrect source judgements was interpreted as reflecting the retrieval of source or contextual information. However, this view was queried when several studies did not show right frontal effects for correct source judgements (Wilding and Rugg, 1997b; Cycowicz et al., 2001; Cycowicz and Friedman, 2003; Ranganth and Paller, 1999), the effect was also present in remember/know paradigms that did not require an overt source judgement (e.g. Duzel et al., 1997; Rugg et al., 1998b; Trott et al., 1999) and has also been recorded in complex item recognition tasks.

Consequently, the account of the right frontal effect was revised to be associated with the strategic processing of the products of recollection. However, following the demonstration that the effect was present for incorrectly classified new items as old (Mecklinger, 2000; Curran et al., 2001), and elicited by words that were remembered in a direct forgetting task, but which belonged to the to-be-forgotten encoding condition (Ullsperger et al., 2000), this interpretation was also discredited in favour of an evaluation or monitoring account. Support for this interpretation came from a false memory study that revealed greater right frontal effects for good performers who also had longer RTs than poor performers, indicating that they were more careful in their decision making (Curran et al., 2001). Further support came from the finding that, during a levels of processing manipulation, the right frontal effect was larger following a shallow encoding task compared to a deep encoding task (Rugg et al., 2000). According to this view, test items that were shallowly encoded will be harder to remember than those that were encoded under deep conditions, resulting in more post-retrieval monitoring following shallow encoding.

The findings of two recent experiments have questioned the current interpretation of the right frontal effect as reflecting post-retrieval evaluation or monitoring processes. Hayama et al. (2008) conducted two experiments. The study phases of both experiments were identical: a series of pictures were presented and participants were required to make one of two semantic judgements about the picture. During the test phase of the first experiment, participants were required to remember the source in which they encountered the picture at study (i.e. the semantic judgement made) or to indicate if the picture was new. In the second experiment they were required to make a further semantic judgement about the old and new pictures. The authors contrasted the ERPs following the semantic and source memory tasks and found significant right frontal effects for both tasks. Following these findings, it was proposed that the right frontal old/new effect is a neural correlate of general decision making processes, rather than evaluation or monitoring of the products of an episodic retrieval attempt.

A number of proposals have therefore been made concerning the functional significance of the late right frontal effect, but the debate is still ongoing. The major problem in identifying the functional significance of the effect may lie in the practice of measuring it over long time periods, which may obscure other shorter sub-components that have different distributions and therefore possibly dissimilar functional interpretations (Friedman and Johnson, 2000; Mecklinger, 2000; Hayama et al., 2008). For example, Duzel et al. (1997) noted right frontal effects of equivalent magnitude for remember and know responses, however the know modulation had a more widespread distribution. Furthermore, in addition to late right frontal distributions, late bilateral distributions have been reported for auditory stimuli (Senkfor and Van Petten, 1998) and for pictorial stimuli (Ranganath and Paller, 1999; 2000; Van Petten et al., 2000). Because the neural substrates of the effect are believed to be located in the PFC (see below) which is itself non-unitary (with different areas relating to various executive functions), this suggests the possibility that measuring the effect over long time periods may mask other qualitatively distinct distributions.

4.1.3.1 Neural Substrates of the Right Frontal Old/New Effect

Evidence suggests that the generators of the right frontal old/new effect are located in the PFC. Studies of frontal lesion patients have shown significant source memory deficits (Janowsky et al., 1999; Schacter et al., 1994); patients with lesions restricted to the right frontal cortex exhibit impairment in retrieval monitoring (Stuss et al., 1994).

4.1.4 The Late Posterior Negativity

The late posterior negativity (LPN) is a bilateral negativity for old items compared to new items that is maximal over the parieto-occipital scalp, is often present around the time participants respond behaviourally and lasts for several hundred milliseconds. The functional significance of the modulation, however, remains unclear. In an exclusion task, Wilding and Rugg (1997b) found a negative correlation between RT and LPN amplitude and therefore concluded that the effect reflected response-related processes, rather than mnemonic operations. However, other studies have questioned this interpretation following the demonstration of similar RTs in conditions that produce the LPN and those that do not (Wilding and Rugg, 1996; 1997a; Rugg et al., 1998b; Cycowicz et al., 2001; Johansson et al., 2002).

Cycowicz et al. (2001) and Cycowicz and Friedman (2003) proposed a different theory, which states that the LPN indexes post-retrieval search processes that are used when the task requires the reconstruction of perceptual detail. Evidence in support of the perceptual details account comes from two reality monitoring tasks, where the LPN was larger for previously perceived pictures than for previously imagined pictures (Johansson et al., 2002; Leynes and Bink, 2002).

The perceptual details account has also been questioned after Friedman et al. (2005) found no difference between LPN amplitudes during item and source memory tasks where the colour of pictorial stimuli were matched at study and test, and where the colours differed between study and test. According to the perceptual details account, a larger LPN would be predicted in the non-matching condition. In addition, LPN’s have been reported for non-pictorial and aural stimuli (e.g. Wilding and Rugg, 1996; Senkfor and Van Petten, 1998; Curran, 1999).

A final theory proposed by Johansson and Mecklinger (2003) states that, like the late right frontal effect, there may be more than one late posterior negativity whose distribution and functional significance vary with tasks demands. Accordingly, the functional significance of the LPN observed in source memory tasks that require the retrieval of specific perceptual detail from the study episode, may be completely different to when the modulation appears in item recognition. For example, a stimulus-locked LPN has been linked to high accuracy in source memory studies (e.g. Johansson et al., 2002), whereas a response-locked effect occurs along with high false alarm rates and long RTs in item recognition (Johansson and Mecklinger, 2003). These findings suggest that the LPN in source memory tasks reflects the reconstruction of perceptual details, whereas the modulation elicited during item recognition indexes evaluation processes that are produced by high levels of response conflict (Nessler and Mecklinger, 2003; Herron and Wilding, 2005).

Despite the evidence described above, the functional significance of the LPN is still not entirely clear, neither are its neural correlates. Suggestions have been made that associate the LPN present in source memory tasks to the posterior parietal cortex (Johanssen and Mecklinger, 2003) or occipito-temporal cortex (Cycowicz et al., 2001; Cycowicz and Friedman, 2003), and the LPN in item recognition to the anterior cingulated cortex (Nessler and Mecklinger, 2003).

This section has presented evidence from item recognition and source memory paradigms to explain the functional significance of the four described ERP old/new effects associated with successful episodic retrieval. As this thesis will use the engagement of these modulations as an indication of the retrieval strategies adopted during episodic retrieval across young and older adults, the following section will therefore review the literature regarding ERPs and strategic retrieval in young adults. The literature for older adults will be discussed in section 4.4.

4.2 ERPs and Strategic Retrieval

The majority of ERP studies investigating strategic retrieval processing have used the recognition memory exclusion task. This paradigm is a type of source memory task where participants distinguish between targets (studied items from one source e.g.

female voice), non-targets (studied items from another source e.g. male voice) and new items. Unlike a source memory task where three separate buttons are pressed for each item at test, in the exclusion task one button is pressed for targets and a second for non-target and new items. As this task is more complex than a normal source memory paradigm and also allows participants to perform the task in more than one way, it places high emphasis on the use of strategies to facilitate retrieval and is therefore ideal for investigating strategic retrieval.

Previous exclusion studies have focussed on the differential engagement of the left parietal effect and, to a lesser extent, the right frontal effect, as an indication of retrieval strategies, with some interesting results. Wilding and Rugg (1997b) presented words in a male or female voice and noted left parietal effects for targets and non-targets. In addition, the right frontal effect was present to target hits but not for correctly identified non-targets. Similarly, in two experiments, one with a response-time limit and the other with no explicit upper limit, Wilding and Sharpe (2004) noted left parietal effects at test for targets and non-targets following the presentation of words in a male or female voice during the study phase. Interestingly, and in-line with the non-unitary nature of the right frontal effect, the modulation was present for targets only at right frontal sites when there was no explicit upper time limit, but a more right centrally distributed effect was recorded for targets only following the response-time limit. This result suggests that different post-retrieval monitoring operations were engaged according to the time available to make memory judgements. Target and non-target left parietal and target only right frontal effects have also been noted for pictures presented in a red or green colour (Cycowicz et al., 2001), and target and non-target left parietal and right frontal effects for objects requiring a function or drawing judgement (Dzulkifli et al., 2005).

The previous studies have reported consistent findings regarding the engagement of the left parietal effect, however, other studies have shown divergent results. For example, after the presentation of words or pictures during the study phase, Herron and Rugg (2003a) noted left parietal effects at test for targets only, and right frontal effects for targets and non-targets. Herron and Rugg (2003b) also reported left parietal effects for targets only but did not report the findings of the right frontal effect. Herron and Wilding (2005) required participants to rate words for pleasantness on a five-point scale and found left parietal and right frontal effects for targets only, while, after a function or drawing judgement about a study word, Dzulkifli and Wilding (2005) noted left parietal effects for targets only and right frontal effects for targets and non-targets. Finally, Fraser et al. (2007), using a different exclusion paradigm where words were only presented in one source at study and at test the studied items were re-presented along with new words and repeated new words, they found left parietal effects for targets only but did not report results of the right frontal effect.

The existing evidence suggests that, during the exclusion task, participants either use the strategy of recollecting targets and non-targets or restricting recollection to targets. Furthermore, adopting the post retrieval monitoring account of the late right frontal effect, evaluation is restricted either to targets only or to both target and non-target items. Because target accuracy was high in the studies showing a target specific strategy, Herron and Wilding (2005) proposed that when the likelihood of target recollection is high, participants focus solely on the recollection of target information as this strategy gives rise to accurate task performance. Further support for this view comes from the aforementioned studies where targets and non-targets were recollected, as all reported relatively low target accuracy. In addition, using words in red or green font as study items, Wilding et al. (2005) reported left parietal effects for targets in two experiments, but for non-targets only in the experiment with low target accuracy.

The studies reporting right frontal effects for targets only employed a simple study task (e.g. repeating the gender the word was spoken in or the colour in which the word was presented). In contrast, studies showing right frontal effects for targets and non-targets adopted more complex study tasks, such as making a function or drawing judgement about the object, therefore the greater complexity of the study task required strategic retrieval processing for all study items.

The exclusion tasks reported in this section failed to provide data regarding the bilateral frontal effect and strategic retrieval. To my knowledge, only one study (Bridson et al., 2006) has directly investigated the putative bilateral frontal correlate of familiarity in exclusion tasks, and has failed to shed light on how familiarity is involved in strategic retrieval. Following the demonstration that the ERPs of target misses were reliably more positive going than those elicited by correct rejections, the authors simply used this as further support for a familiarity interpretation of the effect. In addition, the studies in this section have used either an intrinsic source context (information inherent to the studied word e.g. male or female voice, red or green font colour) or an extrinsic context (information not inherent to the studied word e.g. make a function or drawing judgement about the word, rate the word for pleasantness) without any consideration of the effects of this on strategic retrieval.

4.3 The Effects of Ageing on the ERP Correlates of Recognition

To date, ERP research on the influence of ageing on the neural correlates of episodic retrieval has been somewhat limited. The current section will provide a review of this limited literature, and, because the focus has primarily been on the effects of ageing on left parietal and right frontal effects, these modulations will be examined in particular.

4.3.1 Continuous Recognition Studies

The most common task employed during early ERP investigations of recognition memory and ageing was the continuous recognition paradigm. In this paradigm participants were presented with a series of stimuli, some of which were repeated after different lags (delays), and participants had to differentiate between previously seen and new items (Rugg et al., 1997; Swick and Knight, 1997). Behavioural results indicate that older adults show reduced performance on continuous recognition tasks compared to the young, especially as the delay increases. ERP findings showed that a centro-parietal positive old/new effect (discussed below), significant for all lag conditions in the young group, was reduced in the older group at short lags and non-significant at longer lags. These studies employed visually presented words as stimuli, however, continuous recognition studies using auditory stimuli (Minamoto et al., 2001) and pictorial stimuli (Nielson-Bohlman and Knight, 1995) show that the age-related ERP changes are generalisable beyond visual words. Importantly, Nielson-Bohlam and Knight (1995) noted age equivalence in the ERPs to new items, suggesting that the ERP age difference in the old/new effects indicates changes in retrieval processes.

The centro-parietal effect evident in continuous recognition tasks is more bilaterally distributed than the left parietal correlate of recollection, but they both occur around the same time (approximately 400-900ms post stimulus). The two components are assumed to be related, with the topographic difference simply reflecting design differences between continuous recognition tasks and study/test paradigms (e.g. Friedman, 2000). However, because it is open to debate whether or not the delay even in the long lag condition is great enough to test long-term memory, the centro-parietal modulation may not index long-term memory processes.

It is therefore questionable whether continuous recognition studies provide evidence of age-related changes in episodic memory. The study/test paradigm overcomes the long-term memory criticism, where a longer delay occurs between study and test than the long lag conditions of continuous recognition tasks. Using a study/test paradigm, Morcom and Rugg (2004) found a left parietal effect in young adults for the recognition of words following the encoding of either pictorial or verbal stimuli. This effect was absent in older adults for both pictorial and verbally encoded items, even when performance was age matched.

In line with dual process theory, the absence of the left parietal effect in the Morcom and Rugg study indicates that the elderly were relying less on recollection based remembering than the young. This age difference can be explained by either an ageing deficit in recollection or an under use of recollection when the task can be completed based on familiarity. To address these possibilities, the following section will present the findings regarding age-related changes in the neural correlates of episodic retrieval using a source memory task, which promotes recollection-based retrieval.

4.3.2 Source Memory Studies

During a typical source memory task, items are presented under two study conditions (e.g. different voices or lists) and, at test, participants are required to remember the source by making one-, two-, or three-stage judgements. For example, in a study phase Trott et al. (1997) presented two lists of sentences to young and older adults with the requirement to learn the nouns from each sentence, along with the list in which they were studied. During the test phase, participants were instructed to discriminate between old and new nouns and then, for words judged old, to make a remember/know judgement followed by a source decision. Behaviourally, the elderly had a source memory deficit compared to the young, but no between group difference was present in the rate of remember responses. Electrophysiologically, both correct source judgements and remember responses were associated with a left parietal effect of equivalent magnitude in both age groups. In addition, the right frontal effect was present in the young but was significantly reduced in the elderly. Wegesin et al. (2002) noted comparable findings when they replicated the aforementioned study, including a variation to improve the older adults' near chance performance.

However, other source memory studies are inconsistent with the foregoing findings. Mark and Rugg (1998) required participants to remember the source of words heard in a male or female voice, whereas Li et al. (2004) asked participants to recollect which of two encoding tasks they had performed on pictorial stimuli. Source accuracy did not differ between age groups. Both of these studies found no right frontal differences between age groups, however, they did observe an age-related reduction in the left parietal effect.

A negative left/central old/new effect has also been reported in older adults, maximal at around 1100ms, in three of the previous source memory studies (Trott et al., 1997; Wegesin et al., 2002; Li et al., 2004), and even evident when performance was equated across age groups (Li et al., 2004). Wegesin et al. (2002) compared this negativity to the late posterior negative slow wave (LPN) recorded in young adults, surmising that the more posterior distribution in the young reflected attenuation at central electrodes by the right frontal effect. This interpretation is tentative, however, as Li et al., (2004) showed that when the right frontal effect was equivalent across age groups, the negativity in the elderly was still more centrally distributed. Two alternative accounts of the functional significance of the modulation seen in the elderly are: Wegesin et al. (2002) incorporated a two stage response in their source memory task (old/new then source) and noted that the modulation occurred after the mean RT response for the initial old/new decision. Accordingly, they proposed that the modulation represents the engagement of different/compensatory processes associated with the search for, or retrieval of, source information. Alternatively, following the use of pictorial stimuli, Li et al. (2004) suggested that it reflects older adults greater need to reconstruct perceptual details of the study context to make source decisions. It remains unclear which of these interpretations, if any, reflects the functional significance of the left/central negativities.

Consistent with the notion that the elderly engage compensatory processes to reduce age-related source memory deficits, PET studies have shown that, in certain circumstances, older adults show bilateral prefrontal cortex activation in comparison to right sided only in the young (Backman et al., 1997; Madden et al., 1999; Cabeza et al., 2002). In particular, in a PET study, Cabeza et al (2002) grouped older adults according to their performance on neuropsychological memory tests. During a source recognition task, high performers on the memory tests showed bilateral prefrontal cortex activation, compared to right prefrontal activation only in the low performers.

4.3.3 Ageing and the Bilateral Frontal Effect

To date, very few studies have reported the effects of ageing on early onsetting ERP effects. Collectively, the studies that have reported early frontal modulations (evident between 300 and 600ms post stimulus) showed similar magnitudes across age groups, but a bilateral distribution for the young and a right sided distribution for the elderly (Wegesin et al., 2002; Morcom and Rugg, 2004). These distributional differences, while difficult to interpret, may reflect the age-related engagement of different cognitive processes, or ageing changes in brain morphology that have altered the alignment of the neural generators of the bilateral frontal effect (Rugg and Morcom, 2004).

4.4 ERPs, Ageing and Strategic Retrieval

ERP exclusion ageing studies have used a different paradigm compared to the majority of studies on the young only. Rather than presenting items in two sources at study (e.g. male or female voice) and, at test, requiring young participants to distinguish between targets (studied items from one source), non-targets (studied items from the other source) and new items, one set of study words were presented to young and older adults and the task at test was to discriminate between target (studied) words, new (unstudied) words and non-target lures (new words repeated at test).

Using a paradigm including non-target lures, Dywan et al. (1998; 2001; 2002) demonstrated behavioural and electrophysiological differences between age groups. While target accuracy was equivalent for young and older adults, the elderly made more false alarms to non-targets. In addition, the ERPs revealed an age-related asymmetry, with greater parietal positivities being present for targets compared to non-targets in young adults, in contrast to the elderly showing larger positivities for non-targets than targets. These results imply that, consistent with the inhibition deficit hypothesis of cognitive ageing (see ‘Memory and Ageing’ chapter), while the young group adopted the retrieval strategy of inhibiting/reducing the recollection of irrelevant non-target information, the older group did not do this. The chance that the age-related behavioural difference in the aforementioned studies influenced the ERP differences was excluded when a similar pattern of results was evident even when performance was equated across age groups (Dywan et al., 2001). These findings suggest differences in the retrieval strategies adopted across age groups, with only younger adults being able to reduce the recollection of irrelevant non-target information.

4.5 Limitations of ERP Ageing Research

During recognition tasks, older adults performance is often reduced compared to the young, particularly during source recognition, which promotes recollection rather than familiarity. This age-related performance deficit can be problematic for electrophysiological comparisons across age groups, for two possible reasons (Rugg and Morcom, 2004). Firstly, older adults may exert more effort during tasks that they find more difficult than the young, possibly confounding ageing differences in the neural correlates of successful retrieval with retrieval effort. However, even when performance is equated across age groups the older adults could still find the task more difficult and exert more effort to keep performance equivalent, therefore equating performance does not necessarily control for the confound of effort. Secondly, the proportion of trials associated with a guess response or weak memory trace increases as performance decreases, diluting the neural correlates of successful retrieval. Consequently, smaller ERP effects in older adults compared to younger adults may be the result of increased guessing or weak memory trials in the older group, rather than ageing differences in the engagement of retrieval operations per se. However, the findings from previous ERP ageing studies have demonstrated that age-related differences in ERP effects persist when young and older adults performance is equated (Li et al., 2004; Morcom and Rugg, 2004). These results suggest that the age-related differences in ERP effects observed when performance is reduced in the elderly, are due to differences in the engagement of retrieval operations rather than the aforementioned confounds associated with an age-related performance deficit.

4.6 Conclusion

Together, the studies reported to date have shown that the ERP correlates of recognition memory change with age. However, the pattern of findings is inconsistent, making overall conclusions very difficult. The limited evidence regarding the bilateral frontal effect indicates that the neural correlate of familiarity either has a more right sided distribution in the elderly compared to the young, or the different distributions represent the engagement of different cognitive processes across age groups. Age-related reductions in the size of the left parietal effect are consistent with the dual process view that recollection becomes impaired with age. However, several source memory paradigms have reported age equivalent left parietal effects, therefore age-related declines in recollection have not been found universally. Likewise, some studies report that the putative right fontal correlate of post-retrieval processing is reduced in the elderly, whereas others show age equivalence. However, these inconsistencies in the engagement of post-retrieval processes may reflect the non-unitary nature of the right frontal effect, and a more precise definition of the modulations functional significance will shed extra light on the effects of ageing on post retrieval strategic processing.

The results with regards to the effects of ageing on strategic retrieval are clearer. Under certain circumstances, young adults appear to be able to restrict recollection, and post retrieval monitoring, to relevant (target) information and inhibit/reduce recollection of irrelevant (non-target) information, whereas the elderly do not seem able to do this. Finally, it has been proposed that the negative left/central effect present in the elderly during source memory studies may index compensatory retrieval processes or older adults greater need to reconstruct perceptual details of the study context to make source decisions.

4.7 Thesis Aims

Evidence has accumulated to suggest that normal ageing is associated with a decline in accuracy of the source of information retrieved from episodic memory (e.g. see McIntyre and Craik, 1987; Schacter et al., 1981). The retrieval of source information requires recollection of contextual details surrounding the event, such as when and where the event occurred, along with executive functions, such as working memory, strategy use and planning, to monitor the contextual information retrieved. Due to the complexity of retrieving source information, strategic retrieval is required to maximise performance. Strategic retrieval is the retrieval of episodic information by implementing a self-initiated process (Dzulkifli and Wilding, 2005).

While a decline in recollection with age has been widely linked to older adults source memory deficit (e.g. Dywan and Jacoby, 1990; Jennings and Jacoby, 1993), the role of executive functions, which also show an age-related reduction (e.g. see Moscovitch and Winocur, 1995), is less clear. Neuroimaging studies of young adults have provided considerable evidence that different regions of the prefrontal cortex, which sub-serves our executive functions, are active during episodic memory retrieval, possibly reflecting the engagement of various executive functions (e.g. Nolde et al., 1998; Wagner et al., 1998; Buckner and Wheeler, 2001; Wheeler and Buckner, 2003). One of the aims of the thesis was to establish if there is a relationship between the activation of different regions of the prefrontal cortex during source memory retrieval, and specific executive functions, and whether this relationship is different for young and older adults. This approach will further our understanding of the role of executive functions in the retrieval of source information from episodic memory in young adults. In addition, the approach will also help to understand if an age-related reduction in executive functioning results in the engagement of less effective retrieval strategies, and contributes to the source memory deficit evident in older adults.

The thesis used neuropsychological profiling to assess four executive functions (working memory, strategy use, planning and flexibility of thinking and responding), along with non-executive short-term memory, and involved completing four tests from the Cambridge Automated Neuropsychological Test Battery (CANTAB): Spatial Span, Spatial Working Memory, Stockings of Cambridge, and the ID/ED Set-Shifting task. The Spatial Span task is a non-executive task of spatial short-term memory capacity, while the Spatial Working Memory task is an executive task that assesses working memory for spatial stimuli and strategy use. The Stockings of Cambridge task and the ID/ED Set-Shifting task are executive tasks that measure spatial planning and flexibility of thinking and responding respectively. To a lesser extent, the Stockings of Cambridge task also taps into working memory and behavioural inhibition. The CANTAB is a computerised battery of tests that can be broken down in to their cognitive components in order to provide a detailed view of the functions that are impaired and those that are spared. This reason, along with the fact that the battery has an unrivalled degree of validation, is why its use was favoured over manual tests such as the Wisconsin Card Sorting Test or the Tower of Hanoi.

In addition to neuropsychological profiling, ERP data was recorded during the completion of a source memory exclusion task, to investigate the neural correlates of episodic memory retrieval in young and older adults. The exclusion task was chosen because the majority of ERP studies investigating strategic retrieval have used this task. Pressing one button during the test phase for target items and a second for non-target and new items allows participants to implement various strategies to maximise performance, and is therefore ideal for investigating strategic retrieval. Existing evidence shows that young adults either restrict recollection to target items only or recollect both target and non-target items. Furthermore, monitoring retrieved information is restricted either to targets only or to both target and non-target items. In contrast to young adults, older adults appear unable to inhibit recollection of non-target information, recollecting both targets and non-targets.

A further aim of the thesis was to investigate the effect of the context of source information on strategic retrieval. Previous ERP studies using the exclusion task have adopted intrinsic contexts (information inherent to the studied word e.g. a male or female voice) or extrinsic contexts (information not inherent to the studied word e.g. rate the word for pleasantness) without any consideration of the effects of this on their findings. Two reasons highlight that the type of context may have an influence on strategic retrieval. Firstly, a meta-analysis on the effects of aging on memory for content and context (Spencer and Raz, 1995) noted that the elderly had reduced accuracy for extrinsic context (spatial features of stimuli) compared to intrinsic context (auditory or visual aspects of stimuli), suggesting that the retrieval strategies might differ across contexts. Secondly, the previous ERP studies using the exclusion task in young adults have shown a different, and fairly consistent, pattern of results for the retrieval of intrinsic and extrinsic contexts: recollection of target and non-target items, and monitoring of targets only, has been observed for the retrieval of intrinsic contexts (Wilding and Rugg, 1997b; Cycowicz et al., 2001; Wilding and Sharpe, 2004). In contrast, recollection of targets only, and monitoring of targets and non-targets, has been reported for the retrieval of extrinsic contexts (Herron and Rugg, 2003b; Dzulkifli and Wilding, 2005).

Chapter 5 General Methods

The preceding chapters reviewed the literature against which the current research has been conducted. The direction now turns to the experiments that will form the remainder of the thesis. This chapter contains an overview of the participants, testing sessions, stimulus materials, experimental procedure, behavioural analyses, along with the EEG recording, processing and analysis strategy. When these details deviate from the descriptions in this chapter, a separate methods section will be provided within each experimental chapter, describing any procedures specific to that study.

5.1 Participants

Young participants were members of the Stirling University community; older participants were from the local community. All were right handed, native English speakers, with normal (or corrected to normal) hearing and vision. The young group was aged between 17 and 36 years; the older group between 60 and 80 years. Participants were offered payment at a rate of £5 per hour; however, some of the young group requested part payment in course credits. Informed consent was always obtained prior to testing.

5.2 Testing Sessions

Participants visited the laboratory on two occasions. Three to five days prior to the ERP experimental session, each volunteer was trained on the exclusion task procedure (described in section 5.4) and completed a battery of neuropsychological tests. Neuropsychological testing involved the National Adult Reading Test (NART), the Beck Depression Inventory (BDI, Beck et al., 1961), Logical Memory I and II from the

Weschler Memory Scale – Revised (WMS-R, Weschler, 1987), and the older adults completed the Mini Mental State Examination (MMS, Folstein et al., 1975) to ensure they did not have dementia. Participants also completed four tests from the Cambridge Neuropsychological Test Automated Battery (CANTAB): Spatial Span, Spatial Working Memory, Stockings of Cambridge, and the ID/ED (Intra Dimensional/Extra Dimensional) Set-Shifting task. The instructions given for each task was taken from manuals provided by CENES, the company responsible for the marketing of the CANTAB tests. A description of each test is provided below.

Spatial Span

The Spatial Span task is a non-executive task of spatial short-term memory capacity. The test assesses the participant's ability to remember the spatial locations of a sequence of squares on a touch screen computer monitor. On each trial, a display of nine white boxes is presented on the screen. Participants watch while each white box changes colour before being asked to reproduce the sequence. The sequence begins with two boxes changing colour and increases one box at a time up to a maximum of nine. The participant's spatial span score is defined as the longest sequence that they could reproduce correctly within three attempts.

ID/ED (Intra Dimensional/Extra Dimensional) Set-Shifting

This task assesses a participant's ability to focus attention on specific attributes of compound stimuli (intradimensional stages) and to shift attention when required to a previously irrelevant stimulus dimension (extradimensional stages). The participant is required to learn a series of discriminations in which responding to one of two stimuli is correct and the other wrong. The computer provides immediate feedback automatically.

The task involves nine stages with the participant proceeding to the next stage when a criterion of six consecutive correct responses had been attained. Failure to achieve this criterion within 50 trials results in the premature discontinuation of the test. In the first two stages, participants were tested on simple discrimination and reversal for two stimuli varying in just one dimension (irregular purple filled shapes). A second alternative dimension was then introduced (two different white line configurations) and compound discrimination and reversal were tested. To succeed, participants must continue to respond to the previously relevant dimension (purple shapes) while ignoring the presence of the new irrelevant dimension (white lines).

At the intradimensional shift stage, novel examples of each of the two dimensions are introduced and participants must continue to respond to one of the two examples from the previously relevant dimension (purple shapes) and complete a reversal stage where they followed the other relevant example (second purple shape). The final two stages, the extradimensional shift and reversal stages, commence with the introduction of novel examples of each stimulus dimension. In order to succeed at this stage, the participant has to shift ‘response set’ to the previously irrelevant stimulus dimension (white lines). PET scanning studies have shown that the critical ED shift stage involves regions within the anterior frontal lobe (Rogers et al., 2000). The main measure of performance on this task is the furthest stage successfully attained.

Spatial Working Memory

The Spatial Working Memory task is an executive task that assesses working memory for spatial stimuli and strategy use. The test is a self-ordered searching task (Petrides and Milner, 1982), and Positron Emission Tomography (PET) studies have suggested that it activates the dorsal and ventral prefrontal regions (Mehta et al., 2000; Owen et al., 1996; Robbins et al., 1998). A spatial array of coloured boxes is presented on the screen. The purpose of the task is to collect blue tokens hidden inside the boxes by touching each box so it ‘opens up’ revealing what is inside. Once a blue token is found it is used to fill an empty column on the right corner of the screen. There are four sets with three boxes, four sets with four boxes, four sets with six boxes and four sets with eight boxes. Only one blue token is hidden on each trial within a set, and overall in every set, each coloured box only contains one blue token. The key instruction for participants is that once a blue token is found within a box (in any individual trial), then that box would not contain a token again. Therefore, when searching for another token on the next trial participants must remember not to search in boxes that contained blue tokens on previous trials. Consequently, a between search error (BSE) occurs when a participant returns to a box where a token has already been found on a previous trial.

A strategy score can also be derived from this task. Performance on this task can be facilitated by employing a repetitive search strategy. The optimal strategy involves searching through the boxes in the same order on each trial, while remembering not to search in boxes containing tokens on previous trials (e.g. Fray et al., 1996; Owen et al., 1990). Such a strategy may reduce the load on working memory and would, presumably, enhance performance at all levels of task difficulty. The strategy score is calculated by counting the number of different boxes initially opened on each trial. The lower the score, therefore, the greater the use of the strategy.

Stockings of Cambridge

This task was derived from the ‘Tower of Hanoi’ task and primarily measures spatial planning, and to a lesser extent working memory and behavioural inhibition (Shallice, 1982). Several PET studies have indicated that performing this task activates the right dorsolateral prefrontal cortex (Baker, et al., 1996; Morris et al., 1993; Owen et al., 1996). In this test, two sets of three coloured balls are presented on a touch screen monitor, each arranged in three hanging pockets. Participants are asked to copy the top pattern by moving the balls in the lower half of the screen according to specified rules (a ball underneath another ball cannot be moved; a ball cannot be moved to a place where there is no ball underneath, unless its position will be at the bottom of the pocket). Problems should be solved in a certain minimum number of moves (two, three, four or five moves) and participants are instructed to work out the solution prior to moving any balls. There are three sets requiring two moves, three sets requiring three moves, three sets requiring four moves and three sets requiring five moves. The maximum moves allowed correspond to twice the minimum number possible plus one, or plus two in the case of ‘five move’ problems. If the maximum number of moves is exceeded the computer indicates ‘too many moves’ before beginning the next trial.

Initial and subsequent thinking times during trials are recorded to provide estimates of cognitive speed during the preparatory and execution phases of task performance. For each trial, a yoked control condition is also executed. During these ‘following’ trials, participants are instructed to execute a sequence of single moves as quickly as possible. The ‘following’ trials are exact reproductions of the participant’s earlier planning moves. Initial and subsequent movement times in these ‘following’ trials provide estimates of motor speed. These ‘movement times’ are subtracted from the test condition times that included both ‘thinking times’ and ‘movement times’ in order to provide an estimate of planning times in the test conditions.

Due to the relationship between declining health factors and poor memory performance in older adults (Nolan and Blass, 2002; Backman et al., 2000a) participants rated their health on a 5 point scale: 1 = poor, 2 = could be better, 3 = fair, 4 = good, 5 = excellent.

A rating of 3 or above was necessary for inclusion. In addition, any volunteer with a history of neurological or psychiatric illness, epilepsy, head injury, stroke, drug or alcohol abuse, or who was taking any psychoactive medication, was excluded. Finally, years of education were equated in young and older participants.

The exclusion task procedure training session consisted of a short practice block for the young group and two short practice blocks for the older group. The older group were given an extended training session because pilot studies showed that this was necessary for them to become comfortable with the task.

5.3 Stimulus Materials

The stimuli were generated for use in a recognition memory exclusion task. During the study phase of this task, stimuli were presented in a male or female voice and two decisions were required: a gender decision (voice of presentation) and a task decision (either a liking or action judgement). At test, stimuli were presented visually, and participants were required to make recognition judgements based on either gender or task decisions.

The stimuli consisted of 408 low frequency nouns and verbs (range 1-7 per million, word length 3-9 letters; see Appendix), taken from Kucera and Francis (1967). Auditory recordings were taken from Wilding and Rugg (1997b), digitised at 22kHz with 16-bit resolution. Words were used to form 2 practice study-test blocks (24 randomly selected words) and 8 experimental study-test blocks (48 words randomly allocated to each block for each participant). First, the stimuli were randomly allocated into 3 sets of 128 words. For each participant 2 sets were combined to form the study items, and the remaining set served as new items at test. Each set served as new items equally often, counterbalanced by rotation across participants. Second, within each study list, the factors of voice of presentation and task decisions were fully crossed: half of the items were presented in a male voice, half female, and half of the items from each voice required a liking judgement, half action, counterbalancing the four possible combinations of voice/task pairing.

Two practice study-test blocks were formed, allowing recognition decisions based on voice and task decisions to be practiced separately. Each practice study list comprised 8 items, 2 from each voice/task pairing, and each practice test list contained the original 8 studied items along with 4 new items. For the experimental blocks 8 study lists (each consisting of 32 words) were constructed, containing 8 words from each voice/task pairing. To control for primacy and recency effects, each study block began and ended with 2 filler words (1 from each voice/task pairing) and therefore consisted of 28 experimental items plus 4 fillers. Each of the 8 test blocks therefore contained the original 28 studied items along with 16 new items; two of the new items were employed as fillers, presented at the beginning of the test block. The allocation of stimuli as filler items and the order of presentation within each study-test block were randomly determined for each participant.

5.4 Procedure

Participants were informed that they were to take part in a memory experiment consisting of a number of study/test phases, presented on a standard desktop PC. The experiment was implemented using E-Prime software, and responses were made on a PST Serial Response Box (Psychology Software Tools, Inc., http://www.pstnet.com). Visual stimuli were presented in central vision on a monitor, using bold 18-point

Courier New Font, in upper case white letters on a black background. The presentation of stimuli as white against a black background ensured that the stimuli were clear to read and upper case removed shape information that could be used to recognise words. Auditory stimuli were presented through two speakers placed at either side of the monitor.

At study, participants were informed that a series of words would be presented one at a time in a male or female voice. Each study trial commenced with a '+' presented in the centre of the monitor for 500ms, indicating central fixation, followed by a 200ms blank screen, and then an 'O' or 'X' for 1000ms. Participants were told that an 'O' signalled a liking judgement was required on that trial (i.e., judge whether the word is pleasant or unpleasant), whereas an 'X' signalled an action judgement was required (i.e., judge whether the word is active or passive). A 200ms blank screen was followed by a '+' for 500ms, a further 500ms blank screen, and the auditory study stimulus was then presented (mean duration 645ms). A final 1000ms blank screen was followed a '?' prompting participants to respond. Participants were instructed to respond verbally by: i) repeating the word, ii) stating the gender in which the word was spoken, and iii) making the required task judgement. After responding, participants were required to press any button to initiate the next trial. Participants were told that there were no right or wrong answers to the task judgements. The order of gender and task decisions was counterbalanced across participants, but both decisions were made for each study item.

At test, participants were informed that memory judgements would be required, based on either gender or task information, but that they would only be told which information was relevant before the beginning of the test phase and must therefore encode both gender and task information during the study phase. Each test trial commenced with a central '+' for 500ms, replaced by a blank screen for 200ms. The visual test stimulus was then presented for 300ms, followed by a 3000ms blank period during which participants could respond. Participants were required to make a single response to each test word, indicating whether it was a ‘target’ or ‘non-target’ item. Judgements based on gender were performed during half of the test blocks, judgements based on task during the remaining half, with judgement order determined randomly for each participant. The gender (male or female) and task (action or liking) designated as target was counterbalanced and fully crossed within each group of young and older participants.

When making gender judgements, participants were required to remember whether the test item was presented in the designated target voice at study, responding ‘non-target’ to old items presented in the other voice and new items. When making task judgements, participants were required to remember whether the test item was associated with the designated target judgement, responding ‘non-target’ to old items associated with the other task and new items. Participants were told that the task judgement referred to the type of judgement required at study (action or liking) not the specific response that they made (active/passive or pleasant/unpleasant). Target and non-target responses were made by pressing one of two buttons using left and right index fingers, and the mapping of buttons to responses was counterbalanced within each group of younger and older participants.

The average interval between study and test phases was approximately 2 minutes, during which participants a) were informed of the relevant information (voice or task) to be retrieved in the subsequent test phase, and b) demonstrated to the experimenter which buttons would be used during the test phase. Throughout the experiment participants were instructed to respond as quickly and accurately as possible, and to reduce the number of trials containing EEG artefact, they were instructed to remain relaxed and to maintain central fixation. A short break (of approximately 2 minutes) was given between each study/test block.

The gender the word was spoken in was intrinsic (inherent) to the word, whereas the task judgement made about the word was extrinsic (not inherent) to the word; therefore for the remainder of the thesis the gender will be referred to as the intrinsic context and the task judgement as the extrinsic context. This distinction is important as the purpose of the gender and task judgment were to compare retrieval of intrinsic and extrinsic contexts.

5.5 Behavioural Analyses

The behavioural data were reported separately for each context or age group. Accuracy data (consisting of the proportion of hits to targets and non-targets, and the proportion of correct rejections), sensitivity and bias (Pr [hit-FA] and Br [FA/(1-Pr)], respectively; Snodgrass and Corwin, 1988) were reported along with the reaction time (RT) data to target hits, non-target hits and correct rejections. In Experiment 1a, the accuracy and RT data were analysed using repeated measures ANOVA, with factors of context (intrinsic vs. extrinsic) and response (target vs. non-target vs. correct rejection). Any main effects or interactions were followed up using paired t-tests.

Two discriminability analyses were conducted: the first was within context and compared the hit rate for targets to the false alarm rate for non-targets and new items (i.e. to ensure that Pr was greater than zero), using paired t-tests. As the same button press is used for non-target and new items it is difficult to determine chance performance in the exclusion task. Therefore, an accepted method used in the literature to assess performance is to ensure that the hit rate to targets is significantly greater than the false alarm rate to non-target and new items. The second discriminability analysis compared Pr between contexts and responses using repeated measures ANOVA, with factors of context (intrinsic vs. extrinsic) and response ([target vs. non-target] vs. [target vs. new]). Any interactions were followed up by paired t-tests. Br was assessed using the same ANOVA structure.

Process Dissociation Procedure (PDP) estimates of familiarity and recollection were also calculated. Although the experiments reported in this thesis were based on an ‘exclusion’ condition only, the structure of the task allows it to be treated as one in which an ‘inclusion’ and ‘exclusion’ condition have been embedded (Wilding and Rugg, 1997b). The rationale underlying the calculation of these estimates is as follows: a target item is endorsed as such either when it is recollected or when it is recognised on the basis of familiarity. If these two basis for recognition are independent, then the probability of responding correctly to a target (pT) is given by $pT = pR + pF – pRF$, where pR, pF and pRF are the probabilities of recognising an item on the basis of recollection, familiarity, and recollection and familiarity, respectively. It is further assumed that the incorrect endorsement of a non-target item as a target (pNT) occurs when recollection fails, but the item is nevertheless recognised as old on the basis of familiarity, giving the equation $pNT = pF – pRF$. Given this formulation, pR can be estimated as $pT – pNT$, and pF as $pNT / (1 – pR)$. The PDP estimates were analysed using repeated measures ANOVA, with factors of context (intrinsic vs. extrinsic) and estimate (familiarity vs. recollection). Any interactions were investigated using paired t-tests.

For the age comparison in Experiment 2a, the above behavioural analyses were conducted, except mixed ANOVAs and/or independent t-tests were employed and the factor of context was replaced by that of age (younger vs. older). Also, in Experiment

1b and 2c correlations were performed between the magnitude of the late right frontal effect and performance on the CANTAB tests using Spearman's Rho. Non-parametric analysis was used because, while the ERP data was normally distributed, the CANTAB data was not. Finally, in Experiment 2b analyses comparing performance of the young and old on the CANTAB tests was conducted using mixed ANOVAs and independent t-tests (see Experiment 2b for a full description of the factors employed in the ANOVAs). There is no non-parametric alternative for the mixed ANOVA (Dancey and Reidy, 2004). For the behavioural data, statistical significance was assessed using an alpha level of 0.05. However, as this level is strict, an alpha level between 0.05 and 0.07 was regarded as marginally significant.

5.6 EEG Recording

Data was recorded and processed using Neuroscan software (Compumedics Ltd., http://www.neuro.com). EEG was recorded from 61 Silver/Silver Chloride electrodes embedded in a Quick-Cap (Neuro-medical Supplies, http://www.neuro.com), based on the international 10-20 system (Jasper, 1958). The montage included 7 midline sites (OZ, POZ, PZ, CPZ, CZ, FCZ and FZ), 27 sites over the left hemisphere (O1, PO3, PO5, PO7, P1, P3, P5, P7, CP1, CP3, CP5, TP7, C1, C3, C5, T7, FC1, FC3, FC5, FT7, F1, F3, F5, F7, AF3, AF7 and FP1), and 27 sites over the right hemisphere (O2, PO4, PO6, PO8, P2, P4, P6, P8, CP2, CP4, CP6, TP8, C2, C4, C6, T8, FC2, FC4, FC6, FT8, F2, F4, F6, F8, AF4, AF8 and FP2). An electrode placed at AFZ was used as the ground, and additional reference electrodes were placed on the left and right mastoid processes. Horizontal and vertical EOG were monitored from electrodes placed above and below the left eye and the outer canthi of each eye. Prior to recording, all electrode impedances were adjusted below 5kΩ. EEG recordings were referenced online to the left mastoid and re-referenced offline to the average of the left and right mastoids. All data were recorded continuously with a bandpass filter of 0.01-40 Hz, and digitised at a sampling rate of 125 Hz and a sampling period of 8ms per point.

5.7 ERP Formation

Continuous EEG from each participant was processed to remove data where saturation had occurred, and to remove the effects of eye-blinks (using Neuroscan Ocular Artefact Reduction procedure). The data was then separated into 2104 ms epochs (104ms pre-stimulus and 2000ms post-stimulus), baseline corrected (using the pre-stimulus interval) and digitally smoothed over 5 points. Trials on which baseline drift (the difference in amplitude from the baseline to the end point of each individual epoch) exceeded 75 µV or where horizontal eye movements exceeded +/- 100mV were excluded.

Six average ERP waveforms were formed for each participant in Experiment 1a, using correct responses for each context (intrinsic and extrinsic), in each response category (targets, non-targets and new). As the extrinsic context was only retrieved in Experiment 2a, three average ERP waveforms (targets, non-targets and new) were formed for each participant. A minimum of 16 artefact free trials was required from each participant in each response category, to ensure an acceptable signal-to-noise ratio. Finally, individual participant ERPs were averaged together to form grand average target, non-target and new waveforms for both contexts.

5.8 ERP Analyses

5.8.1 Magnitude Analyses

Magnitude analyses were conducted to ascertain the presence of significant old/new effects within contexts or age groups, and to assess whether reliable old/new effects differ quantitatively (in size) between contexts or age groups. The ERP amplitude data for each context or age group was initially analysed separately using consecutive 100ms time bins to ascertain the presence and time course of reliable voltage differences. Repeated-measures ANOVA employed the factors of response ‘R’ (target vs. non-target vs. new), location ‘L’ (anterior vs. posterior), hemisphere ‘H’ (left vs. right) and site ‘S’ [inferior vs. mid vs. superior (see Figure 6 for electrode sites)]. The preceding analyses, together with visual inspection of the waveforms, were used to inform the choice of appropriate latency periods to reflect the evolution of the ERP effects throughout the epoch.

The mean amplitudes from each response (target, non-target and new) were then calculated for each latency period and subjected to analysis by repeated-measures ANOVA. An initial global ANOVA was conducted employing factors of response ‘R’ (target vs. non-target vs. new), location ‘L’ (anterior vs. posterior), hemisphere ‘H’ (left vs. right) and site ‘S’ (inferior vs. mid vs. superior). As interest lies solely in ERP old/new effects, only main effects and interactions involving the factor of response are reported. Main effects and interactions involving the factor of response were followed up by subsidiary ANOVAs and/or post hoc t-tests investigating all possible paired comparisons. For example, a global response (target vs. non-target vs. new) by location (anterior vs. posterior) interaction was investigated using a series of two-way ANOVAs with factors of response (target vs. new; non-target vs. new; target vs. non-target) and location (anterior vs. posterior).

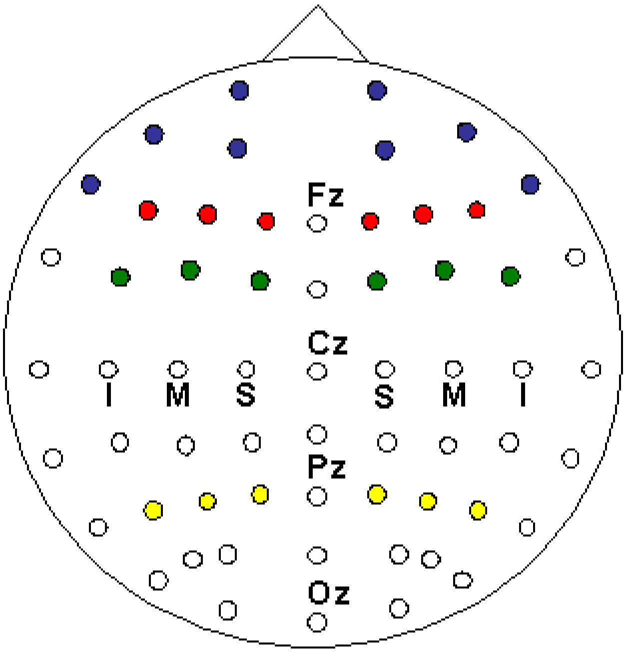

Figure 6. Schematic map of the 61 EEG electrode sites. S represents superior sites, M shows midline sites and I indicates inferior sites. Electrodes shown in red and yellow are included in the main ERP analyses in Experiment 1a and 2a, and those used in the additional analysis in Experiment 2a are depicted in green. Electrodes employed in the analysis of Experiment 1b and 2c and the additional analysis in Experiment 1a are shown in blue and red. Only the main ERP analyses in Experiment 1a and 2a are described in this chapter; see the methods section of individual experimental chapters for details of the other analyses.

Between context analyses were conducted using difference waveforms (target minus new, non-target minus new and target minus non-target). Similar to the within context analyses, global analyses were conducted, but the factor of context was now included: context ‘C’ (intrinsic vs. extrinsic), response ‘R’ (target minus new vs. non-target minus new vs. target minus non-target), location ‘L’ (anterior vs. posterior), hemisphere ‘H’ (left vs. right) and site ‘S’ (inferior vs. mid vs. superior). Here, as interest lies solely in differences in the ERP old/new effects between contexts, the reported results were restricted to those involving the factor of context. Main effects and interactions involving the factor of context were followed up by subsidiary ANOVAs and/or post hoc t-tests examining each response separately if context by response interactions were present. For example, a global context (intrinsic vs. extrinsic) by response (target minus new vs. non-target minus new vs. target minus non-target) by location (anterior vs. posterior) interaction was investigated using two-way ANOVAs of separate responses with factors of context (intrinsic vs. extrinsic) and location (anterior vs. posterior). If context and response did not interact in the global ANOVA, subsidiary analyses were conducted on data collapsed across responses. For the between age magnitude comparison in Experiment 2a, the same above ERP analyses were conducted, except mixed ANOVAs were employed and the factor of context was replaced by that of age (younger vs. older).

In the subsidiary analyses, four-way interactions (e.g. response by location by hemisphere by site) were investigated using three-way ANOVAs (e.g. response by hemisphere by site of separate locations). Any three-way interactions (e.g. response by location by hemisphere) were explored using two-way ANOVAs [e.g. response by hemisphere (collapsed across site) of separate locations]. Finally, two-way interactions (e.g. response by location) were followed up using paired or independent t-tests [e.g. of separate locations (collapsed across hemisphere and site)]. The subsidiary analyses are only reported for the highest order global interactions (e.g. a global RxLxH interaction will not be followed up if an RxLxHxS interaction is present). This approach was adopted because the highest order interactions provide a complete description of the data. In addition, for brevity, not all subsidiary analyses are reported. For example, if a three way RxLxH interaction reflected a left parietal effect, only the result of the final t-test comparing responses at separate left and right parietal hemispheres would be reported, the intermediate RxH interaction when split by location would not be presented.

5.8.2 Topographic Analyses

Topographic analyses assess whether qualitative differences in significant ERP old/new effects are present across time windows, contexts or age groups. Topographic comparisons were only performed when the relevant within-context/age magnitude analyses revealed robust ERP effects. Topographic ANOVAs were conducted using difference waveforms (target minus new, non-target minus new) for each latency period following normalisation (across all 61 EEG electrodes) using the maximum/minimum method (McCarthy and Wood, 1985). Within-context and within-age comparisons were conducted to assess qualitative differences in the ERP effects over time. An initial global ANOVA was conducted, employing factors of epoch ‘E’ (latency period 1 vs. latency period 2 vs. latency period 3 vs. latency period 4) by response ‘R’ (target minus new vs. non-target minus new) by location ‘L’ (anterior vs. posterior) by hemisphere ‘H’ (left vs. right) by site (inferior vs. mid vs. superior). As interest lies solely in distributional changes over time, only main effects and interactions involving the factor of epoch are reported.

Main effects and interactions involving the factor of epoch were followed up by subsidiary ANOVAs and/or post hoc t-tests of appropriate paired contrasts of separate responses if epoch by response interactions were present. For example, a global epoch (latency period 1 vs. latency period 2 vs. latency period 3 vs. latency period 4) by response (target minus new vs. non-target minus new) by location (anterior vs. posterior) interaction would be investigated using a series of two way ANOVAs of separate responses with factors of epoch (latency period 1vs. latency period 2; latency period 2 vs. latency period 3; latency period 3 vs. latency period 4) and location (anterior vs. posterior). If epoch and response did not interact in the global ANOVA, subsidiary analyses were conducted on data collapsed across responses.

Between-context and between-age comparisons were performed using ANOVAs of the same design as the equivalent magnitude comparisons, without the response level target minus non-target. Interactions in the subsidiary topographic analyses were investigated in the same way as for the magnitude analyses. For the ERP data, statistical significance was assessed using an alpha level of 0.05. However, as this level is strict, consistent with the behavioural data an alpha level between 0.05 and 0.07 was regarded as marginally significant.

The preceding description of the methods applies to the majority of studies in the thesis. Each experimental chapter details any differences to these methods in their own methods section (i.e. in Experiment 2a only the extrinsic context was retrieved; Experiment 1a, 1b and 2c include additional frontal analyses using all frontal electrodes to further investigate the late right frontal effect; and finally due to the more widespread distribution of the left sided negativities in the elderly, additional fronto-central analyses were conducted in Experiment 2a). The focus now turns to the first experimental chapter.

Chapter 6 Experiment 1a

6.1 Introduction

In everyday life, our memory for prior events often requires us to remember an episode in the context in which it happened. For example, if you remember hearing the famous quote by Sir Winston Churchill ‘The price of greatness is responsibility’ you may be asked who said it. Similarly, if you remember watching a film last weekend you may be asked what you thought of it. These scenarios both provide an example of source memory. One important distinction between these two scenarios is that the source memory is either intrinsic or extrinsic to the prior event (e.g. in the Sir Winston Churchill and film scenarios respectively).

From the perspective of dual process theory, as source memory tasks require the retrieval of context, familiarity alone is insufficient for successful remembering; recollection is required. In accordance with this view, previous ERP studies of source memory retrieval have found the putative mid-frontal correlate of familiarity and the left parietal correlate of recollection (e.g. see Bridson et al., 2006; Herron and Wilding, 2005). In addition, the putative late right frontal correlate of executive/post retrieval processing has also been elicited during source memory tasks (e.g. see Wilding, 1999). It remains unclear, however, whether differences in the engagement of these three retrieval processes can elucidate the strategies people employ during source memory retrieval. This first experimental chapter therefore investigates whether people use different strategies (as indexed by behaviour) depending on the type of context (intrinsic or extrinsic), and examines differences in the engagement of the three retrieval processes across contexts, to further reveal the retrieval strategies used.

The majority of previous ERP studies investigating retrieval strategies have used the source memory exclusion task. These studies have investigated retrieval strategies by examining variations in the left parietal correlate of recollection, and to a lesser extent, the late right frontal effect, rather than exploring whether differences in behaviour produce variations in all three retrieval processes. In addition, the studies have used either intrinsic or extrinsic contexts without any consideration of whether this influences their findings.

Close inspection of previous ERP studies indicates that, separately, they provide some evidence for a dissociation of the retrieval strategies employed for intrinsic and extrinsic contexts. Although the behavioural evidence is very mixed, in general higher accuracy and slower reaction times are evident for the retrieval of extrinsic context, suggesting differences in retrieval strategies between contexts. The ERP evidence is clearer, however. The majority of studies employing extrinsic contexts have reported target specific strategies, i.e. the left parietal correlate of recollection was present only for target items (Herron and Rugg, 2003a; Herron and Rugg, 2003b; Herron and Wilding, 2005; Dzulkifli and Wilding, 2005). In contrast, the majority of studies employing an intrinsic context have reported target and non-target strategies, i.e. the left parietal correlate of recollection was present for target and non-target items (Wilding and Rugg, 1997b; Cycowicz et al., 2001; Wilding and Sharpe, 2004; Wilding et al., 2005).

The aforementioned studies have not widely reported the late right frontal effect in relation to strategic retrieval, therefore the effect of context on post-retrieval monitoring is less clear than that of recollection. However, the available findings suggest that late right frontal effects are frequently present for targets and non-targets when an extrinsic context is employed (Herron and Rugg, 2003b; Dzulkifli and Wilding, 2005; Dzulkifli et al., 2005), while late right frontal effects are often evident for targets only following the use of an intrinsic context (Wilding and Rugg, 1997b; Cycowicz et al., 2001; Wilding and Sharpe, 2004).

The comparison of the behavioural data and ERP correlates of intrinsic and extrinsic contexts is confounded by the fact that different studies have been used to investigate each type of context; these studies have employed different experimental designs (e.g. some studies have included study/test delays) and separate participant groups. The present experiment aims to eliminate these confounds by using a single paradigm for both intrinsic and extrinsic contexts, therefore allowing a direct comparison of their behavioural performance and ERP correlates without the confounds of experimental design or separate participant groups.

In the current experiment, young participants' EEG was recorded while they studied a series of words spoken in a male or female voice (intrinsic context). In addition, they made an action or liking judgement about the word (extrinsic context). During the test phase, participants were instructed to discriminate between target, non-target and new items (targets were old items from one gender or judgement; non-targets were old items from the other gender or judgement). The retrieval of intrinsic or extrinsic contexts was required in separate blocks. The key prediction was that retrieval strategies would differ for intrinsic and extrinsic contexts (as indexed by behavioural performance) and this would be associated with variation in the accompanying ERP effects, thus further elucidating the retrieval strategies employed.

6.2 Methods

6.2.1 Participants

Fifty-six young participants took part in the experiment. The data from 11 participants was discarded: 3 due to insufficient behavioural trial numbers, 7 due to high proportions of noise (electrode drift and alpha activity) and 1 due to equipment failure. The remaining 45 participants (23 female) were aged between 18 and 36 years (mean age 24). All other aspects of the methods are described in the ‘General Methods’ chapter.

6.3 Results

6.3.1 Behaviour

The behavioural data are reported in Table 1 (below). Accuracy was slightly greater in the extrinsic context than the intrinsic context, and for correct rejections followed by non-targets then targets. An ANOVA analysing the accuracy data (see ‘General Methods’ chapter for the structure of this and the other behavioural data ANOVAs) revealed a main effect of response [F(2,88) = 171.31, p < 0.001], but no significant main effect of context or interaction between response and context, therefore accuracy did not differ between contexts. Pairwise comparisons, collapsed across the factor of context, revealed that accuracy was greater for new responses than non-targets [t(44) = -15.72, p < 0.001] and targets [t(44) = -16.27, p < 0.001]. In turn, accuracy to non-targets was greater than targets [t(44) = -3.85, p < 0.001].

	Intrinsic Context	Extrinsic Context
Accuracy		
Hits/Target	0.65 (0.14)	0.67 (0.14)
Hits/Non-Target	0.72 (0.15)	0.73 (0.13)
Correct Rejection	0.94 (0.06)	0.95 (0.06)
Sensitivity (Pr)		
Target vs. Non-Target	0.37 (0.25)	0.40 (0.23)
Target vs. New	0.59 (0.16)	0.62 (0.16)
Bias (Br)		
Target vs. Non-Target	0.44 (0.12)	0.45 (0.11)
Target vs. New	0.15 (0.11)	0.13 (0.13)
PDP Estimates		
Familiarity	0.44 (0.20)	0.45 (0.19)
Recollection	0.37 (0.18)	0.40 (0.21)
RT(ms)		
Hits/Target	1365 (278)	1498 (273)
Hits/Non-Target	1415 (301)	1563 (307)
Correct Rejection	1136 (260)	1135 (251)

Table 1. Mean behavioural data for Experiment 1a (standard deviation in brackets). Accuracy, sensitivity, bias and the PDP estimates did not differ between contexts, while reaction times did differ between contexts. Reaction times were slower for the extrinsic context for target and non-target responses. There was no significant difference in the response times for correct rejections between contexts.

Table 1 shows that within each context Pr was greater than zero suggesting that participants were able to discriminate targets from non-targets and new items. This was confirmed by paired t-tests, which revealed that, for both contexts, more target responses were made to targets than to non-targets and new items, [Intrinsic context, target vs. non-target: $t(44) = 10.02$, $p < 0.001$, target vs. new: $t(44) = 24.46$, $p < 0.001$; Extrinsic context, target vs. non-target: $t(44) = 11.81$, $p < 0.001$, target vs. new: $t(44) = 26.03$, $p < 0.001$].

Table 1 also shows that Pr was greater in the extrinsic context than the intrinsic context, and for target compared to new than target compared to non-target. An ANOVA comparing discriminability (Pr) between contexts revealed a main effect of response

[F(1,44) = 247.18, p < 0.001], showing that, unsurprisingly, it was more difficult to discriminate between targets and non-targets than targets and new items. There was no significant main effect of context or interaction between context and response, indicating that discriminability was equivalent between contexts.

Bias (Br) was more liberal in the extrinsic context than the intrinsic context when discriminating target and non-target items, and more conservative when discriminating target and new items (see Table 1). However, an ANOVA comparing bias between contexts only revealed a main effect of response [F(1,44) = 415.97, p < 0.001], showing that participants adopted a more conservative bias when discriminating targets from new items than targets from non-targets. Again, there was no significant main effect of context or interaction between context and response, therefore bias was equivalent between contexts.

Table 1 shows that the PDP estimated that the contribution of familiarity and recollection was greater in the extrinsic context than the intrinsic context, and, in general, the contribution of familiarity was greater than recollection. However, an ANOVA comparing the estimates of familiarity and recollection revealed no main effects of estimate or context, or interaction between the factors, showing that the contribution of familiarity and recollection remained constant within and between contexts.

Reaction times were generally slower in the extrinsic context, except for correct rejections, where the intrinsic context was associated with slightly longer decision times (see Table 1). An ANOVA comparing the reaction times revealed a main effect of context [F(1,44) = 15.76, p < 0.001] and response [F(2,88) = 130.35, p < 0.001] and an interaction between context and response [F(2,88) = 11.97, p < 0.001]. Pairwise comparisons revealed slower reaction times for the extrinsic context for target responses [t(44) = -3.69, p = 0.001] and non-target responses [t(44) = -4.48, p < 0.001]. There was no significant difference in the response time for correct rejections across contexts.

6.3.1.1 Summary of Behavioural Data

The accuracy, sensitivity, bias and PDP data suggests that performance was similar for intrinsic and extrinsic contexts. Longer RTs for targets and non-targets in the extrinsic context, however, suggests that in order to keep performance equivalent across contexts, different strategies may have been adopted for each context.

6.3.2 Event-Related Potentials

6.3.2.1 Intrinsic Context

Figure 7 and Figure 8 show the grand average target, non-target and new waveforms for the intrinsic context condition from 36 electrode sites in Figure 7 and a close up of 6 sites in Figure 8. The mean number of trials contributing to the waveforms was 33 target, 36 non-target and 48 new. The waveforms begin to diverge over fronto-central sites from approximately 300ms post-stimulus onset, with target and non-target waveforms becoming more positive than new waveforms. This divergence exhibits a bilateral distribution, and is greater for target compared to non-target waveforms. An old/new positivity is also evident over parieto-central sites from approximately 400ms post stimulus onset, and is of greater magnitude for targets compared to non-targets. This effect appears to be maximal at left parietal sites and although it begins to decline around 700ms, the effect continues until approximately 1000ms. From about 900ms, a prominent old/new effect is a bilateral negativity over parieto-centro-occipital sites, which looks to be larger for targets compared to non-targets from approximately 1100-1500ms. An old/new positivity is also present over right frontal sites from approximately 900ms. This effect appears to be larger for targets compared to non-targets at sites F2, F4, F6 and AF8. Finally, an old/new negativity, of possible greater magnitude for targets compared to non-targets, is evident from about 1300ms at sites AF7, F7 and F5.

6.3.2.2 Extrinsic Context

Figure 9 and Figure 10 show the grand average target, non-target and new waveforms for the extrinsic context, again from 36 electrode sites in Figure 9 and a close up of 6 sites in Figure 10. The mean number of trials contributing to the waveforms was 35 target, 37 non-target and 48 new. The bilateral fronto-central divergence apparent in the intrinsic context from 300ms is delayed for the extrinsic context, beginning at approximately 500ms. In accordance with the intrinsic context, this divergence appears to be larger for target compared to non-target waveforms. An old/new positivity is also evident over parieto-central sites from approximately 400ms, and is of greater magnitude for targets compared to non-targets from approximately 600-800ms. This effect appears to be maximal at left parietal sites and, although it is in decline from approximately 700ms, the effect continues until approximately 1500ms (in contrast to 1000ms in the intrinsic context). From about 900ms, a prominent old/new effect is a bilateral negativity over parieto-centro-occipital sites, which looks to be larger for non-targets compared to targets from approximately 1700ms (compared to targets greater than non-targets from 1100-1500ms in the intrinsic context). An old/new positivity is also present over right frontal sites from approximately 900ms. This effect appears to be larger for targets compared to non-targets at sites F2, F4, F6, FP2, AF4 and AF8.

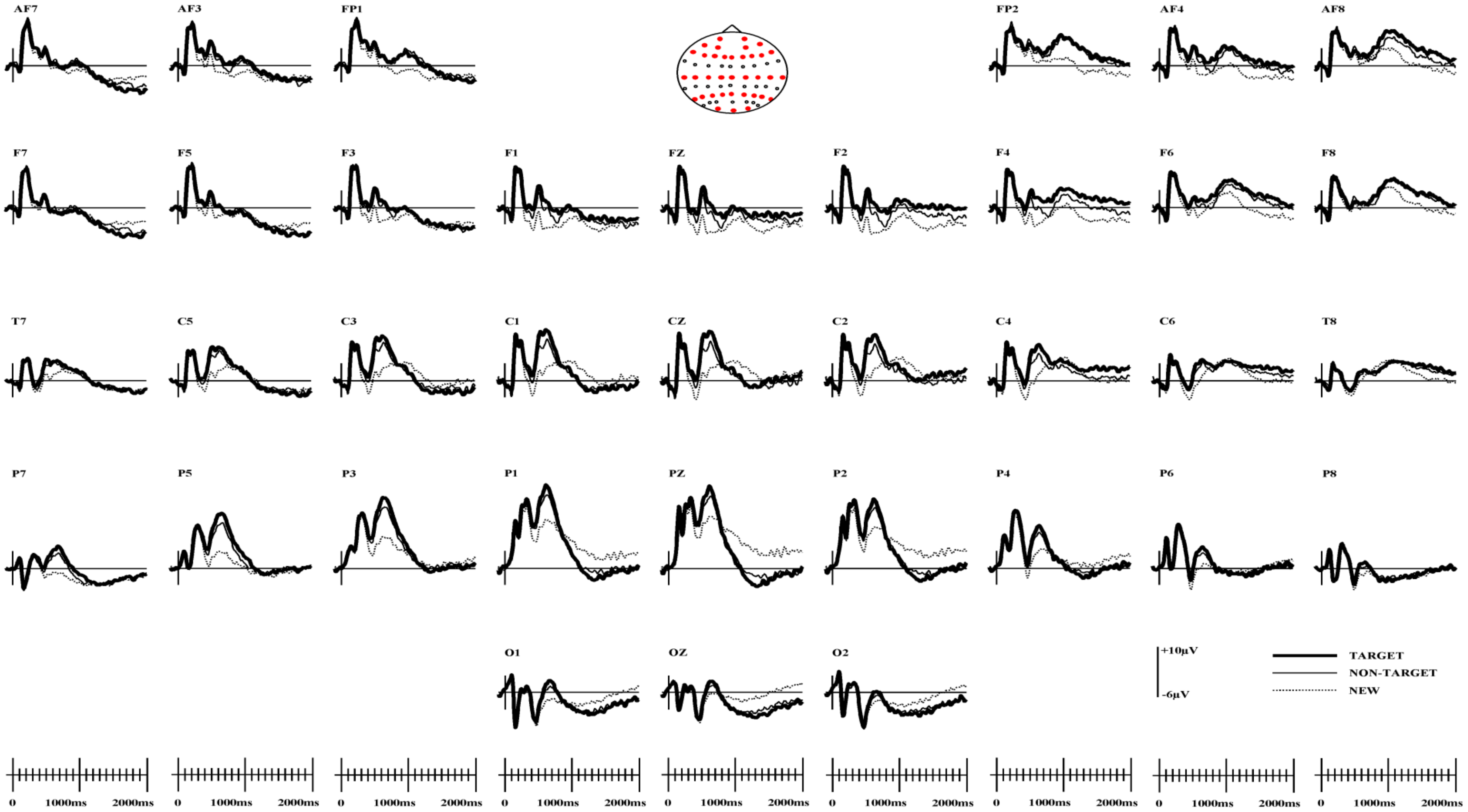

Figure 7. Grand average ERP waveforms for correctly classified target, non-target and new items for the intrinsic context. 36 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16µV.

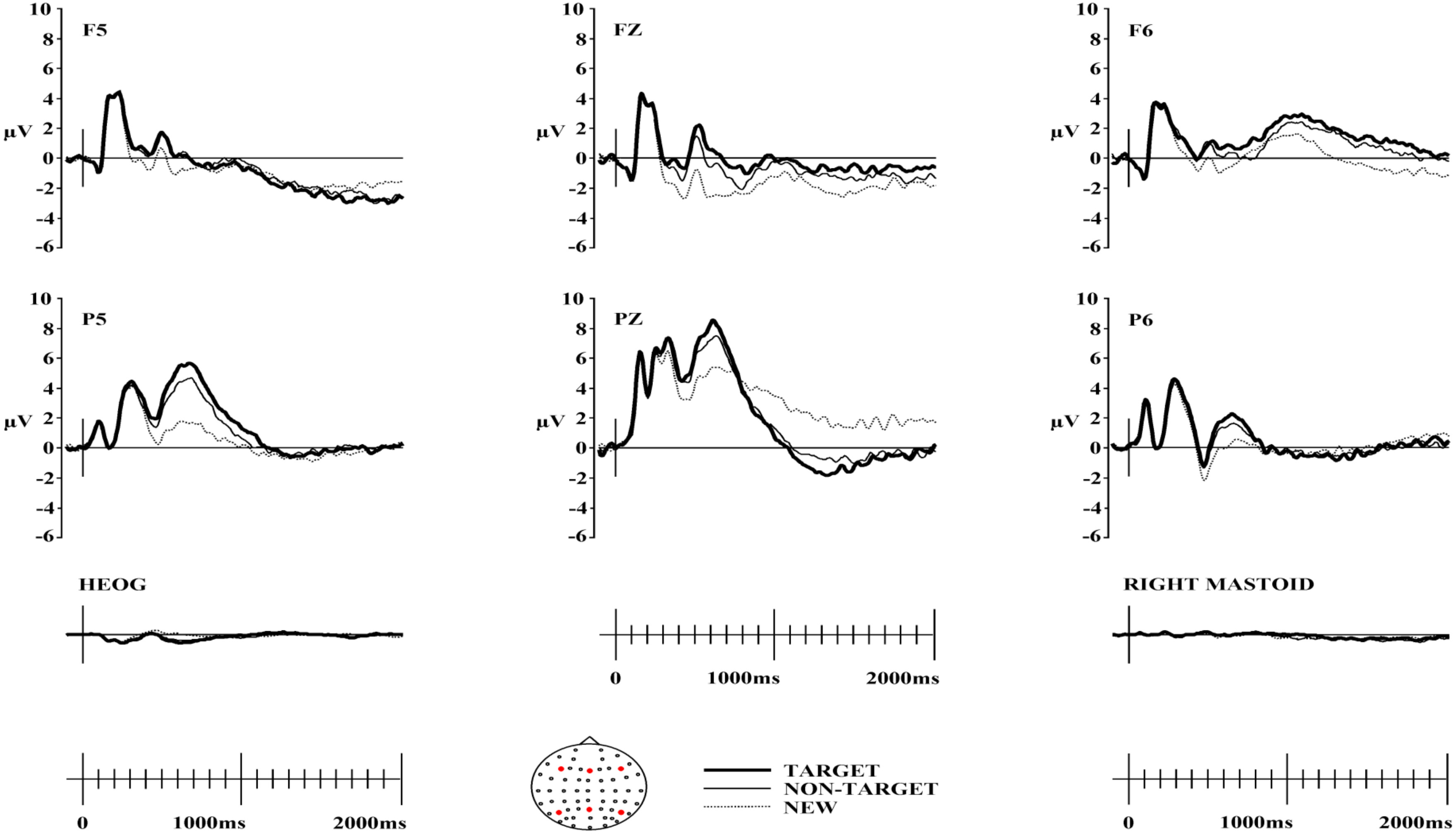

Figure 8. Grand average ERP waveforms for correctly classified target, non-target and new items for the intrinsic context. A close up of 6 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16μV.

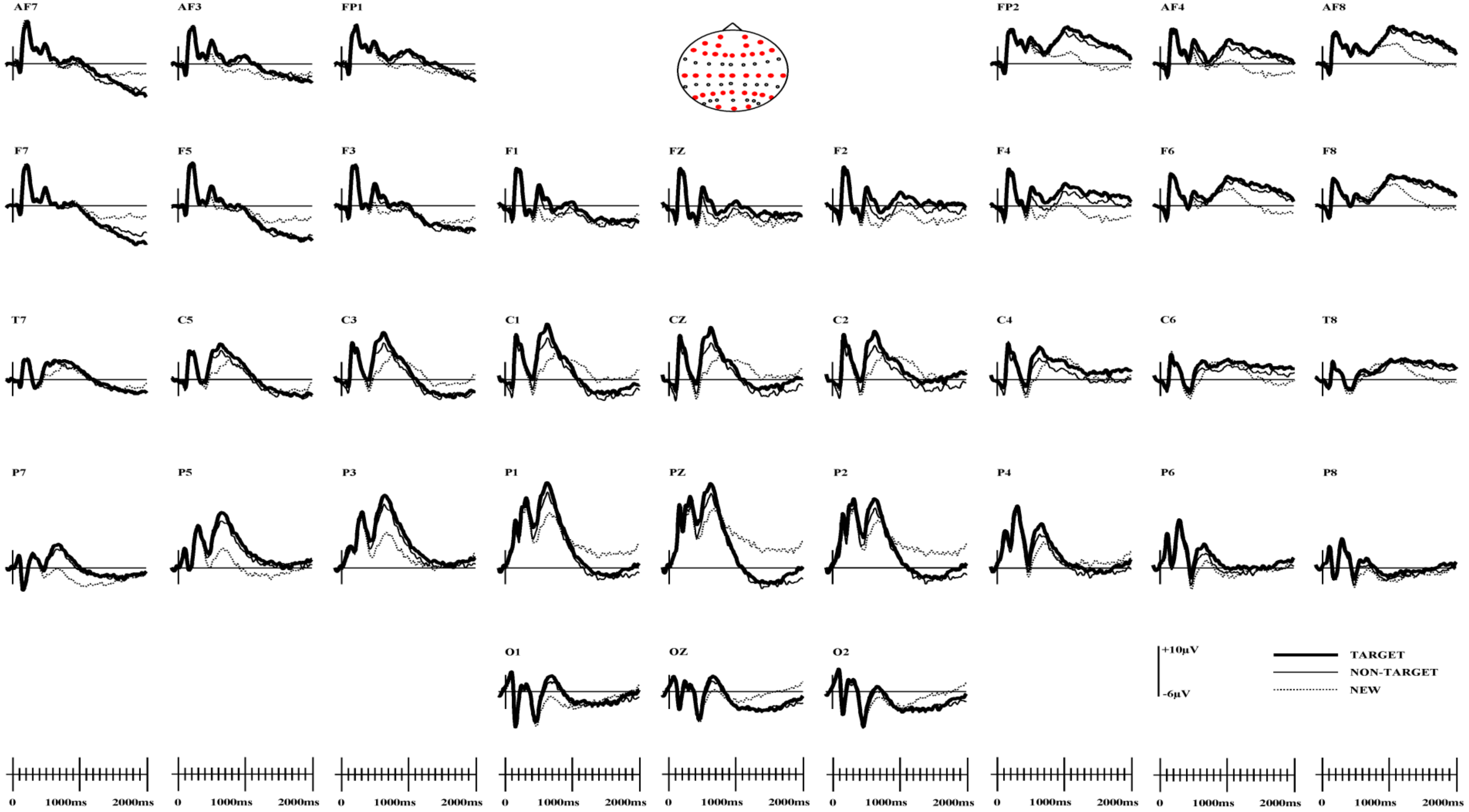

Figure 9. Grand average ERP waveforms for correctly classified target, non-target and new items for the extrinsic context. 36 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16µV.

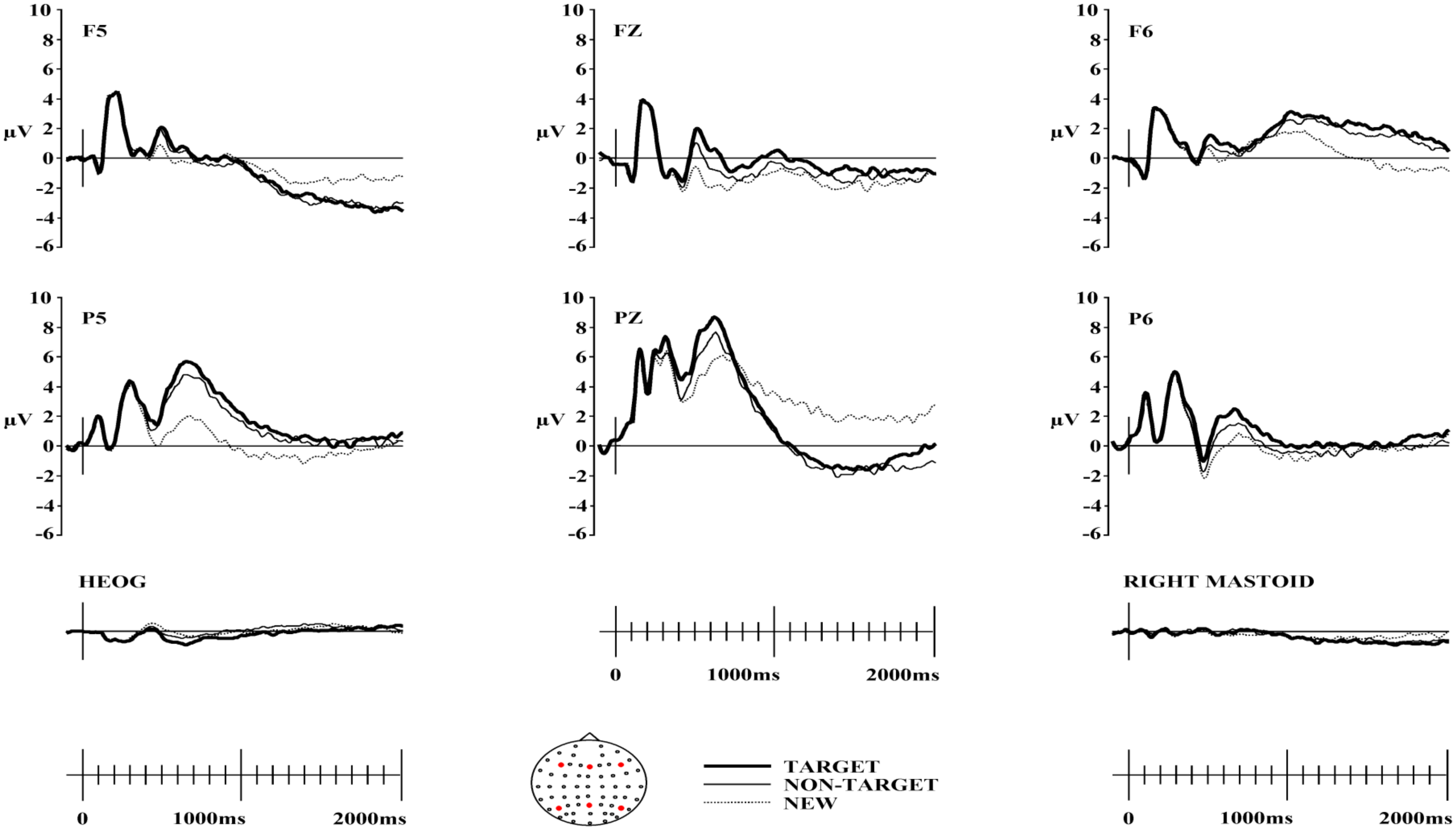

Figure 10. Grand average ERP waveforms for correctly classified target, non-target and new items for the extrinsic context. A close up of 6 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16µV.

Finally, an old/new negativity, of possible greater magnitude for targets compared to non-targets, is evident from about 1300ms at sites AF7, F7 and F5 (see Figure 9).

6.3.2.3 Rationale for the ERP Analyses

The aim of the ERP analyses was to compare early bilateral frontal, left parietal and late right frontal old/new effects elicited by the retrieval of intrinsic and extrinsic contexts during an exclusion task. With this aim in mind, preliminary analyses (see ‘General methods’ chapter for details) showed that the following time windows best captured the evolution of the ERP effects over time for both context conditions: 300-450ms, 450-900ms, 900-1300ms and 1300-2000ms. The distributions of the effects in these time windows are illustrated in the topographic maps shown in Figure 11 and Figure 12 (p135 and 136). Within-context magnitude and topographic ANOVAs were conducted to assess the presence of significant ERP modulations within each latency window, and any qualitative differences across latency windows, respectively. Between-context magnitude and topographic ANOVAs were conducted to examine quantitative and qualitative differences between the ERP correlates of intrinsic and extrinsic contexts within each latency window. Precise details of the ERP analysis strategy for this and the other experiments can be found in the ‘General Methods’ chapter.

6.3.2.4 Within-Context Magnitude Analyses

6.3.2.4.1 Intrinsic Context

The global magnitude analyses revealed main effects and interactions involving the factor of response for all four latency windows (see Table 2 below). The highest order

ANOVA result from 300-450ms was a two-way response by site interaction, and from 450-900ms, 900-1300ms and 1300-2000ms the highest order results were four-way response by location by hemisphere by site interactions. These results were further examined with subsidiary analyses investigating all possible paired comparisons (target vs. new; non-target vs. new; target vs. non-target).

Latency Window	Target vs. Non-Target vs. New
<u>300-450ms</u>	
R	F(1.61,70.68)=12.26,p<0.001
RxS	F(2.18,95.89)=9.72,p<0.001
<u>450-900ms</u>	
R	F(1.83,80.39)=22.88,p<0.001
RxH	F(1.93,85.02)=3.30,p=0.04
RxS	F(2.30,101.36)=7.59,p<0.001
RxLxH	F(1.71,75.24)=14.30,p<0.001
RxLxS	F(2.37,104.17)=13.95,p<0.001
RxLxHxS	F(2.53,111.36)=6.82,p=0.001
<u>900-1300ms</u>	
RxL	F(1.93,84.91)=3.99,p=0.02
RxS	F(2.42,106.32)=7.89,p<0.001
RxLxH	F(1.71,75.29)=7.74,p=0.002
RxLxS	F(2.77,121.73)=32.74,p<0.001
RxLxHxS	F(2.11,92.79)=2.80,p=0.06
<u>1300-2000ms</u>	
RxL	F(1.86,81.63)=5.66,p=0.006
RxH	F(1.62,71.29)=3.73,p=0.04
RxS	F(2.32,101.89)=5.43,p=0.004
RxLxH	F(1.93,84.79)=11.43,p<0.001
RxLxS	F(2.54,111.94)=26.60,p<0.001
RxLxHxS	F(2.76,121.40)=3.32,p=0.03

Table 2. Results of the global magnitude analyses for the intrinsic context condition. R, L, H and S represent the factors of response, location, hemisphere and site respectively. Main effects and interactions involving the factor of response were present for all four latency windows.

<u>Target vs. New:</u> Subsidiary analyses investigating the global response by site interaction in the 300-450ms time window (Table 2) also gave rise to a response by site interaction [F(1.20,53.00) = 24.49, p < 0.001], indicating that while target waveforms were more positive than new waveforms at all sites [superior – t(44) = 6.68, p < 0.001;

mid – $t(44) = 6.62$, $p < 0.001$; inferior – $t(44) = 5.91$, $p = 0.002$], the difference was greater at the superior site [superior site = Mean 1.37μV; mid site = Mean 1.11μV; inferior site = Mean 0.75μV]. Although the results do not reveal a significant interaction with location, they are nonetheless consistent with the presence of a significant bilateral frontal effect. As can be seen in Figure 11(A) this effect overlapped in time with the onset of the parietal old/new effect.

The greater positivity of target waveforms compared to new waveforms continued into the 450-900ms epoch (Figure 11, B). Subsidiary analysis investigating the global response by location by hemisphere by site interaction (Table 2) also revealed a response by location by hemisphere by site interaction [$F(1.40,61.62) = 10.69$, $p = 0.001$] in the target versus new contrast. This interaction reflected the left parietal effect: target waveforms were more positive than new waveforms at all left parietal sites [superior – $t(44) = 4.67$, $p < 0.001$; mid – $t(44) = 6.93$, $p < 0.001$; inferior – $t(44) = 8.04$, $p < 0.001$], this difference was greatest, however at the mid and inferior sites [superior site = Mean 1.97μV; mid site = Mean 2.96μV; inferior site = Mean 2.89μV]. A main effect of response at the posterior right hemisphere [$F(1,44) = 16.12$, $p < 0.001$] most likely reflected spread of the left parietal effect. Target waveforms were also more positive than new waveforms at all anterior sites [superior – $t(44) = 5.41$, $p < 0.001$; mid – $t(44) = 4.86$, $p < 0.001$; inferior – $t(44) = 2.59$, $p = 0.01$], this difference was greater, however, at the superior site [superior site = Mean 2.28μV; mid site = Mean 1.82μV; inferior site = Mean 0.85μV], most probably reflecting the early bilateral onset of the late right frontal effect.

As is clear in Figure 11 (C and D), the right frontal effect and late posterior negativity were well established from 900-1300ms and continued throughout the 1300-2000ms latency window. Subsidiary analyses investigating the global response by location by hemisphere by site interactions (Table 2) revealed interactions involving response by location by hemisphere [900-1300ms - $F(1,44) = 11.59$, $p = 0.001$; 1300-2000ms - $F(1,44) = 18.03$, $p < 0.001$] and response by location by site [900-1300ms - $F(1.37,60.13) = 56.25$, $p < 0.001$; 1300-2000ms - $F(1.34,59.00) = 42.38$, $p < 0.001$] in the target versus new contrast. The response by location by hemisphere interaction reflected old/new positivities at the anterior right hemisphere [900-1300ms - $t(44) = 3.11$, $p = 0.003$; 1300-2000ms - $t(44) = 3.87$, $p < 0.001$], whereas the response by location by site interaction reflected old/new negativities at the posterior superior site [900-1300ms - $t(44) = -4.03$, $p < 0.001$; 1300-2000ms - $t(44) = 2.67$, $p = 0.01$]. Despite the appearance of anterior left hemisphere negativities (Figure 11, C and D), these were not statistically significant, and the left parietal effect was no longer robust.

Non-Target vs. New: Subsidiary analyses investigating the global response by site interaction in the 300-450ms time window (Table 2) also gave rise to a significant response by site interaction [$F(1.18,51.75) = 7.29$, $p = 0.007$], indicating that while old waveforms were more positive than new waveforms at all sites [superior – $t(44) = 3.25$, $p = 0.002$; mid – $t(44) = 3.05$, $p = 0.004$; inferior – $t(44) = 2.92$, $p = 0.006$], the difference became greater towards superior sites [superior site = Mean 1.01μV; mid site = Mean 0.82μV; inferior site = Mean 0.60μV]. As for the target versus new comparison, the non-target versus new contrast revealed no interaction with location, possibly because a bilateral frontal effect was overlapping in time with the onset of parietal activity (Figure 11, E).

The greater positivity of non-target waveforms compared to new waveforms continued into the 450-900ms epoch (Figure 11, F). Subsidiary analysis investigating the global response by location by hemisphere by site interaction (Table 2) also revealed a response by location by hemisphere by site interaction [$F(1.48,64.91) = 3.13$, $p = 0.06$]

in the non-target versus new contrast. Consistent with the target versus new contrast, this interaction reflected the left parietal effect: non-target waveforms were more positive than new waveforms at all left parietal sites [superior – t(44) = 2.89, p = 0.006; mid – t(44) = 4.28, p < 0.001; inferior – t(44) = 4.75, p < 0.001], this difference was greatest, however at the mid and inferior sites [superior site = Mean 1.46μV; mid site = Mean 2.13μV; inferior site = Mean 1.95μV]. A main effect of response at the posterior right hemisphere [F(1,44) = 5.52, p = 0.02] most likely reflected spread of the left parietal effect. Non-target waveforms were also more positive than new waveforms at all anterior sites [superior – t(44) = 3.02, p = 0.004; mid – t(44) = 2.88, p = 0.006; inferior – t(44) = 2.04, p = 0.05], this difference was greater, however, at the superior site [superior site = Mean 1.45μV; mid site = Mean 1.14μV; inferior site = Mean 0.65μV], most probably reflecting the early bilateral onset of the late right frontal effect.

As can be seen in Figure 11 (G and H), the right frontal effect and late posterior negativity were well established from 900-1300ms and continued into the 1300-2000ms latency window. As for the target versus new comparison, subsidiary analyses investigating the global response by location by hemisphere by site interactions (Table 2) revealed interactions involving response by location by hemisphere [900-1300ms - F(1,44) = 5.32, p = 0.03; 1300-2000ms - F(1,44) = 11.87, p = 0.001] and response by location by site [900-1300ms - F(1.57,69.06) = 25.93, p < 0.001; 1300-2000ms - F(1.52,66.85) = 20.31, p < 0.001]. The response by location by hemisphere interaction reflected old/new positivites at the anterior right hemisphere [900-1300ms - t(44) = 2.32, p = 0.03; 1300-2000ms - t(44) = 2.08, p = 0.04], whereas the response by location by site interaction reflected old/new negativites at the posterior superior site [900-1300ms - t(44) = -2.50, p = 0.02; 1300-2000ms - t(44) = -2.13, p = 0.04]. Despite the appearance of anterior left hemisphere negativities (Figure 11, G and H), these were not statistically significant, and the left parietal effect was no longer robust.

Target vs. Non-Target: Subsidiary analyses investigating the global response by site interaction from 300-450ms (Table 2) produced no significant results, suggesting that there were no magnitude differences between targets and non-targets during this part of the epoch (Figure 11, A and E). During the 450-900ms time window, however, the left parietal effect and bilateral frontal activity were greater for targets (Figure 11, B and F): subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 2) also revealed a response by location by hemisphere by site interaction [$F(1.35,59.46) = 4.69$, $p = 0.02$], indicating that target waveforms were more positive than non-target waveforms at anterior superior and mid sites [superior – $t(44) = 1.85$, $p = 0.07$; mid – $t(44) = 1.83$, $p = 0.07$] and left parietal mid and inferior electrodes [mid – $t(44) = 2.24$, $p = 0.03$; inferior – $t(44) = 2.71$, $p = 0.01$].

Subsidiary analyses investigating the global response by location by hemisphere by site interactions from 900-1300ms and 1300-2000ms (Table 2) revealed no significant results, implying that there were no magnitude differences between targets and non-targets during these time windows. Targeted t-tests of data from left and right frontal and parietal sites also failed to produce significant results. However, visual inspection of the waveforms (see Figure 7) suggests that if the target/non-target difference at left parietal sites from 450-900ms was significant then the target/non-target difference at right frontal sites from 900-1300ms and 1300-2000ms should also be significant. As Table 3 shows, the reason that no significant differences were found at right frontal sites may be because there was greater variance at these sites than at left parietal sites, resulting in reduced power to detect differences.

Latency Window and Electrode Site	Target/Non-Target Amplitude Difference in µV. SD in Brackets.
450-900ms	
P1	0.50 (2.80)
P3	0.83 (2.48)
P5	0.94 (2.33)
900-1300ms	
F2	0.71 (3.65)
F4	0.87 (3.25)
F6	0.55 (4.34)
1300-2000ms	
F2	0.97 (3.68)
F4	1.10 (3.94)
F6	0.54 (3.89)

Table 3. Target/non-target difference in µV (SD) for the left parietal effect (450-900ms) and the late right frontal effect (900-1300ms and 1300-2000ms) in the intrinsic context condition. Although the amplitude difference is similar at left parietal and right frontal sites, the variance is greater at right frontal sites, possibly resulting in reduced power to detect right frontal differences.

6.3.2.4.2 Extrinsic Context

The global magnitude analyses revealed interactions and/or main effects involving the factor of response for all four latency windows (see Table 4 below). The highest order ANOVA result from 300-450ms was a main effect of response, and from 450-900ms, 900-1300ms and 1300-2000ms the highest order results were four-way response by location by hemisphere by site interactions. Consistent with the intrinsic context, these results were further examined with subsidiary analyses investigating all possible paired comparisons (target vs. new; non-target vs. new; target vs. non-target).

Latency Window	Target vs. Non-Target vs. New
300-450ms	
R	F(1.88,82.48)=3.17,p=0.05
450-900ms	
R	F(1.95,85.86)=19.37,p<0.001
RxH	F(1.97,86.61)=9.07,p<0.001
RxS	F(2.45,107.84)=5.05,p=0.005
RxLxH	F(1.82,80.02)=12.90,p<0.001
RxLxS	F(2.25,99.08)=16.40,p<0.001
RxHxS	F(2.57,113.04)=6.45,p=0.001
RxLxHxS	F(2.96,130.37)=6.16,p=0.001
900-1300ms	
RxS	F(2.06,90.66)=20.19,p<0.001
RxLxH	F(1.79,78.65)=19.51,p<0.001
RxLxS	F(2.07,91.27)=35.79,p<0.001
RxLxHxS	F(3.12,137.06)=9.86,p<0.001
1300-2000ms	
RxL	F(1.53,67.30)=3.93,p=0.035
RxH	F(1.50,65.88)=5.48,p=0.012
RxS	F(2.06,90.63)=17.32,p<0.001
RxLxH	F(1.81,79.77)=30.61,p<0.001
RxLxS	F(2.15,94.50)=28.21,p<0.001
RxHxS	F(1.85,81.20)=3.18,p=0.05
RxLxHxS	F(2.95,129.72)=11.95,p<0.001

Table 4. Results of the global magnitude analyses for the extrinsic context condition. R, L, H and S represent the factors of response, location, hemisphere and site respectively. Interactions and/or main effects involving the factor of response were present for all four latency windows.

Target vs. New: Subsidiary analyses investigating the global main effect of response in the 300-450ms time window (Table 4) revealed a target/new difference [t(44) = 2.29, p=0.03], indicating that target waveforms were generally more positive than new waveforms. However, inspection of the topography during this time window (see Figure 12, A) shows a target/new positivity that appears maximal at parietal sites. Consequently, targeted t–tests were used to examine data from parietal sites, revealing significant differences at all sites [P1 – t(44) = 2.67, p = 0.01; P3 – t(44) = 2.76, p = 0.008; P5 – t(44) = 2.29, p = 0.03; P2 – t(44) = 2.33, p = 0.03; P4 – t(44) = 2.12, p = 0.04; P6 – t(44) = 2.94, p = 0.005]. Importantly, targeted t-tests of data from frontal sites revealed no significant differences at any site; therefore, despite the impression given in Figure 12 (A) there was no statistically significant bilateral frontal effect in the extrinsic context condition.

By 450-900ms old/new effects were present at the frontal location (Figure 12, B). Subsidiary analyses investigating the response by location by hemisphere by site interaction in the global ANOVA (Table 4) also revealed a response by location by hemisphere by site interaction in the target versus new contrast. Analyses at the frontal location produced significant target/new differences at frontal superior [$t(44) = 4.33$, $p < 0.001$] and mid sites [$t(44) = 3.80$, p = < 0.001], which probably reflected the early bilateral onset of the late right frontal effect. In contrast, at the posterior location, the left parietal effect was significant at all left parietal sites [superior – $t(44) = 4.35$, $p < 0.001$; mid – $t(44) = 7.59$, $p < 0.001$; inferior – $t(44) = 8.77$, $p < 0.001$], greatest, however, at mid and inferior sites [superior site = Mean 1.97μV; mid site = Mean 3.05μV; inferior site = Mean 3.04μV]. A main effect of response at the posterior right hemisphere [$F(1,44) = 12.22$, $p = 0.001$] probably reflected spread of the left parietal effect.

The right frontal effect, continuation of the left parietal effect and presence of the late posterior negativity were evident from 900-1300ms (Figure 12, C). Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 4) also revealed a response by location by hemisphere by site interaction [$F(1.72,75.84) = 12.08$, $p < 0.001$]: analysis at the posterior location revealed a significant negativity at the left hemisphere superior site and a positivity at mid and inferior sites [superior – $t(44) = -2.16$, $p = 0.04$; mid – $t(44) = 2.62$, $p = 0.01$; inferior – $t(44) = 4.18$, $p < 0.001$]. A significant negativity was also present at the right hemisphere superior site [$t(44) = -3.29$, $p = 0.002$]. Meanwhile, analysis at the frontal location revealed a significant difference at the right hemisphere only [t(44) = 2.63, p = 0.01], therefore, in accordance with the intrinsic context, the left hemisphere negativity was not statistically significant during this latency window (Figure 12, C).

By 1300-2000ms the anterior left hemisphere negativity was statistically significant. Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 4) also produced a response by location by hemisphere by site interaction [F(1.73,75.97) = 16.13, p < 0.001]. This interaction reflected a left frontal negativity (Figure 12, D) at the inferior site [t(44) = -1.94, p = 0.06], which was not significant during this time window for the intrinsic context. A right frontal effect was also present, as reflected by a main effect of response at the right hemisphere [F(1,44) = 11.62, p = 0.001]. The left parietal effect was no longer robust, but the late posterior negativity was statistically significant at the posterior left hemisphere superior site [t(44) = -3.41, p = 0.001], and the posterior right hemisphere superior and mid sites [superior – t(44) = -3.82, p < 0.001; mid – t(44) = -1.86, p = 0.07].

Non-Target vs. New: Subsidiary analyses investigating the global main effect of response from 300-450ms (Table 4) revealed no significant results, suggesting that there were no magnitude differences between non-targets and new items during this part of the epoch (Figure 12, E). By 450-900ms, the response by location by hemisphere by site interaction [F(1.53,67.23) = 8.80, p = 0.001] in the subsidiary analyses investigating the global response by location by hemisphere by site interaction reflected the left parietal effect and possible early bilateral onset of the late right frontal effect (Figure 12, F): robust old/new differences were present at frontal superior [t(44) = 2.19, p = 0.03] and mid sites [t(44) = 2.07, p = 0.05] and at all left parietal sites [superior – t(44) = 3.32, p = 0.002; mid – t(44) = 7.06, p < 0.001; inferior – t(44) = 8.25, p < 0.001], becoming greater, however, towards inferior sites [superior site = Mean 1.19μV; mid site = Mean

2.34μV; inferior site = Mean 2.53μV]. No main effects or interactions were present at the posterior right hemisphere.

The right frontal effect, continuation of the left parietal effect and presence of the late posterior negativity were evident from 900-1300ms (Figure 12, G). Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 4) also revealed a response by location by hemisphere by site interaction [$F(1.65,72.65) = 14.03$, $p < 0.001$]: analysis at the posterior location revealed a significant negativity at the left hemisphere superior site [$t(44) = -3.40$, $p = 0.001$] and a positivity at the inferior site [$t(44) = 4.01$, $p < 0.001$]. A significant negativity was also present at the right hemisphere superior site [$t(44) = -4.40$, $p < 0.001$]. Meanwhile, analysis at the frontal location revealed a significant difference at the right hemisphere only [$t(44) = 2.31$, $p = 0.03$] therefore, again, in accordance with the intrinsic context, the left hemisphere negativity was not statistically significant during this latency window (Figure 12, G).

As in the target versus new contrast, by 1300-2000ms the anterior left hemisphere negativity was statistically significant. Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 4) also produced a response by location by hemisphere by site interaction [$F(1.67,73.44) = 13.88$, $p < 0.001$]. This interaction reflected a left frontal negativity at the inferior site [$t(44) = -2.60$, $p = 0.01$], which, again, was not significant during this time window for the intrinsic context, and a right frontal effect at the mid and inferior sites [mid – $t(44) = 2.90$, $p = 0.006$; inferior – $t(44) = 3.47$, $p = 0.001$]. The left parietal effect was no longer robust, but the late posterior negativity was statistically significant at the posterior left hemisphere superior site [$t(44) = -4.40$, $p < 0.001$], and the posterior right hemisphere superior and mid sites [superior – $t(44) = -4.78$, $p < 0.001$; mid – $t(44) = -2.66$, $p = 0.01$]. To view the topography of these effects, see Figure 12 (H).

Target vs. Non-Target: Subsidiary analyses investigating the global main effect of response in the 300-450ms time window (Table 4) revealed a target/non-target difference [t(44) = 2.00, p = 0.05], indicating that target waveforms were generally more positive than non-target waveforms. However, statistically significant old/new effects were only present at parietal sites for targets and no differences were found for non-targets (Figure 12, A and E). Consequently, targeted t-tests of data from frontal and parietal locations were conducted (collapsed across hemisphere and site), revealing significant differences at the parietal location only [t(44) = 2.81, p = 0.007].

During the 450-900ms time window the left parietal effect and bilateral frontal activity were greater for targets than non-targets (Figure 12, B and F). Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 4) revealed a response by site interaction [F(1.29,56.83) = 4.85, p = 0.02], which showed that although targets were more positive than non-targets at all sites, this difference became greater towards superior sites [superior: t(44) = 2.57, p = 0.01; mid: t(44) = 2.51, p = 0.02; inferior: t(44) = 2.25, p = 0.03]. Because analyses of the old/new effects revealed bilateral frontal and left parietal effects, targeted t-tests of data from these regions were conducted to determine if target/non-target differences were present. Significant differences were found at frontal superior and mid sites [superior: t(44) = 2.09, p = 0.04; mid: t(44) = 1.90, p = 0.07], and left parietal superior and mid sites [superior: t(44) = 1.87, p = 0.07; mid: t(44) = 1.83, p = 0.07].

Subsidiary analyses investigating the global response by location by hemisphere by site interactions from 900-1300ms and 1300-2000ms (Table 4) revealed no significant results, suggesting that there were no magnitude differences between targets and non-targets in these time windows. Targeted t-tests on right and left frontal and parietal sites also failed to show any significant effects. As for the intrinsic context, it was surprising that target/non-target differences were not present at right frontal sites (Figure 9). Again, as Table 5 shows, this lack of significance may be explained by greater variance for the right frontal effect than the left parietal effect, resulting in reduced power to detect differences.

Latency Window and Electrode Site	Target/Non-Target Amplitude Difference in μV. SD in Brackets.
450-900ms	
P1	0.77 (2.76)
P3	0.71 (2.60)
P5	0.51 (2.38)
900-1300ms	
F2	0.96 (3.18)
F4	0.85 (3.10)
F6	0.45 (3.82)
1300-2000ms	
F2	0.72 (3.82)
F4	0.81 (3.84)
F6	0.54 (3.03)

Table 5. Target/non-target difference in μV (SD) for the left parietal effect (450-900ms) and the late right frontal effect (900-1300ms and 1300-2000ms) in the extrinsic context condition. Although the amplitude difference is similar at left parietal and right frontal sites, the variance is greater at right frontal sites, possibly resulting in reduced power to detect right frontal differences.

6.3.2.4.3 Within Context Topographic Analyses

Figure 11 and Figure 12 illustrate the change in distribution of the old/new effects over time. Figure 11 shows the intrinsic context condition; there is a change in distribution over successive latency periods from a fronto/centro/parietal effect to a left parietal effect followed by a right frontal effect and a late posterior negativity. Figure 12 shows the extrinsic context condition; there is a change in distribution over successive latency periods from a parietal effect to a left parietal effect and a frontal effect, followed by a right frontal effect, late posterior negativity and finally a left frontal negativity. The change over time is similar for targets and non-targets in both contexts.

Within context topographic analyses were conducted to assess qualitative differences in the ERP effects over successive latency windows. The precise details of these analyses are described in the ‘General Methods’ chapter. For both contexts, global analyses revealed interactions involving the factor of epoch, but no epoch by response interactions (see Table 6), suggesting that there were qualitative differences in the ERP effects over time, and that these differences were similar for targets and non-targets. Consequently, subsidiary analyses were performed on data collapsed across targets and non-targets (with the exception of the 300-450ms vs. 450-900ms comparison for the extrinsic context, which was only performed for targets because there were no significant modulations for non-targets from 300-450ms), and the factor of response was removed from the analyses. For both contexts, three subsidiary topographic comparisons were conducted (300-450 ms vs. 450-900 ms, 450-900 ms vs. 900-1300 ms, 900-1300 ms vs. 1300-2000 ms).

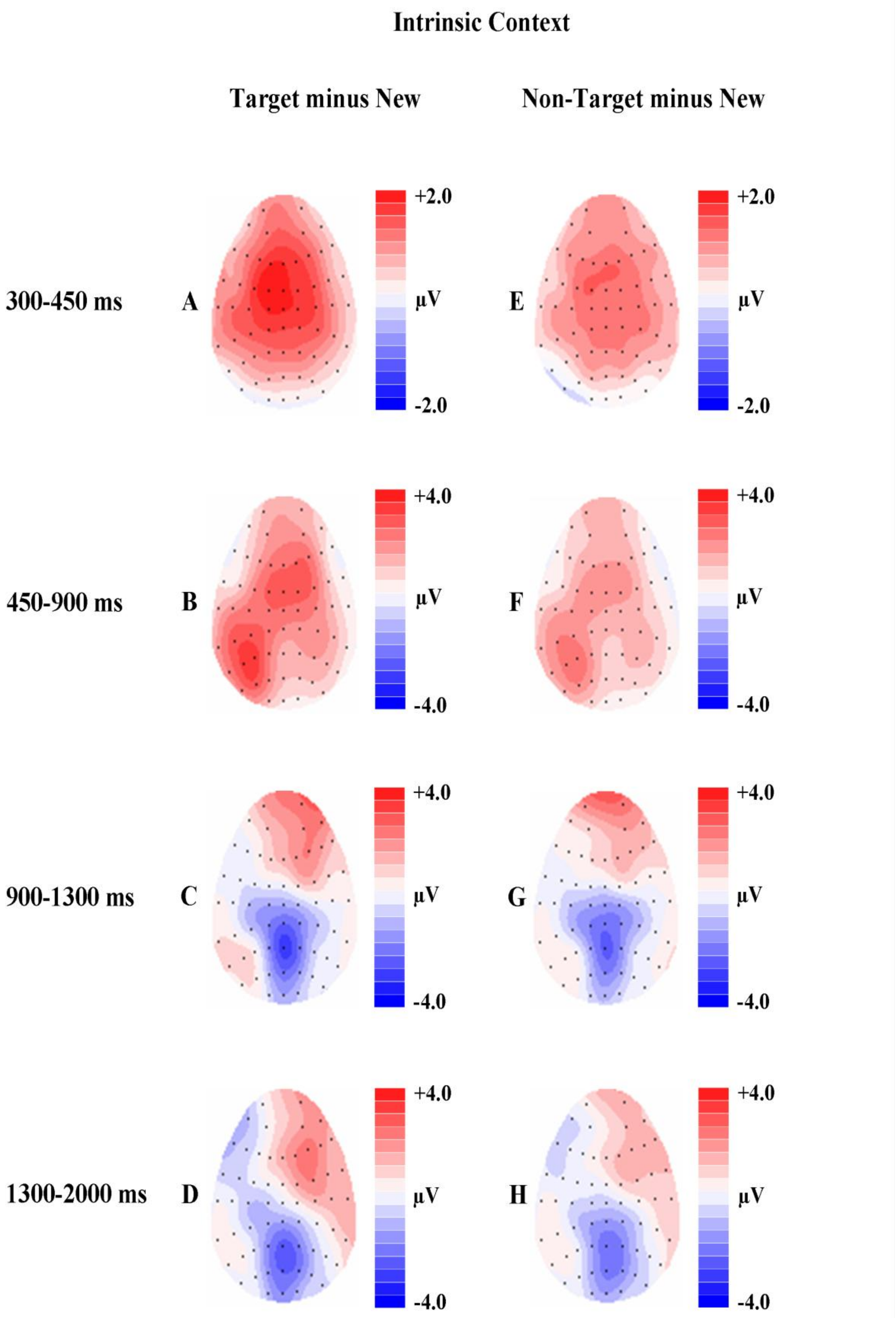

Figure 11. Topographic maps illustrating the scalp distribution of ERP effects for the intrinsic context. Each map is shown as if looking down onto the top of the head with frontal sites towards the top of the page.

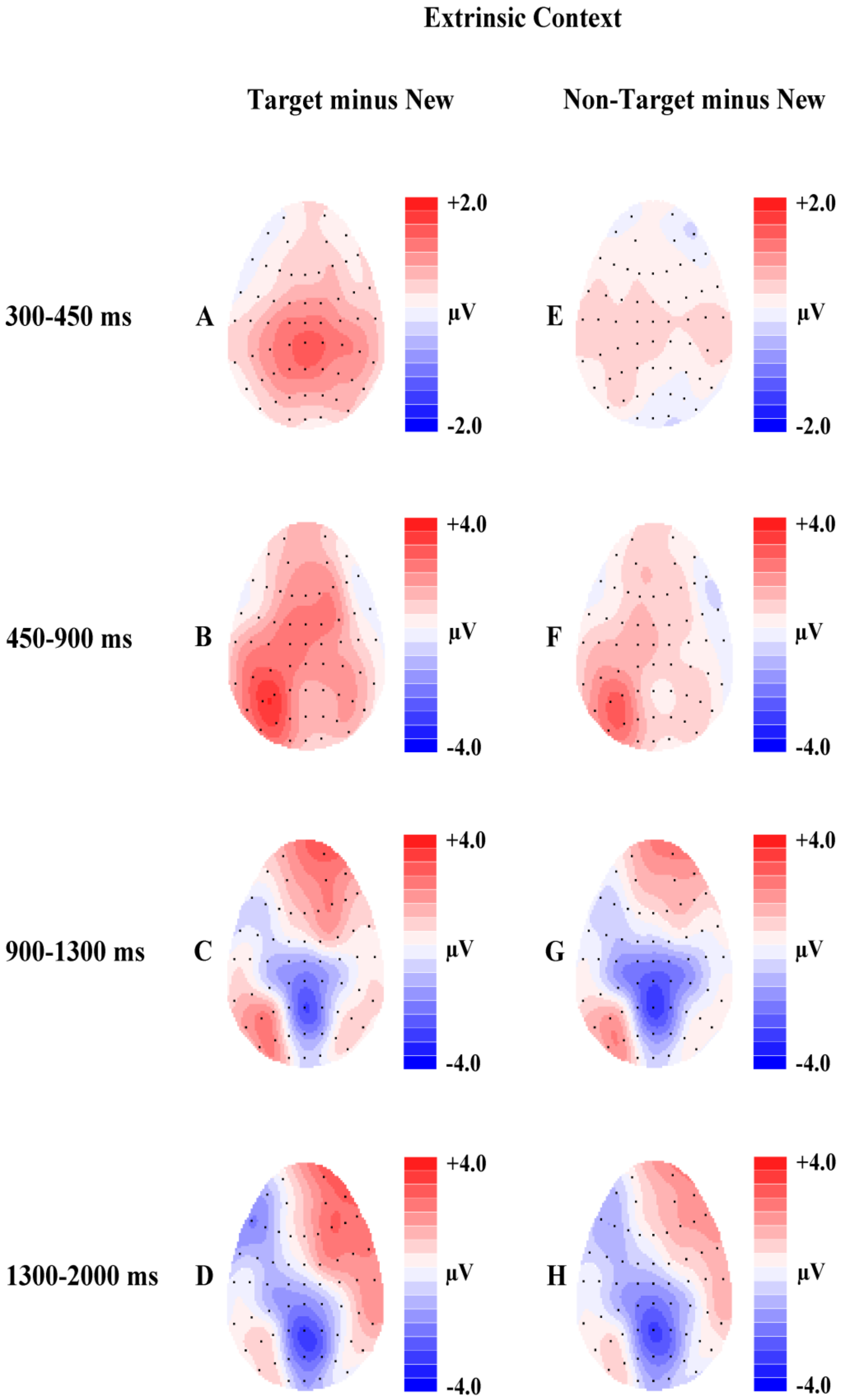

Figure 12. Topographic maps illustrating the scalp distribution of ERP effects for the extrinsic context. Each map is shown as if looking down onto the top of the head with frontal sites towards the top of the page.

	Intrinsic Context	Extrinsic Context
ExL	F(2.25,99.04)=5.00,p=0.006	F(1.65,72.68)=6.83,p=0.003
ExH	F(2.13,93.70)=5.38,p=0.005	F(1.55,68.07)=8.06,p=0.002
ExS	F(2.44,107.47)=30.36,p<0.001	F(1.37,60.08)=10.69,p=0.001
ExLxH	F(2.57,113.13)=14.79,p<0.001	F(1.53,67.22)=6.04,p=0.008
ExLxS	F(2.81,123.78)=17.89,p<0.001	F(2.08,91.38)=13.54,p<0.001
ExHxS	F(2.43,106.87)=3.39,p=0.03	F(2.06,90.59)=5.71,p=0.004
ExLxHxS	F(3.20,140.83)=4.83,p=0.003	F(2.23,98.28)=5.20,p=0.005

Table 6. Results of the within context global topographic analyses of rescaled difference waveforms, comparing all four latency windows. E, L, H and S represent the factors of epoch, location, hemisphere and site respectively. Interactions involving the factor of epoch were present for both contexts.

Intrinsic Context: Subsidiary analyses investigating the global epoch by location by hemisphere by site interaction (Table 6) also revealed an epoch by location by hemisphere by site interaction [F(1.41,61.84) = 12.73, $p < 0.001$] from 300-450ms vs. 450-900ms. This interaction reflected a change in distribution over time; anteriorly the effect was widespread in the first latency period and became more sharply focussed towards the midline in the second latency period, whereas at the posterior electrodes the effect was bilaterally distributed in the first latency period and became a clear left parietal effect in the second latency period (Figure 11, A,B,E and F).

Subsidiary analyses from 450-900 ms vs. 900-1300 ms revealed an epoch by location by hemisphere by site interaction [F(1.37,60.22) = 3.18, $p = 0.06$], which reflected a progression from a left parietal effect and a bilateral frontal effect in the 450-900ms time window, to the late right frontal effect and late posterior negativity in the 900-1300ms time window (Figure 11, B,C,F and G). By contrast, the 900-1300 ms vs. 1300-2000 ms subsidiary ANOVA failed to produce any significant results involving the factor of epoch, indicating that the distributions in these latency regions were similar (Figure 11, C,D,G and H).

Extrinsic Context: Subsidiary analyses investigating the global epoch by location by hemisphere by site interaction (Table 6) also revealed an epoch by location by hemisphere by site interaction [F(1.34,58.74) = 4.45, p = 0.03] from 300-450ms vs. 450-900ms. This interaction reflected a progression from a bilaterally distributed parietal effect in the first latency period to a clear left parietal effect in the second latency period (Figure 12, A and B).

Subsidiary analyses from 450-900ms vs. 900-1300ms revealed an epoch by location by hemisphere by site interaction [F(1.46,64.32) = 5.04, p = 0.02], which reflected a progression from a left parietal effect and a bilateral frontal effect from 450-900ms to the late right frontal effect and late posterior negativity in the 900-1300ms time window (Figure 12, B,C,F and G). Subsidiary analyses from 900-1300ms vs. 1300-2000ms revealed an epoch by location by hemisphere interaction [F(1,44) = 8.67, p = 0.005], which marked the decline of the left parietal effect and the evolution of a left frontal negativity in the latter time window (Figure 12, C,D,G and H).

6.3.2.4.4 Additional Within Context Frontal Analyses

The previous within context topographic analyses revealed that the late right frontal effects from 900-1300ms and 1300-2000ms were topographically similar within contexts. However, visual inspection of the maps (Figure 11 and Figure 12 C and G) suggests that the F line electrodes (F1, F3, F5, F2, F4 and F6) were not capturing where the effect was maximal from 900-1300ms and may therefore have prevented the detection of topographic differences between 900-1300ms and 1300-2000ms. Consequently, within context topographic analyses were repeated, including all frontal electrodes (F1, F3, F5, F7, AF3, AF7, FP1, F2, F4, F6, F8, AF4, AF8, FP2) to investigate more fully whether the right frontal effects from 900-1300ms and 1300-2000ms were qualitatively different. As the purpose of the analyses was to investigate topographic differences at frontal sites, the factor of location was removed from the analyses. The within context global topographic ANOVA included factors of epoch ‘E’ (900-1300ms vs. 1300-2000ms) response ‘R’ (target minus new vs. non-target minus new) hemisphere ‘H’ (left vs. right) and site ‘S’ (F1, F3, F5, F7, AF3, AF7, FP1, F2, F4, F6, F8, AF4, AF8, FP2). Any main effects or interactions involving the factor of epoch were investigated using subsidiary analyses (see ‘General Methods’ Chapter for the structure of the subsidiary analyses).

For both contexts, global analyses revealed main effects and interactions involving the factor of epoch, but no epoch by response interactions (see Table 7), suggesting that there were qualitative differences in the frontal ERP effects over time, and that these differences were similar for targets and non-targets. Consequently, subsidiary analyses were performed on data collapsed across targets and non-targets and the factor of response was removed from the analyses.

	Intrinsic Context	Extrinsic Context
ExH	F(2.29,100.57)=6.79,p=0.001	F(1.32,58.13)=30.11,p<0.001
ExHxS	F(6.04,209.92)=4.77,p=0.04	F(3.63,159.88)=10.77,p<0.001

Table 7. Results of the additional within context global topographic analyses of frontal sites from 900-1300ms and 1300-2000ms, using rescaled difference waveforms. E, H and S represent the factors of epoch, hemisphere and site respectively. Main effects and interactions involving the factor of epoch were present for both contexts.

Intrinsic Context: Importantly, (and in contrast to the previous topographic analyses that included the F line electrodes only, and revealed no significant differences involving the factor of epoch) subsidiary analyses investigating the global epoch by hemisphere by site interaction (Table 7) revealed a change in distribution over time from a right prefrontal effect from 900-1300ms to a right frontal effect from 1300-2000ms (Figure 11 compare C and G to D and H).

Extrinsic Context: Subsidiary analyses revealed that the global epoch by hemisphere by site interaction (Table 7) marked the evolution of a left frontal negativity in the latter time window and, importantly (and again in contrast to the previous findings including F line electrodes only) a progression from a right prefrontal effect from 900-1300 ms to a right frontal effect from 1300-2000 ms (Figure 12 compare C and G to D and H).

6.3.2.5 Summary of the ERP Effects Elicited Separately by Intrinsic and Extrinsic Contexts

The intrinsic context condition produced the putative bilateral frontal correlate of familiarity from 300-450ms for targets and non-targets. This effect was of equivalent magnitude for targets and non-targets. The left parietal correlate of recollection and a bilateral anterior frontal effect were present from 450-900ms for targets and non-targets, effects that were statistically larger for targets. A right prefrontal effect and the late posterior negativity were present for targets and non-targets from 900-1300ms, along with a right frontal effect and the late posterior negativity for targets and non-targets from 1300-2000ms. These effects were of equivalent magnitude for each response from 900-1300ms and 1300-2000ms.

In contrast to the intrinsic context condition, the extrinsic context condition produced no significant early bilateral frontal effects. The left parietal correlate of recollection was significant from 450-900ms and 900-1300ms for targets and non-targets, and this effect was greater in magnitude for targets from 450-900ms. A bilateral anterior frontal effect was significant for targets and non-targets from 450-900ms and this was greater in magnitude for targets. A right prefrontal effect and late posterior negativity were present for targets and non-targets from 900-1300ms, along with a right frontal effect, late posterior negativity and a left frontal negativity for targets and non-targets from 1300-2000ms; there were no magnitude differences between targets and non-targets in these last two time windows.

6.3.2.6 Between-Context Magnitude and Topographic Analyses

Robust effects were present for targets and non-targets during each latency window in the intrinsic context, therefore between context magnitude analyses were conducted on the difference waveforms for each window. From 300-450ms target/non-target magnitude differences were present in the extrinsic context and from 450-900ms target/non-target differences were present in the intrinsic and extrinsic contexts. As a result, the between context magnitude analyses of the first two latency windows included a third level of response (target minus new, non-target minus new and target minus non-target). The remaining two windows did not include the target minus non-target level. There were no significant modulations in the extrinsic context for non-targets from 300-450ms; therefore topographic comparisons were performed only for targets during this latency period (i.e. the factor of response was removed from the analyses).

Table 8 shows the results of the between context global magnitude and topographic analyses. As is clear from the table, there were no interactions with response, therefore subsidiary analyses were performed on data collapsed across this factor. The presence of the bilateral frontal effect in the intrinsic context but not in the extrinsic context was confirmed by the subsidiary paired t-test comparing data from the frontal location [t(44) = 2.76, p = 0.008], conducted to investigate the context by location interaction in the 300-450 ms magnitude ANOVA (Table 8). Importantly, by contrast, there was no difference at posterior sites [t(44) = 0.005, p = 1.0]. The more posterior distribution of effects in the extrinsic context from 300-450ms was indicated by the subsidiary analyses investigating the context by location interaction in the 300-450ms topographic ANOVA (Table 8).

Subsidiary analyses investigating the context by location by site interaction in the 900-1300ms magnitude ANOVA revealed a difference at posterior inferior sites [t(44) = 2.10, p = 0.04], which reflects the continuing presence of declining parietal activity in the extrinsic context from 900-1300ms. The late posterior negativity did not differ between contexts. The lack of significant magnitude differences from 1300-2000ms suggests that the left frontal negativity also did not differ between contexts. Although the effect was only robust in the extrinsic context, visual inspection of the data suggests that it was also present in the intrinsic context (Figure 11, D and H).

Latency Window	Magnitude	Topographic
300-450 ms		
CxL	F(1,44)=4.15,p=0.05	F(1,44)=3.93,p=0.05
450-900 ms	No significant results	No significant results
900-1300 ms		
CxLxS	F(1.22,53.73)=5.69,p=0.02	No significant results
1300-2000 ms	No significant results	No significant results

Table 8. Results of the between context global magnitude and topographic analyses of difference and rescaled difference waveforms respectively. C, L and S represent the factors of context, location and site respectively. The between context magnitude analyses of the first two latency windows included three levels of response (target minus new, non-target minus new and target minus non-target). The remaining two windows did not include the target minus non-target level. The between context topographic comparisons were performed only for targets from 300-450ms (i.e. the factor of response was removed from the analyses). Results revealed no interactions between context and response, therefore subsidiary analyses were performed on data collapsed across response.

6.3.2.7 Additional Between Context Frontal Analyses

The previous between context topographic analyses revealed that the right prefrontal effect from 900-1300ms was topographically similar across contexts. However, because the F line electrodes (F1, F3, F5, F2, F4 and F6) were not capturing where the effect was maximal from 900-1300ms (see Figure 11 and Figure 12, C and G) this may have prevented the detection of topographic differences across contexts during this time window. Consequently, between context topographic analyses were repeated, including all frontal electrodes (F1, F3, F5, F7, AF3, AF7, FP1, F2, F4, F6, F8, AF4, AF8, FP2) to investigate more fully whether the right prefrontal effect from 900-1300ms was qualitatively different across contexts. As the purpose of the analyses was to investigate topographic differences at frontal sites, the factor of location was removed from the analyses.

The between context global topographic ANOVA included factors of context ‘C’ (intrinsic vs. extrinsic) response ‘R’ (target minus new vs. non-target minus new) hemisphere ‘H’ (left vs. right) and site ‘S’ (F1, F3, F5, F7, AF3, AF7, FP1, F2, F4, F6, F8, AF4, AF8, FP2). The between context global topographic analyses failed to reveal main effects or interactions involving the factor of context, therefore, consistent with the previous analyses including F line electrodes only, the right prefrontal effect was topographically similar across contexts.

6.3.2.8 Summary of the Differences in the ERP Effects Elicited by Intrinsic and Extrinsic Contexts

The bilateral frontal effect was significant from 300-450ms for targets and non-targets, but only in the intrinsic context condition. By contrast, from 900-1300ms, an extended left parietal effect was present in the extrinsic context condition for targets and non-targets, along with a left frontal negativity from 1300-2000ms. The magnitude and topography of the left parietal effect and bilateral anterior frontal effect (from 450-900ms), right prefrontal effect (from 900-1300ms), right frontal effect (from 1300-2000ms) and late posterior negativity (from 900-1300ms and 1300-2000ms) appeared equivalent in both contexts.

6.4 Discussion

The aim of Experiment 1a was to investigate whether young adults adopt different retrieval strategies depending on the type of context (intrinsic or extrinsic) retrieved. Differences in behavioural performance across contexts were used as an index of dissimilar retrieval strategies, while variations in the engagement of the three ERP retrieval processes (the putative mid frontal correlate of familiarity, the left parietal correlate of recollection and the putative late right frontal correlate of executive/post retrieval processing), were examined to further reveal the retrieval strategies used. Equivalent behavioural accuracy, sensitivity, bias and PDP estimates indicated that performance was similar across contexts. However, longer reaction times for targets and non-targets in the extrinsic context suggested that a different retrieval strategy was adopted to keep performance equivalent.

The ERP data revealed that the putative bilateral frontal correlate of familiarity was significant for targets and non-targets solely in the intrinsic context, whereas the left parietal effect and three frontal effects were significant for targets and non-targets in both contexts and were of equivalent magnitude and topography between contexts. Together the behavioural and ERP data suggested that young adults adopted different retrieval strategies depending on whether an intrinsic or an extrinsic context was retrieved: familiarity based remembering occurred only for the retrieval of intrinsic context, whereas there was as a common reliance on recollection and executive/post retrieval monitoring across contexts. Differences in retrieval strategies therefore appeared to be linked to familiarity.

6.4.1 Bilateral Frontal Correlate of Familiarity

It is highly unlikely that the bilateral frontal effect is linked to executive/post retrieval processing because the weight of evidence supports a familiarity interpretation of the effect (Rugg and Curran, 2007). Consistent with the findings from Experiment 1a, previous ERP studies have also found the bilateral frontal effect only for certain types of information. For example, during an associative recognition memory task, Rhodes and Donaldson (2007) found that word pairs related purely by association were rated as having a more unitised representation than word pairs sharing either an association and semantic relationship, or a semantic relationship only. According to Graf and Schachter (1989) unitisation occurs when previously separate items are processed as a single unit. Importantly, for current purposes, the bilateral frontal effect in the Rhodes and Donaldson study was elicited solely by association word pairs, whereas by contrast, the left parietal effect was elicited equally by all three conditions. On the basis of these findings, Rhodes and Donaldson argued that unitisation enhances familiarity based remembering, while leaving recollection based remembering unaffected. Convergent results have been found in other event-related potential studies that have shown the bilateral frontal effect to be larger for associations that are rated as more unitized (Jager et al., 2006; Ecker and Zimmer, 2007) or when the encoding conditions promote unitisation (Opitz and Cornell, 2006).

Further support for the claim that unitisation enhances familiarity based remembering comes from a behavioural study of recognition memory for faces. Yonelinas et al. (1999) reported that familiarity can support associative recognition for faces when the faces are upright, but not when they are inverted. As faces are normally processed holistically, the authors concluded that the upright faces were encoded as a coherent entity leading to a reliance on familiarity. Finally, recent behavioural studies have investigated the effects of unitisation on associative recognition in amnesic patients with hippocampal damage who have deficits in recollection but show preserved familiarity. Patients showed poor associative recognition for unrelated word pairs, however their performance was somewhat preserved if the word pairs formed compound words (Giovanello et al., 2006) or if random word pairs were encoded as compound words (Quamme et al., 2007).

Taken together, the findings from the aforementioned studies may provide an explanation for the results of Experiment 1a: in the intrinsic context, because the gender the word was spoken in was an inherent part of the word, the gender and the word became unitised, enhancing familiarity based remembering and resulting in faster identification of target and non-target items. Unitisation did not occur for the extrinsic context, however, as the judgement made was not an inherent part of the word. The findings from this study add to a growing body of evidence that suggests that unitisation enhances familiarity based remembering during source memory, as well as in associative recognition. Using fMRI, Staresina and Davachi (2006) examined source memory for colour-word associations. Participants were scanned while they encoded words presented on a red, yellow, green or blue background. The study task was to imagine the item as though it was the same colour as the background (e.g. the word ‘elephant’ on a red background would signal that the participant should imagine a red elephant). Accurate source recollection was measured by the ability to remember the colour associated with each word. The authors found that activation in the hippocampus and perirhinal cortex was present at encoding for items that were remembered at retrieval along with the correct source. Previous studies have postulated that the perirhinal cortex is critical for familiarity based remembering but not recollection based remembering. Because Staresina and Davachi’s encoding task encouraged participants to encode source information as an inherent feature of the item, the unexpected activation in the perirhinal cortex may reflect familiarity based remembering as a result of the unitisation of the item and its context.

A recent source memory behavioural study also supports the unitisation claim. Diana et al. (2008) showed participants words that were presented either on a red or yellow background. In the unitised encoding condition, they were told to form a mental image of the item in the same colour as the background colour (e.g. the word ‘pig’ presented against a yellow background signified the participant should imagine a yellow pig). In the non-unitised encoding condition participants were informed to make an animacy judgement (i.e. is the item alive?) if the word was presented against a red background and to make a size judgement (i.e. would this item fit in a shoe box?) if the word was presented against a yellow background. Based on receiver operating characteristics and response deadline performance, Diana et al. noted that familiarity made a greater contribution to source memory retrieval when the source and item were unitised during encoding. The contribution of familiarity to source memory therefore depends on the way the item and source information are initially processed.

6.4.2 Bilateral Frontal Correlate of Familiarity and the PDP Estimates

The fact that the PDP estimates did not reveal an increased contribution of familiarity in the intrinsic context despite the bilateral frontal correlate of familiarity being significant only in the intrinsic context appears to be problematic for a unitisation account. However, these discrepant results can be reconciled in the following way. The PDP is reliant on different patterns of behavioural performance across conditions to detect differences in the contribution of familiarity and recollection. For example, the PDP assumes that if familiarity contributed more to condition one than condition two, more non-targets would be mistaken for targets in condition one, resulting in a greater false alarm rate to non-targets. The resultant PDP estimate for familiarity would therefore be higher in condition one than two. Importantly, however, even if familiarity was greater in condition one than two, the false alarms to non-targets could remain constant across conditions if recollection was equivalent, and hence corrected the false alarms due to familiarity in condition one. In the current experiment, unitisation resulted in greater familiarity for targets and non-targets in the intrinsic context, creating a familiarity 'boost' and speeded up accurate identification of old items. Recollection, indexed by the left parietal effect, occurred after familiarity and may have corrected potential false alarms to non-targets as a result of familiarity. In contrast in the extrinsic context, recollection was still keeping performance equivalent to the intrinsic context, however there was no familiarity 'boost' resulting in slower identification of old items. The common reliance on recollection across contexts ensured that the false alarm rate to non-targets remained constant between conditions, resulting in the PDP estimates for familiarity being equivalent. Support for the contention that recollection corrects false alarms due to familiarity comes from a study by Hintzman and Curran (1994). Using a response deadline method where a test item was presented, followed by a tone after a 175ms, 450ms or 750ms lag that signalled an immediate old or new recognition response, Hintzman and Curren noted that false alarms to new items decreased as lag increased. These findings suggested that recollection occurred as the lag increased, correcting false alarms to new items.

6.4.3 Left Parietal Correlate of Recollection

The finding that the left parietal effect was significant for targets and non-targets in the extrinsic context is contrary to the majority of ERP studies that have found left parietal effects for targets only in the extrinsic context. One exclusion study by Dzulkifli et al., (2005), employed an extrinsic context (a function or drawing judgement about words) and found that after a 40-minute delay between study and test, left parietal effects were present for targets and non-targets. Consistent with the fact that this delay increased task demands, lowered target accuracy and resulted in the recollection of target and non-target items, it may be the case that combining intrinsic and extrinsic in one paradigm also increased task demands and made recollection of only target items an insufficient strategy for good performance.

Although the left parietal effect was equivalent in magnitude and topography across contexts, it did, however, continue into the 900-1300ms time window for both targets and non-targets in the extrinsic context only. Based on the assumption that differences in the latency of two qualitatively similar ERPs suggests that the underlying cognitive process takes longer in one condition than the other (Rugg and Coles, 1995), the extended left parietal effect in the extrinsic context suggests that recollection took longer in this condition. As recollection was the primary basis for retrieval in the extrinsic context whereas participants relied on familiarity and recollection in the intrinsic context, it follows that in the absence of a familiarity ‘boost’ recollection took longer in the extrinsic context.

6.4.4 Late Right Frontal Correlate of Post Retrieval/Executive Processing

The late right frontal effect was fractionated into three temporally and topographically distinct frontal effects from 450-900ms, 900-1300ms and 1300-2000ms: a bilateral anterior frontal effect, a right prefrontal effect and a right frontal effect respectively. Based on the current interpretation of the late right frontal effect reflecting the engagement of executive/post retrieval monitoring processes, or as recently suggested, general decision making processes, the findings from this experiment suggest that different post retrieval monitoring or decision making processes may be engaged over time. Consistent with this proposal, Friedman and Johnson (2000) and Mecklinger (2000) have suggested that the major problem in identifying the functional significance of the late right frontal effect may lie in the practice of measuring it over long time periods; this practice may obscure other shorter sub-components that have different distributions and therefore possibly reflect the engagement of different processes. Experiment 1a does not speak to what these different post retrieval processes might be, this issue will be investigated in Experiment 1b.

6.4.5 Left Frontal Negativity

A left frontal negativity was present from 1300-2000ms in the extrinsic context. Similar effects have been observed in older adults in source memory studies (Trott et al., 1999; Wegesin et al., 2002; Li et al., 2004), although these have typically been more centrally distributed than the effect reported here. The functional significance of these negativities is unclear, however the CARA (Cortical Asymmetry of Reflective Activity) model (Nolde et al., 1998) proposes that the left prefrontal cortex can be additionally activated when a task is more demanding. This theory has proved influential in the literature with numerous PET studies (e.g. Lekeu et al., 2001) and fMRI studies (e.g. Hunkin et al., 2000; Hayes et al., 2004; Marklund et al., 2007; Mitchell et al., 2008) supporting its assumptions. As familiarity was not benefiting performance in the extrinsic context, it may be the case that retrieval of extrinsic context was more demanding requiring the recruitment of additional frontal processes to monitor performance.

6.4.6 Retrieval Orientation

The current findings cannot be explained by retrieval orientation effects. Previous ERP studies have shown that rememberers can adopt a 'retrieval orientation' that biases how retrieval cues are processed so as to maximize the likelihood of retrieval success (Robb and Rugg, 2002). The electrophysiological index of retrieval orientation is a magnitude difference between the ERPs evoked by new test items from 500-900ms over fronto-central sites (Dzulifli and Wilding, 2005). Dzulkifli and Wilding identified this retrieval orientation effect in a study in which recollection of only targets occurred in one condition, whereas recollection of targets and non-targets occurred in the other condition, therefore leading to the conclusion that retrieval orientations reflect processes responsible for prioritising information associated with target items. In keeping with the electrode locations employed in Dzulkifli and Wilding's analysis (F5, FZ, F6, C5, CZ, C6, P5, PZ, P6) targeted t-tests of these sites revealed no significant differences between the new items from the intrinsic and extrinsic contexts from 500-900ms. As targets and non-targets were recollected for both contexts in the current study, the absence of a retrieval orientation effect is in support of Dzulkifli and Wilding (2005) conclusion.

The following chapter assesses whether the magnitude of the bilateral anterior frontal effect (450-900ms), the right prefrontal effect (900-1300ms) and the right frontal effect (1300-2000ms) correlates with performance on the CANTAB tasks of executive functioning (see 'General Methods' chapter for a list of the CANTAB tasks). The aim of Experiment 1b was to resolve conflict in the literature over the functional significance of the late right frontal old/new effect, and hence further our understanding of the role of executive functions in the retrieval of source information from episodic memory in young adults.

Chapter 7 Experiment 1b

7.1 Introduction

Executive control is thought to be sub served by the frontal lobes (Aron et al., 2004), and is a generic term for a set of higher order cognitive processes (e.g. working memory, planning and flexibility of thinking and responding) that can be used to coordinate episodic memory. The link between executive control and episodic memory is clear from patients with frontal lobe damage. Although not amnesic, these patients have problems with pre-ecphoric strategic retrieval (i.e. focussing retrieval onto relevant information) and post-ecphoric strategic retrieval (i.e. monitoring the accuracy of retrieved information).

The timing of the late right frontal effect, recorded in ERP studies, has led to its interpretation as a putative neural correlate of post-ecphoric strategic retrieval. The effect usually onsets around the same time as the left parietal correlate of recollection, but is maximal over the right frontal scalp, and frequently continues until the end of a two second recording epoch. There has been considerable debate in the literature, however, as to the precise functional significance of this effect.

As discussed in section 4.1.3, the late right frontal effect was first reported in source memory studies (Wilding and Rugg, 1996; 1997a). Because the modulation appeared larger for correct source judgements than for incorrect source judgements, it was originally considered to index the retrieval of source or contextual information. This interpretation was questioned, however, following demonstrations that the effect is not always present for correct source judgements (e.g. see Wilding and Rugg, 1997b; Cycowicz et al., 2001; Cycowicz and Friedman, 2003). Consequently, the account of the effect was revised to be an indication of the strategic processing of the products of recollection. This view was also discredited, however, when several studies suggested that the modulation is not always dependent upon retrieval success. For example, the effect has been elicited by forgotten words in a directed forgetting task (Ullsperger et al., 2000), and often appears equivalent for true and false recognition (Mecklinger, 2000; Curran et al., 2001). The previous findings have led to the current interpretation of the late right frontal effect as being related to post retrieval evaluation or monitoring processes. Evidence in support of this account comes from a false memory study that found the late right frontal effect only in good performers, where their longer reaction times suggested that they were more careful in their decision making than poorer performers (Curran et al., 2001).

The findings of two recent experiments have questioned the current interpretation of the right frontal effect as reflecting post-retrieval evaluation or monitoring processes. Hayama et al. (2008) conducted two experiments. The study phases of both experiments were identical: a series of pictures were presented and participants were required to make one of two semantic judgements about the picture. During the test phase of the first experiment, participants were required to remember the source they encountered the picture at study (i.e. the semantic judgement made) or indicate if the picture was new. In the second experiment they were required to make a further semantic judgement about the old and new pictures. The authors contrasted the ERPs following the semantic and source memory tasks and found significant right frontal effects for both tasks. Following these findings, it was proposed that the right frontal old/new effect is a neural correlate of general decision making processes, rather than evaluation or monitoring of the products of an episodic retrieval attempt.

As stated previously, executive control is a generic term for a range of higher order cognitive processes, therefore the interpretation of the late right frontal effect as being an index of post retrieval evaluation/monitoring or, as recently suggested, general decision making processes, appears too broad. If the effect does reflect the engagement of executive processes, further elucidation of the functional significance of the modulation will provide an indication of specific executive functions that are engaged post retrieval.

The current experiment aims to further investigate the functional significance of the late right frontal effect by assessing whether the magnitude of the effect correlates with performance on tests of executive functioning taken from the Cambridge Neuropsychological Test Automated Battery (CANTAB). The CANTAB neuropsychological tests were developed over 21 years ago at the University of Cambridge, with the aim of providing sensitive, reliable and detailed assessments of cognitive functioning. Because the tests are computerised they can be broken down into their cognitive components in order to provide a detailed view of the functions that are impaired and those that are spared. The CANTAB was chosen for assessment of executive functioning in this thesis because it has become a world leader in computerised cognitive testing with more than 500 academic institutions worldwide using the tests, and it has been quoted in over 600 scientific papers; the CANTAB has an unrivalled degree of validation.

The participants were from Experiment 1a, and the magnitude of the late right frontal effect recorded during the exclusion task in that study was correlated with performance on the CANTAB tests. Participants completed four tests from the CANTAB battery: the non-executive Spatial Span task, and three tests of executive functioning: IDED Set Shifting task, Spatial Working Memory and the Stockings of Cambridge (see 'General

Methods' chapter for a description of the tasks). If the current interpretation of the late right frontal effect as being an index of executive/post retrieval control or general decision making processes are correct, it is predicted that the magnitude of the late right frontal effect will correlate with performance on the CANTAB tests, thus resolving conflict in the literature over the functional significance of the effect.

7.2 Methods

7.2.1 Participants

Participants were those that took part in Experiment 1a. Fifty-six participants contributed to the experiment. The data from 11 participants was discarded: 3 due to insufficient behavioural trial numbers, 7 due to high proportions of noise (electrode drift and alpha activity) and 1 due to equipment failure. The remaining 45 participants (23 female) were aged between 18 and 36 years (mean age 24). All other aspects of the methods are described in the 'General Methods' chapter.

7.3 Results

The within and between context topographic analyses from Experiment 1a demonstrated the presence of three temporally and topographically distinct frontal old/new effects (bilateral anterior frontal effect from 450-900ms, right prefrontal effect from 900-1300ms and right frontal effect from 1300-2000ms). These effects were topographically similar for both target and non-target responses, and intrinsic and extrinsic contexts. Consequently, all following behavioural, ERP and correlation analyses were performed using data collapsed across context and response.

7.3.1 Behaviour

The behavioural data are reported in Table 9 (below). Hits represent data from Experiment 1a collapsed across contexts and responses (targets and non-targets). Correct rejections are for all new responses, collapsed across contexts. Accuracy was greater for correct rejections than hits and reaction times were faster for correct rejections compared to hits. These results were confirmed by paired t-tests [Accuracy: t(44) = -18.74, p < 0.001; RT: t(44) = 13.36, p < 0.001].

Accuracy	
Hits	0.69 (0.10)
Correct Rejection	0.94 (0.05)
RT(ms)	
Hits	1460 (268)
Correct Rejection	1135 (236)

Table 9. Mean (SD) behavioural data for Experiment 1b. Hits represent data collapsed across contexts and responses (targets and non-targets). Correct rejections are for new responses collapsed across contexts. Accuracy was greater for correct rejections than hits, and reaction times were faster for correct rejections compared to hits.

7.3.2 Rationale for the ERP and Correlation Analyses

The aim of the ERP magnitude analyses was firstly to demonstrate that significant frontal and left parietal old/new effects were present when data was collapsed across context and response (the putative bilateral frontal correlate of familiarity was significant in the intrinsic context only, whereas the left frontal negativity was significant in the extrinsic context only) and secondly to determine at which electrode sites the effects were maximal. The global magnitude ANOVA included factors of response ‘R’ [old (collapsed across context and target and non-target responses) vs. new (collapsed across context)], hemisphere ‘H’ (left vs. right) and site (F1, F3, F5, F7, AF3, AF7, FP1, F2, F4, F6, F8, AF4, AF8, FP2). Figure 13 shows the grand average old and new waveforms from 36 electrode sites. The mean number of trials contributing to the waveforms was 35 old and 48 new.

The purpose of the ERP topographic analyses was to confirm that distinct frontal old/new effects were present when data was collapsed across context and response. The global topographic analyses included factors of epoch ‘E’ (300-450 ms vs. 450-900 ms vs. 900-1300 ms vs. 1300-2000 ms), hemisphere ‘H’ (left vs. right) and site ‘S’ (F1, F3, F5, F7, AF3, AF7, FP1, F2, F4, F6, F8, AF4, AF8, FP2). The distributions of the old/new effects are illustrated in the topographic map shown in Figure 14.

Subsequent correlation analyses were then conducted to assess if the magnitude of the effects (collapsed across the two electrode sites where the effects were maximal) correlated with performance on tests of executive functioning, to determine the likely functional significance of the three frontal old/new effects.

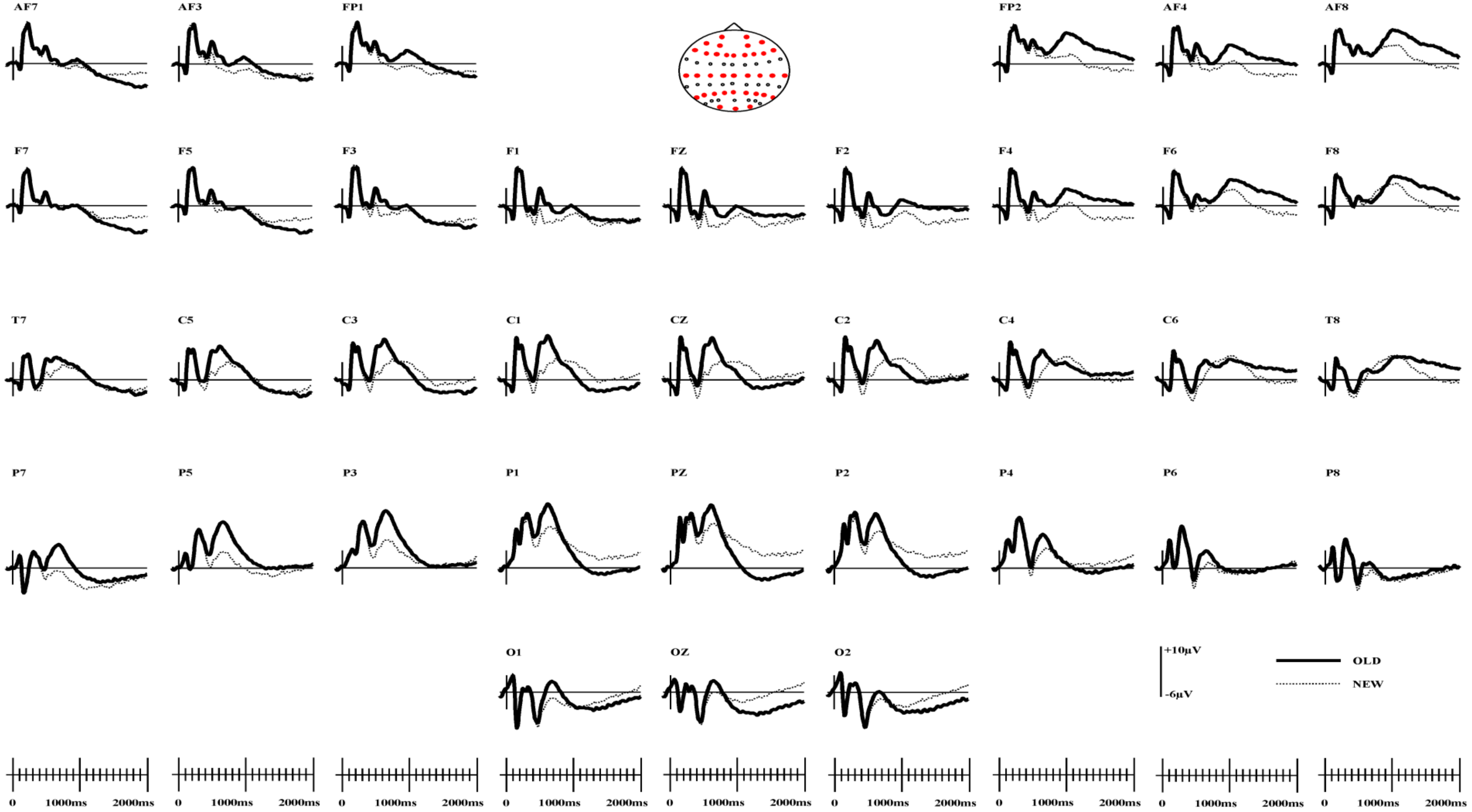

Figure 13. Grand average ERP waveforms for correctly classified old (collapsed across context and target and non-target responses) and new (collapsed across context) items. 36 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16µV.

7.3.2.1 ERP Magnitude Analyses

The global magnitude analyses revealed main effects and/or interactions involving the factor of response for all four latency windows (see Table 10). The highest order ANOVA results from 300-450ms and 450-900ms were two-way response by site interactions, and three-way response by hemisphere by site interactions from 900-1300ms and 1300-2000ms. These interactions were further examined with subsidiary analyses.

Latency Window	Old vs. New
300-450ms	
R	F(1,44)=7.83,p=0.008
RxS	F(2.75,120.83)=13.66,p<0.001
450-900ms	
R	F(1,44)=13.01,p=0.001
RxS	F(2.43,107.06)=27.04,p<0.001
900-1300ms	
R	F(1,44)=6.97,p=0.01
RxH	F(1,44)=11.10,p=0.002
RxS	F(2.06,90.76)=8.24,p<0.001
RxHxS	F(2.85,125.57)=3.04,p=0.03
1300-2000ms	
RxH	F(1,44)=25.56,p<0.001
RxHxS	F(2.13,93.53)=9.07,p<0.001

Table 10. Results of the global magnitude analyses. Old items are collapsed across contexts and responses (target and non-target). New items are collapsed across contexts. R, H and S represent the factors of response, hemisphere and site respectively. Main effects and/or interactions involving the factor of response were present for all four latency windows.

Subsidiary paired t-tests investigating the global response by site interaction from 300-450ms (Table 10) confirmed the presence of a significant bilateral frontal effect (Figure 14, A) at all frontal sites, except AF7/AF8 [F1/F2 – t(44) = 3.74, p = 0.001; F3/F4 – t(44) = 3.54, p = 0.001; F5/F6 – t(44) = 2.94, p = 0.005; F7/F8– t(44) = 2.06, p = 0.05;

AF3/AF4– t(44) = 2.75, p = 0.009; FP1/FP2– t(44) = 2.11, p = 0.04]. The effect was maximal at F1/F2 [Mean 0.83μV].

The positivity of old waveforms compared to new waveforms at frontal sites continued into the 450-900ms latency window (Figure 14, B). Subsidiary paired t-tests investigating the global response by site interaction (Table 10) revealed that the bilateral anterior frontal effect was significant at all frontal sites, apart from F7/F8 and AF7/AF8 [F1/F2 – t(44) = 5.78, p < 0.001; F3/F4 – t(44) = 5.36, p < 0.001; F5/F6 – t(44) = 2.52, p = 0.02; AF3/AF4 – t(44) = 4.37, p < 0.001; FP1/FP2– t(44) = 2.82, p = 0.007]. Again, the effect was maximal at F1/F2 [Mean 1.53μV]. To assess the significance of the left parietal effect from 450-900ms (Figure 14, B), targeted t-tests of left parietal sites (P1, P3 and P5) were conducted, revealing significant differences at all sites [P1 – t(44) = 5.28, p < 0.001; P3 – t(44) = 8.42, p < 0.001; P5 – t(44) = 10.03, p < 0.001]. Examination of the data revealed that the effect was maximal at P3 [Mean 2.62μV] and P5 [Mean 2.61μV].

From 900-1300ms, old greater than new differences persisted at frontal sites (Figure 14, C). Subsidiary analyses investigating the global response by hemisphere by site interaction (Table 10) revealed significant differences at left frontal sites AF3 and FP1 [AF3 – t(44) = 2.47, p = 0.02; FP1 – t(44) = 3.05, p = 0.004] and at all right frontal sites [F2 – t(44) = 2.76, p = 0.008; F4 – t(44) = 3.35, p = 0.002; F6 – t(44) = 2.72, p = 0.009; F8 – t(44) = 2.23, p = 0.03; AF4 – t(44) = 3.60, p = 0.001; AF8 – t(44) = 3.18, p = 0.003; FP2 – t(44) = 4.00, p < 0.001], indicating the presence of the right prefrontal effect. The effect was maximal at FP2 [Mean 2.20μV] and AF4 [Mean 1.64μV].

The right frontal effect was significant in the 1300-2000ms time window, along with the appearance of the left frontal negativity (Figure 14, D). Subsidiary analyses investigating the global response by hemisphere by site interaction (Table 10) revealed significant new greater than old negativities at left hemisphere sites F5 and F7 [F5 – t(44) = -2.17, p = 0.04; F7 – t(44) = -2.54, p = 0.02], and old greater than new positivities at all right frontal sites [F2 – t(44) = 3.00, p = 0.004; F4 – t(44) = 4.06, p < 0.001; F6 – t(44) = 4.41, p < 0.001; F8 – t(44) = 4.04, p < 0.001; AF4 – t(44) = 3.36, p = 0.002; AF8 – t(44) = 3.45, p = 0.001; FP2 – t(44) = 3.18, p = 0.003]. The right frontal effect was maximal at F4 [Mean 1.72μV] and F6 [Mean 1.67μV].

7.3.2.2 ERP Topographic Analyses

Figure 14 illustrates the change in distribution of the old/new effects over time. The description and topographic analyses will only focus on the frontal and left parietal effects. There is a change in distribution over successive latency periods from a bilateral frontal effect to a left parietal effect, followed by a late right frontal effect and finally a left frontal negativity.

The global topographic analyses revealed main effects and interactions involving the factor of epoch (Table 11). Consequently, three subsidiary topographic comparisons were conducted (300-450ms vs. 450-900ms, 450-900ms vs. 900-1300ms, 900-1300ms vs. 1300-2000ms), investigating the highest order epoch by hemisphere by site interaction.

	Old minus New
E	F(1.84,81.02)=5.98,p=0.005
ExH	F(1.91,84.06)=12.82,p<0.001
ExS	F(1.82,211.93)=11.63,p<0.001
ExHxS	F(6.04,265.95)=5.14,p<0.001

Table 11. Results of the global topographic analyses of rescaled difference waveforms, comparing all four latency windows. Old items are collapsed across contexts and responses (target and non-target). New items are collapsed across contexts. E, H and S represent the factors of epoch, hemisphere and site respectively. Main effects and interactions involving the factor of epoch were present.

Subsidiary analyses for the 300-450ms vs. 450-900ms comparison, investigating the global epoch by hemisphere by site interaction (Table 11) revealed an epoch by site interaction [F(2.59,114.11) = 4.28, p = 0.009]. This interaction reflected a change in distribution over time from a widespread frontal effect in the first latency period to a frontal effect more sharply focussed towards the midline in the second latency period (Figure 14, A and B).

For the 450-900ms vs. 900-1300ms comparison, subsidiary analyses investigating the global epoch by hemisphere by site interaction (Table 11) also revealed an epoch by hemisphere by site interaction [F(3.24,142.57) = 4.82, p = 0.002]. This interaction demonstrated a change in distribution over time from a bilateral anterior frontal effect from 450-900ms to a right prefrontal effect from 900-1300ms (Figure 14, B and C).

For the 900-1300ms vs. 1300-2000ms contrast, subsidiary analyses investigating the global epoch by hemisphere by site interaction (Table 11) also revealed an epoch by hemisphere by site interaction [F(2.46,108.08) = 7.86, p < 0.001]. This interaction reflected a change in distribution over time from a right prefrontal effect from 900-1300ms to a right frontal effect from 1300-2000ms, and also reflected the evolution of the left frontal negativity in the latter time window (Figure 14, C and D).

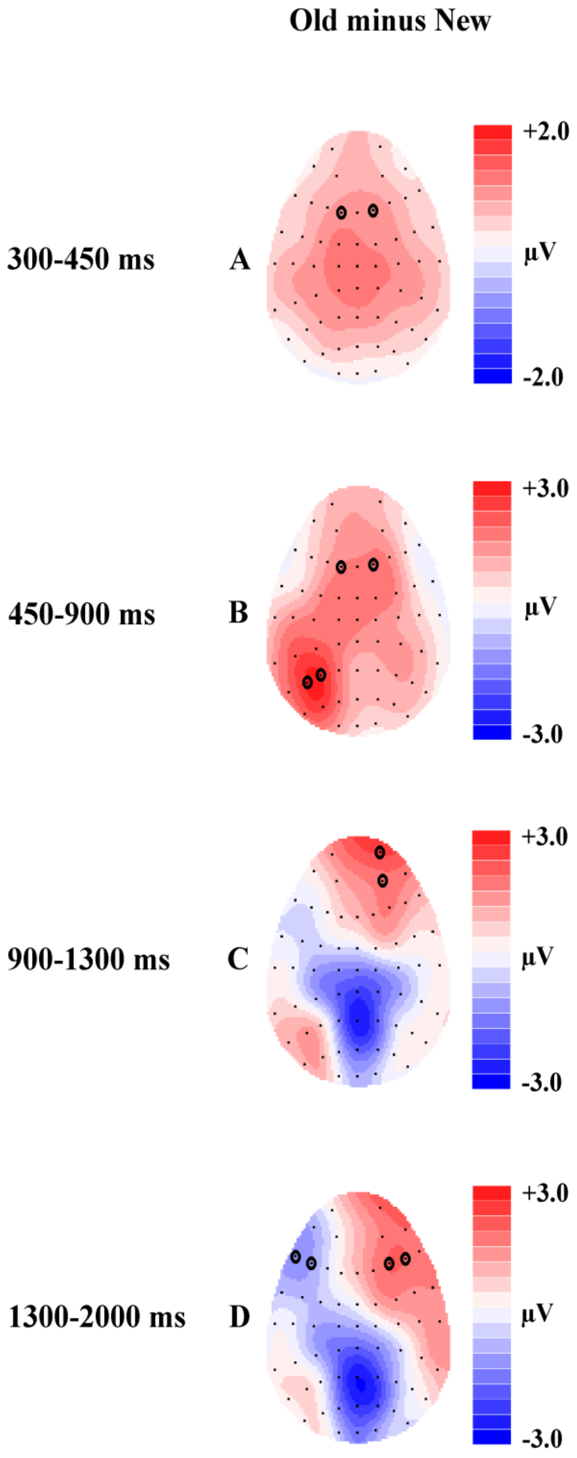

Figure 14. Topographic maps illustrating the scalp distribution of ERP effects. Each map is shown as if looking down onto the top of the head with frontal sites towards the top of the page. Old items are collapsed across contexts and responses (target and non-target). New items are collapsed across contexts. The highlighted electrodes are those used in the correlation analyses. There is a change in distribution over successive latency periods from a bilateral frontal effect to a left parietal effect followed by a right frontal effect, and finally a left frontal negativity.

7.3.2.3 Neuropsychological Data

7.3.2.3.1 Test Performance

As stated previously, participants completed four tests from the CANTAB battery: the non-executive Spatial Span task, and the following executive tasks - Spatial Working Memory, Stockings of Cambridge and the IDED Set Shifting task (see 'General Methods' chapter for a description of the tasks). Table 12 shows the results of the main measures from these tasks, which were subsequently correlated with the ERP data. Mean scores refer to data averaged across participants and, where appropriate, stages of each task. The scores were in line with normative data using the CANTAB (see Robbins et al., 1998; De Luca et al., 2003).

CANTAB Task and Main Measures	Mean Score
Spatial Span Task	
Span Score	7.23
Total Errors	13.49
ID/ED Attention Set-Shifting Task	
Mean Errors Across All Stages	1.21
Mean Errors at ED Shift	3.67
Mean Errors up to ED Shift	0.76
Mean Response Time Across All Stages (msec)	1993
Spatial Working Memory Task	
Mean Between Search Errors Across All Stages	3.01
Strategy Score	28.91
Mean Time Across All Stages (msec)	135684
Stockings of Cambridge Task	
Stages Solved in Minimum Moves	10.22
Mean Initial Thinking Time Across All Stages (msec)	10321
Mean Subsequent Thinking Time Across All Stages (msec)	4932
Mean Number of Excess Moves Across All Stages	0.41

Table 12. Results of the performance on the CANTAB tests. The results were in line with normative data using the CANTAB.

7.3.2.3.2 Inter-Relationship Between Cognitive Tests

Correlations were performed between the spatial span score and the mean between search errors across all stages of the Spatial Working Memory task, to assess the role of short-term memory capacity on working memory performance. There were no significant correlations between the spatial span score and the between search errors, suggesting no relationship between short-term memory capacity and working memory performance.

Furthermore, to investigate if there was a relationship between strategy use and working memory performance, correlations were performed between the strategy score and the mean between search errors across all stages, revealing a positive correlation ($r = 0.69$, $p < 0.001$). Greater use of strategy was associated with reduced errors, therefore better working memory performance, on the Spatial Working Memory task.

7.3.2.4 ERP and Neuropsychological Correlation Analyses

Correlations were performed on the old minus new data, collapsed across the two sites where the frontal and left parietal effects were maximal (300-450ms: F1 and F2; 450-900ms: F1 and F2, P3 and P5; 900-1300ms: FP2 and AF4; 1300-2000ms: F5 and F7, F4 and F6). The sites used in the correlation analyses are highlighted on Figure 14. The two maximal sites were chosen for consistency across all time windows. The effects in the first two time windows were bilateral, therefore an average of two sites (one from each hemisphere) was necessary. By contrast, the effects in the latter two time windows were left or right sided and one electrode site could therefore have been used for the correlation analyses. However, as variation at individual sites will be larger than for an average of two sites, it was important to choose two sites across all time windows to ensure equivalent comparisons. Correlations involving behavioural accuracy and reaction time on the exclusion task were performed using data collapsed across hits and correct rejections (see Table 9).

300-450ms: There were no significant correlations between the magnitude of the putative bilateral frontal correlate of familiarity (Figure 14, A) and performance on any of the neuropsychological tests (see Table 13). However, there was a significant positive correlation between the magnitude of the effect and behavioural accuracy on the exclusion task (r = .29, p = .05), but not reaction time (see Figure 15).

CANTAB Task and Main Measures	R	r square	p value
Spatial Span Task			
Span Score	0.08	0.01	0.62
Total Errors	0.03	0.00	0.84
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	0.04	0.00	0.79
Mean Errors at ED Shift	-0.02	0.00	0.88
Mean Errors up to ED Shift	0.00	0.00	0.98
Mean Response Time Across All Stages (msec)	-0.16	0.03	0.29
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	-0.10	0.01	0.52
Strategy Score	-0.14	0.02	0.35
Mean Time Across All Stages (msec)	-0.09	0.01	0.55
Stockings of Cambridge Task			
Stages Solved in Minimum Moves	0.16	0.03	0.28
Mean Initial Thinking Time Across All Stages (msec)	0.15	0.02	0.32
Mean Subsequent Thinking Time Across All Stages (msec)	-0.17	0.03	0.26
Mean Number of Excess Moves Across All Stages	-0.19	0.04	0.22

Table 13. Results of the correlation analyses between the magnitude of the putative Bilateral Frontal Correlate of Familiarity from 300-450ms and performance on the CANTAB tests. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F1 and F2, where the Bilateral Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on any of the CANTAB tests.

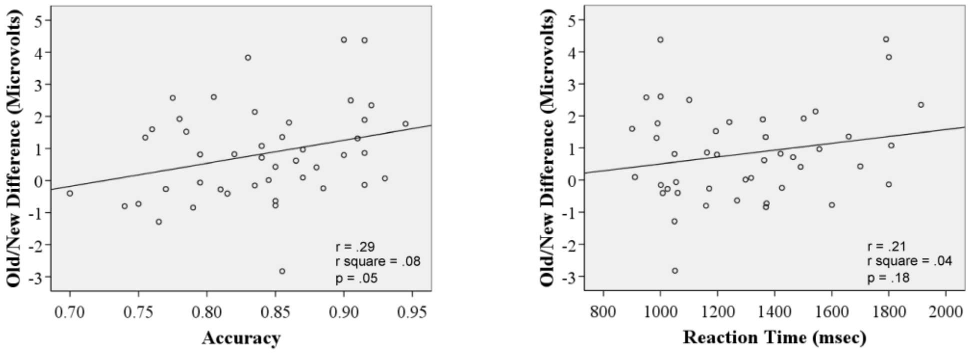

Figure 15. Scatterplots depicting the relationship between the magnitude of the putative Bilateral Frontal Correlate of Familiarity from 300-450ms and behavioural performance on the exclusion task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F1 and F2, where the Bilateral Frontal Effect was maximal. Accuracy and reaction time are data from Table 9 collapsed across hits and correct rejections. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There was a significant positive correlation between the magnitude of the effect and accuracy, but not reaction time.

450-900ms: There were no significant correlations between the magnitude of the left parietal correlate of recollection (Figure 14, B) and performance on any of the neuropsychological tests (see Table 14). However, there was a significant positive correlation between the magnitude of the effect and behavioural accuracy on the exclusion task (r = -.28, p = .06), but not reaction time (see Figure 16). There were no significant correlations between the magnitude of the bilateral anterior frontal effect (Figure 14, B) and performance on the Spatial Span task or the ID/ED Set-Shifting task (see Table 15). As can be seen in Figure 17, however, significant negative correlations were found between the magnitude of the bilateral anterior frontal effect and Spatial Working Memory Mean Between Search Errors (r = -.40, p = .01), Strategy Score (r = -.30, p = .05) and Mean Time (r = -.33, p = .03). There were also significant positive correlations (Figure 18) between the magnitude of the effect and the Stockings of Cambridge Sets Solved in Minimum Moves (r = .40, p = .01), Mean Initial Thinking Time (r = .28, p = .07), and significant negative correlations with Mean Subsequent Thinking Time (r = -.28, p = .07) and Mean Number of Excess Moves (r = -.30, p = .04). The magnitude of the effect also correlated positively with behavioural accuracy on the exclusion task (r = .37, p = .01) and reaction time (r = .34, p = .02) (Figure 19).

CANTAB Task and Main Measures	r	r square	p value
Spatial Span Task			
Span Score	-0.13	0.02	0.40
Total Errors	-0.13	0.02	0.38
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	-0.02	0.00	0.88
Mean Errors at ED Shift	-0.03	0.00	0.70
Mean Errors up to ED Shift	-0.01	0.00	0.84
Mean Response Time Across All Stages (msec)	0.06	0.00	0.70
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	-0.08	0.01	0.61
Strategy Score	-0.14	0.02	0.36
Mean Time Across All Stages (msec)	-0.01	0.00	0.54
Stockings of Cambridge Task			
Stages Solved in Minimum Moves	0.10	0.01	0.52
Mean Initial Thinking Time Across All Stages (msec)	-0.17	0.03	0.28
Mean Subsequent Thinking Time Across All Stages (msec)	-0.07	0.00	0.67
Mean Number of Excess Moves Across All Stages	-0.07	0.00	0.65

Table 14. Results of the correlation analyses between the magnitude of the Left Parietal Correlate of Recollection from 450-900ms and performance on the CANTAB tests. Correlations were performed using the ERP old minus new data (microvolts), collapsed across sites P3 and P5, where the Left Parietal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on any of the CANTAB tests.

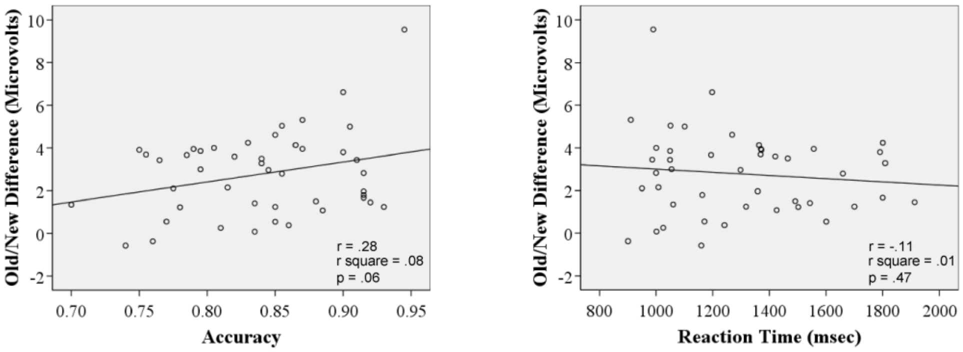

Figure 16. Scatterplots depicting the relationship between the magnitude of the Left Parietal Correlate of Recollection from 450-900ms and behavioural performance on the exclusion task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites P3 and P5, where the Left Parietal Effect was maximal. Accuracy and reaction time are data from Table 9 collapsed across hits and correct rejections. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There was a significant positive correlation between the magnitude of the effect and accuracy, but not reaction time.

CANTAB Task and Main Measures	r	r square	p value
Spatial Span Task			
Span Score	0.05	0.00	0.75
Total Errors	0.04	0.00	0.79
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	-0.24	0.06	0.11
Mean Errors at ED Shift	-0.27	0.07	0.08
Mean Errors up to ED Shift	0.01	0.00	0.96
Mean Response Time Across All Stages (msec)	0.05	0.00	0.77

Table 15. Results of the correlation analyses between the magnitude of the Bilateral Anterior Frontal Effect from 450-900ms and performance on the Spatial Span Task and the ID/ED Attention Set-Shifting Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F1 and F2, where the Bilateral Anterior Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on the Spatial Span Task or the ID/ED Attention-Set Shifting Task.

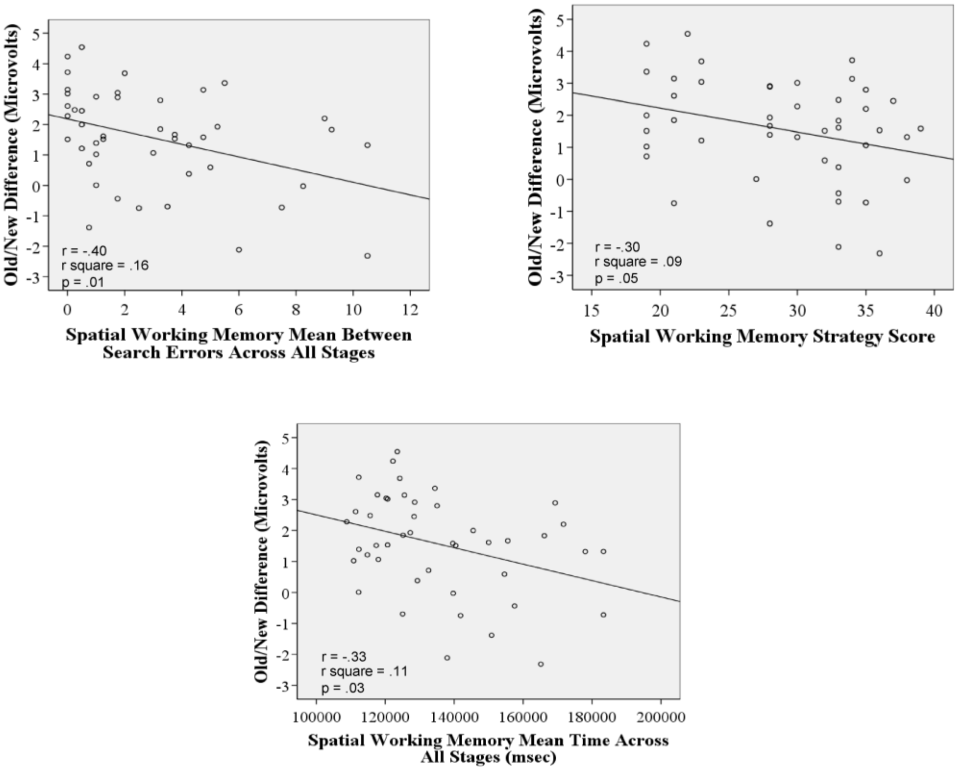

Figure 17. Scatterplots depicting the relationship between the magnitude of the Bilateral Anterior Frontal Effect from 450-900ms and performance on the Spatial Working Memory Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F1 and F2, where the Bilateral Anterior Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the task. There were significant negative correlations between the magnitude of the effect and the Mean Between Search Errors, Strategy Score and Mean Time.

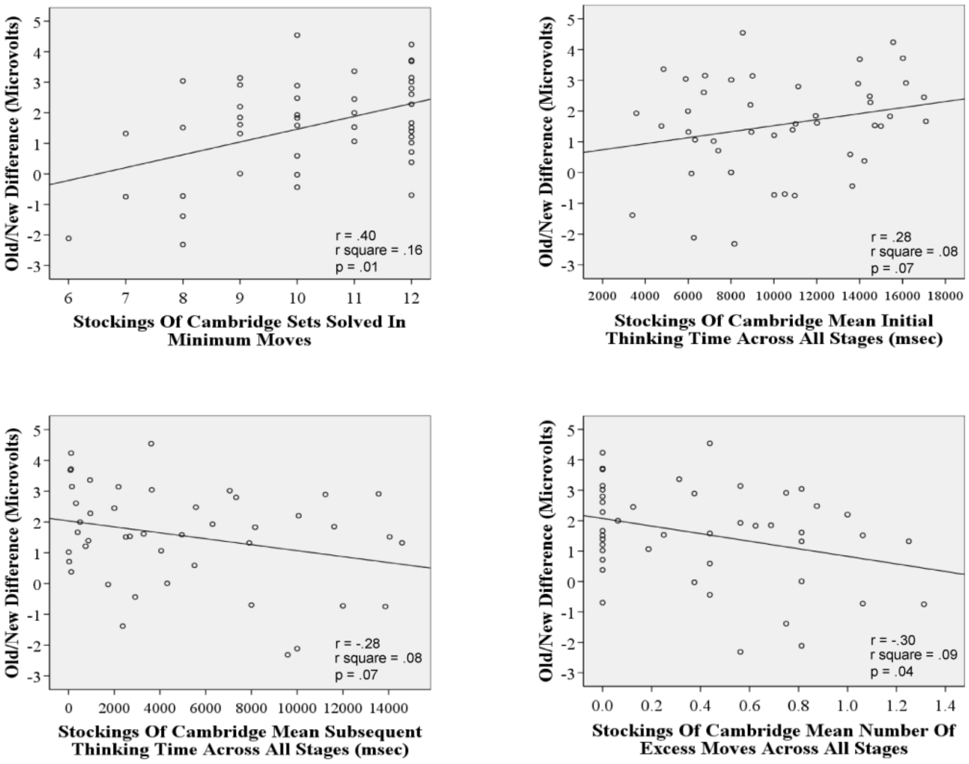

Figure 18. Scatterplots depicting the relationship between the magnitude of the Bilateral Anterior Frontal Effect from 450-900ms and performance on the Stockings Of Cambridge Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F1 and F2, where the Bilateral Anterior Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the task. There were significant positive correlations between the magnitude of the effect and the Sets Solved In Minimum Moves, Mean Initial Thinking Time, and significant negative correlations with Mean Subsequent Thinking Time and the Mean Number Of Excess Moves.

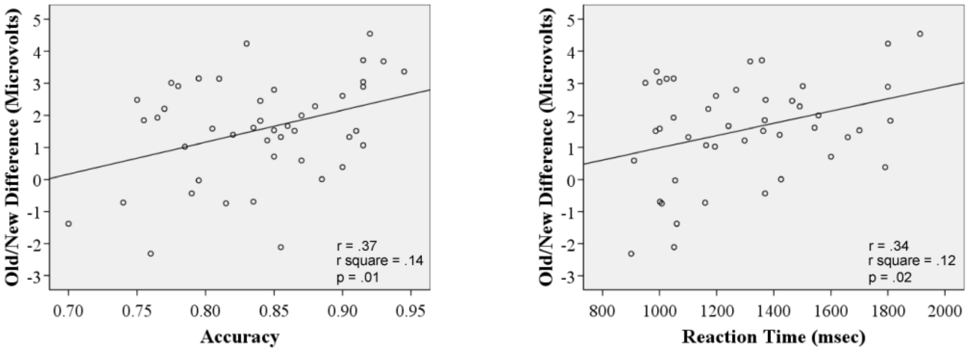

Figure 19. Scatterplots depicting the relationship between the magnitude of the Bilateral Anterior Frontal Effect from 450-900ms and behavioural performance on the exclusion task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F1 and F2, where the Bilateral Anterior Frontal Effect was maximal. Accuracy and reaction time are data from Table 9 collapsed across hits and correct rejections. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There were significant positive correlations between the magnitude of the effect and accuracy and reaction time.

900-1300ms: There were no significant correlations between the magnitude of the right prefrontal effect (Figure 14, C) and performance on the Spatial Span task or the ID/ED Set-Shifting task (Table 16). As can be seen in Figure 20, significant negative correlations were found between the magnitude of the effect and Spatial Working Memory Mean Between Search Errors (r = -.31, p = .04) and Mean Time (r = -.30, p = .04). However, the magnitude of the right prefrontal effect did not correlate significantly with Spatial Working Memory Strategy Score. There were also significant positive correlations (Figure 21) between the magnitude of the effect and the Stockings of Cambridge Sets Solved in Minimum Moves (r = .35, p = .02), Mean Initial Thinking Time (r = .37, p = .01), and significant negative correlations with Mean Subsequent Thinking Time (r = -.47, p = .001) and Mean Number of Excess Moves (r = -.32, p = .04). The magnitude of the effect also correlated positively with behavioural accuracy on the exclusion task (r = .32, p = .03) and reaction time (r = .33, p = .03) (Figure 22).

CANTAB Task and Main Measures	r	r square	p value
Spatial Span Task			
Span Score	0.16	0.03	0.30
Total Errors	-0.09	0.01	0.54
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	-0.27	0.07	0.08
Mean Errors at ED Shift	-0.15	0.02	0.32
Mean Errors up to ED Shift	-0.16	0.03	0.30
Mean Response Time Across All Stages (msec)	0.15	0.02	0.34

Table 16. Results of the correlation analyses between the magnitude of the Right Prefrontal Effect from 900-1300ms and performance on the Spatial Span Task and the ID/ED Attention Set-Shifting Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites FP2 and AF4, where the Right Prefrontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on the Spatial Span Task or the ID/ED Attention-Set Shifting Task.

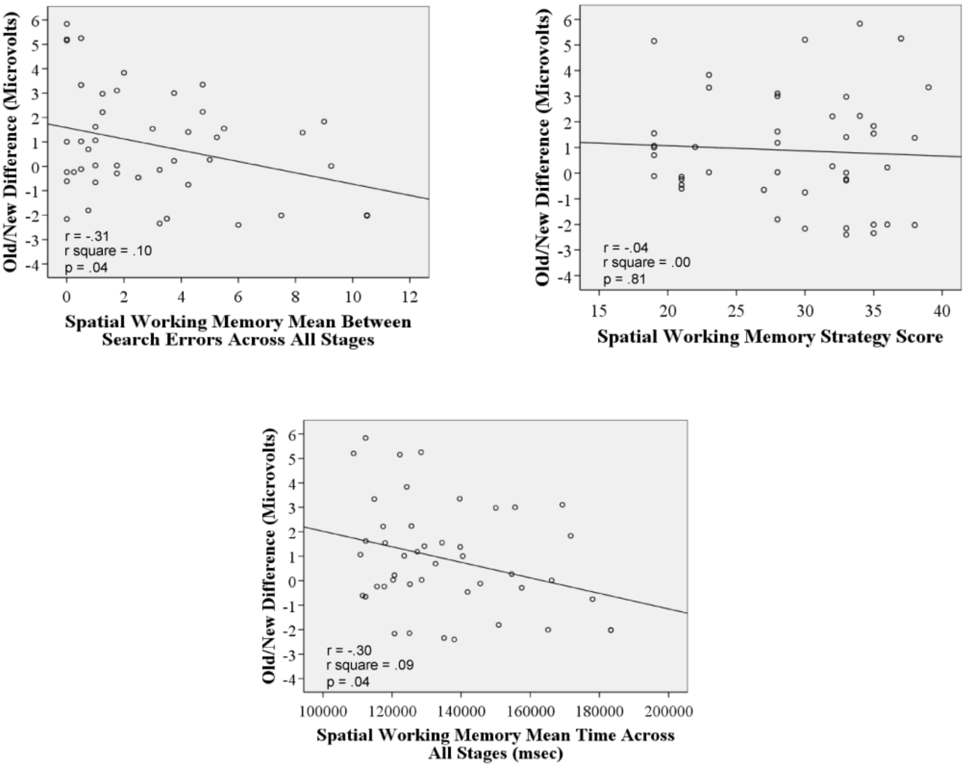

Figure 20. Scatterplots depicting the relationship between the magnitude of the Right Prefrontal Effect from 900-1300ms and performance on the Spatial Working Memory Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites FP2 and AF4, where the Right Prefrontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the task. There were significant negative correlations between the magnitude of the effect and the Mean Between Search Errors and Mean Time, but no significant correlation with Strategy Score.

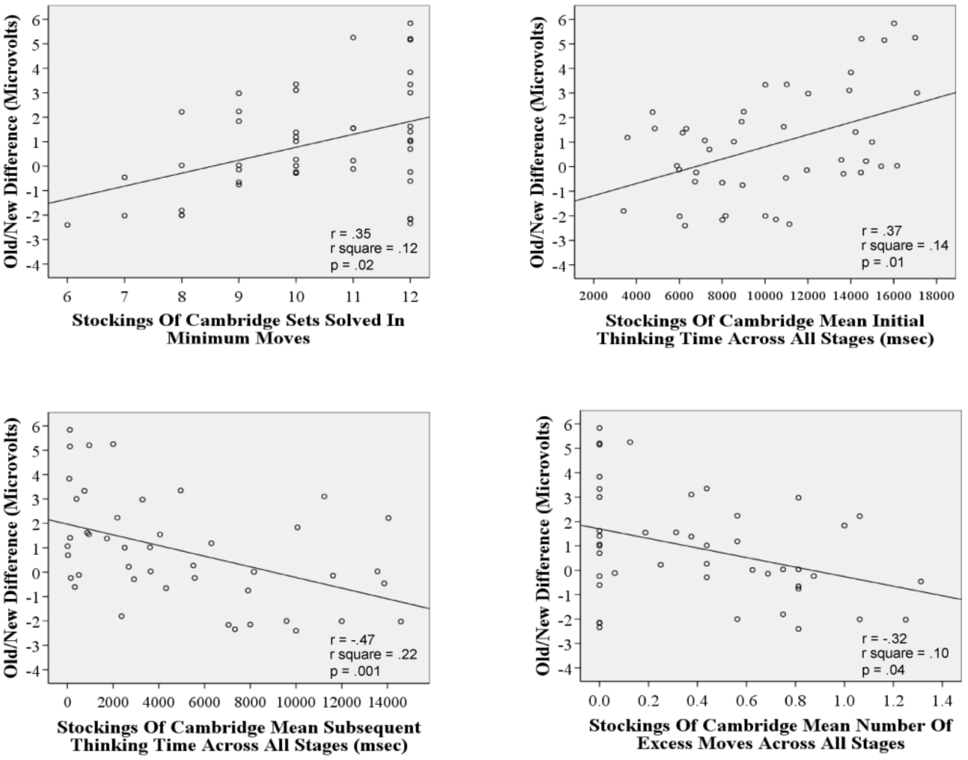

Figure 21. Scatterplots depicting the relationship between the magnitude of the Right Prefrontal Effect from 900-1300ms and performance on the Stockings Of Cambridge Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites FP2 and AF4, where the Right Prefrontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the task. There were significant positive correlations between the magnitude of the effect and the Sets Solved In Minimum Moves, Mean Initial Thinking Time, and significant negative correlations with Mean Subsequent Thinking Time and the Mean Number Of Excess Moves.

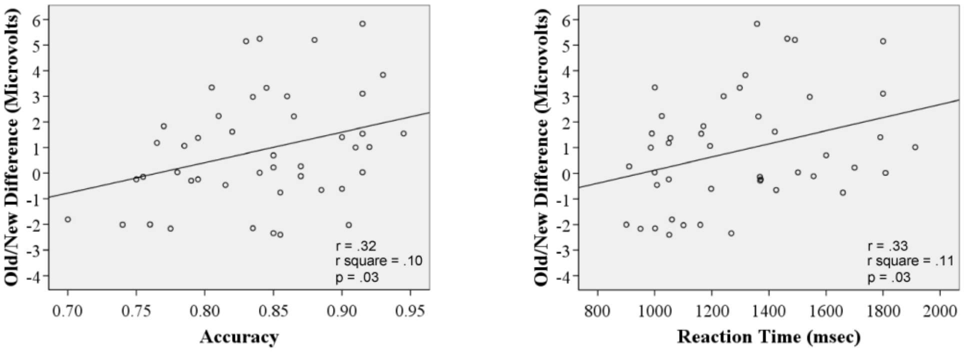

Figure 22. Scatterplots depicting the relationship between the magnitude of the Right Prefrontal Effect from 900-1300ms and behavioural performance on the exclusion task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites FP2 and AF4, where the Right Prefrontal Effect was maximal. Accuracy and reaction time are data from Table 9 collapsed across hits and correct rejections. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There were significant positive correlations between the magnitude of the effect and accuracy and reaction time.

1300-2000ms: There were no significant correlations between the magnitude of the left frontal negativity (Figure 14, D) and performance on any of the neuropsychological tests or behavioural performance on the exclusion task (see Table 17). There were also no significant correlations between the magnitude of the right frontal effect (Figure 14, D) and performance on the Spatial Span task or the ID/ED Set-Shifting task or on any part of the Spatial Working Memory task (Table 18). There were significant positive correlations (Figure 23) between the magnitude of the right frontal effect and the Stockings of Cambridge Sets Solved in Minimum Moves (r = .33, p = .03), Mean Initial Thinking Time (r = .41, p = .01), and significant negative correlations with Mean Subsequent Thinking Time (r = -.31, p = .04) and Mean Number of Excess Moves (r = -.29, p = .05). The magnitude of the effect also correlated positively with behavioural accuracy on the exclusion task (r = .29, p = .06) and reaction time (r = .41, p = .01) (Figure 24).

CANTAB Task and Main Measures	r	r square	p value
Spatial Span Task			
Span Score	0.07	0.00	0.66
Total Errors	-0.05	0.00	0.75
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	0.03	0.00	0.82
Mean Errors at ED Shift	0.15	0.02	0.32
Mean Errors up to ED Shift	-0.08	0.01	0.60
Mean Response Time Across All Stages (msec)	0.10	0.01	0.50
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	-0.26	0.07	0.09
Strategy Score	0.06	0.00	0.72
Mean Time Across All Stages (msec)	-0.13	0.02	0.38
Stockings of Cambridge Task			
Stages Solved in Minimum Moves	0.18	0.03	0.23
Mean Initial Thinking Time Across All Stages (msec)	0.20	0.04	0.19
Mean Subsequent Thinking Time Across All Stages (msec)	-0.28	0.08	0.08
Mean Number of Excess Moves Across All Stages	-0.23	0.05	0.13
Exclusion Task Behavioural Performance			
Accuracy	-0.10	0.01	0.54
Reaction Time (msec)	-0.06	0.00	0.68

Table 17. Results of the correlation analyses between the magnitude of the Left Frontal Negativity from 1300-2000ms and performance on the CANTAB tests and behavioural performance on the exclusion task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F5 and F7, where the Left Frontal Negativity was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on any of the Neuropsychological tasks or behavioural performance on the exclusion task.

CANTAB Task and Main Measures	R	r square	p value
Spatial Span Task			
Span Score	-0.10	0.01	0.51
Total Errors	0.25	0.06	0.11
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	-0.13	0.02	0.39
Mean Errors at ED Shift	-0.16	0.03	0.31
Mean Errors up to ED Shift	0.16	0.03	0.29
Mean Response Time Across All Stages (msec)	0.05	0.00	0.75
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	0.08	0.01	0.59
Strategy Score	0.15	0.02	0.33
Mean Time Across All Stages (msec)	-0.05	0.00	0.73

Table 18. Results of the correlation analyses between the magnitude of the Right Frontal Effect from 1300-2000ms and performance on the Spatial Span Task, ID/ED Attention Set-Shifting Task and the Spatial Working Memory Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F4 and F6, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on the Spatial Span Task, ID/ED Attention Set-Shifting Task or the Spatial Working Memory Task.

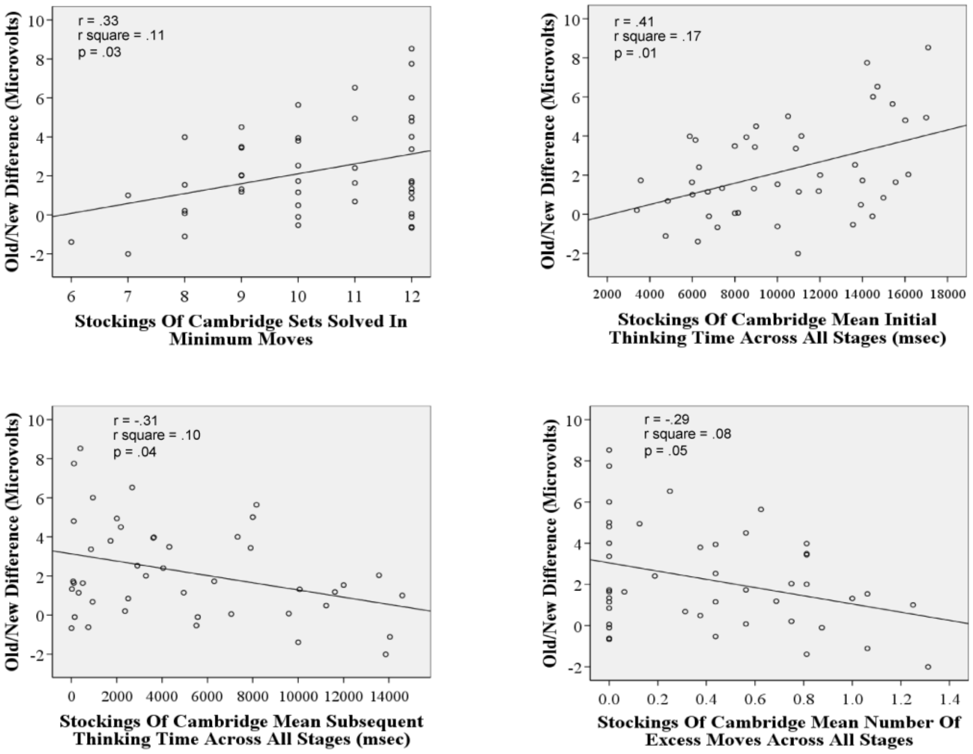

Figure 23. Scatterplots depicting the relationship between the magnitude of the Right Frontal Effect from 1300-2000ms and performance on the Stockings Of Cambridge Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F4 and F6, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the task. There were significant positive correlations between the magnitude of the effect and the Sets Solved In Minimum Moves, Mean Initial Thinking Time, and significant negative correlations with Mean Subsequent Thinking Time and the Mean Number Of Excess Moves.

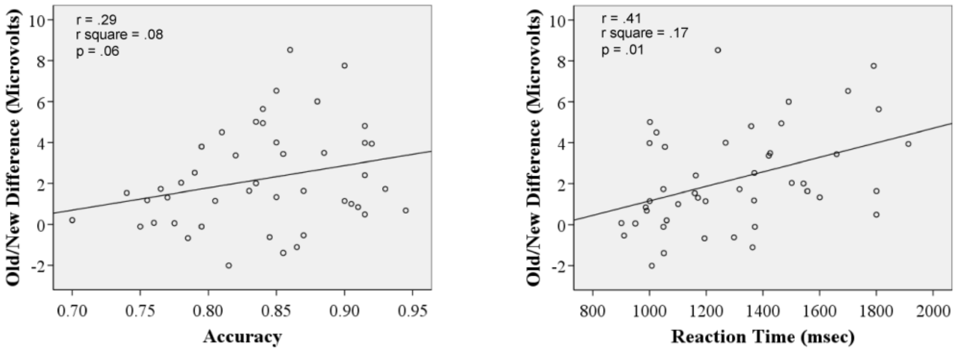

Figure 24. Scatterplots depicting the relationship between the magnitude of the Right Frontal Effect from 1300-2000ms and behavioural performance on the exclusion task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F4 and F6, where the Right Frontal Effect was maximal. Accuracy and reaction time are data from Table 9 collapsed across hits and correct rejections. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There were significant positive correlations between the magnitude of the effect and accuracy and reaction time.

7.3.2.4.1 Summary of Results

The putative bilateral frontal correlate of familiarity and the left parietal correlate of recollection did not significantly correlate with performance on any of the neuropsychological tests. The effects did, however, significantly increase as behavioural accuracy improved, but did not significantly correlate with behavioural reaction time. This result suggests that these old/new effects are not related to the non-executive function of short-term memory, the executive functions of attentional set shifting (or flexibility of thinking and responding), working memory, strategy use, planning or behavioural reaction time on the exclusion task, but are related to behavioural accuracy on the exclusion task.

The left frontal negativity did not significantly correlate with performance on any of the neuropsychological tests or behavioural performance, suggesting that this effect is not related to the non-executive or executive functions mentioned above, or to behavioural accuracy and reaction time on the exclusion task. In contrast, there were significant correlations between the magnitude of the three late frontal effects and performance on the neuropsychological tests and behavioural performance. Importantly, and of particular interest, each effect correlated with the neuropsychological tests in different ways.

The magnitude of the bilateral anterior frontal effect, from 450-900ms, did not significantly correlate with performance on any part of the Spatial Span task or the Attention Set-Shifting task. The magnitude of the effect did, however, decrease as the number of Spatial Working Memory Between Search Errors and Time increased, and as the use of the optimal strategy decreased. The magnitude of the effect also increased as the Stockings of Cambridge Number of Sets Solved in Minimum Moves and Initial Thinking Time increased, and decreased as Subsequent Thinking Time and Number of Excess Moves increased. The magnitude of the effect increased as behavioural accuracy and reaction time increased. These results suggest that the bilateral anterior frontal effect is not related to short-term memory or flexibility of thinking and responding, but is related to working memory, strategy use, planning and behavioural accuracy and reaction time on the exclusion task.

The magnitude of the right prefrontal effect, from 900-1300ms, did not significantly correlate with performance on any part of the Spatial Span task or the Attention Set-Shifting task. The magnitude of the effect did, however, decrease as the number of Spatial Working Memory Between Search Errors and Time increased. There were no significant correlations with strategy score. The magnitude of the effect also increased as the Stockings of Cambridge Number of Sets Solved in Minimum Moves and Initial Thinking Time increased, and decreased as Subsequent Thinking Time and Number of Excess Moves increased. The magnitude of the effect increased as behavioural accuracy and reaction time increased. These results suggest that the right prefrontal effect is not related to short-term memory, flexibility of thinking and responding or strategy use, but is related to working memory, planning and behavioural accuracy and reaction time on the exclusion task.

The magnitude of the right frontal effect, from 1300-2000ms, did not significantly correlate with performance on any part of the Spatial Span task, the Attention Set-Shifting task or the Spatial Working Memory task. The magnitude of the effect did increase, however, as the Stockings of Cambridge Number of Sets Solved in Minimum Moves and Initial Thinking Time increased, and decreased as Subsequent Thinking Time and Number of Excess Moves increased. The magnitude of the effect increased as behavioural accuracy and reaction time increased. These results suggest that the right frontal effect is not related to short-term memory, flexibility of thinking and responding, strategy use or working memory, but is related to planning and behavioural accuracy and reaction time on the exclusion task.

7.4 Discussion

The aim of Experiment 1b was to further investigate the functional significance of the three late frontal effects from Experiment 1a, by assessing whether the magnitude of the effects correlated with performance on neuropsychological tests taken from the CANTAB. The three late frontal effects (the bilateral anterior frontal effect from 450-900ms, the right prefrontal effect from 900-1300ms and the right frontal effect from 1300-2000ms) correlated with the neuropsychological tests in different ways. The bilateral anterior frontal effect was not related to short-term memory or flexibility of thinking and responding, but was related to working memory, strategy use, planning and behavioural accuracy and reaction time on the exclusion task. The right prefrontal effect was not related to short-term memory, flexibility of thinking and responding or strategy use, but was related to working memory, planning and behavioural accuracy and reaction time on the exclusion task. The right frontal effect was not related to short-term memory, flexibility of thinking and responding, strategy use or working memory, but was related to planning and behavioural accuracy and reaction time on the exclusion task. Furthermore, the putative bilateral frontal correlate of familiarity, the left parietal correlate of recollection and the left frontal negativity were not related to short-term memory, flexibility of thinking and responding, strategy use, working memory or planning, however the bilateral frontal and left parietal effects were related to behavioural accuracy on the exclusion task.

7.4.1 Bilateral Frontal Correlate of Familiarity

The majority of evidence suggests that the bilateral frontal effect provides an index of familiarity (Rugg and Curran, 2007). It was therefore unsurprising that the effect did not significantly correlate with performance on any of the neuropsychological tests. While the results cannot speak to the familiarity interpretation of the effect, they do imply that it is not related to the executive functions assessed in this experiment. The size of the effect was related to behavioural accuracy suggesting that greater activation was associated with higher accuracy on the exclusion task. As the bilateral frontal effect is a core memory retrieval effect, as opposed to a post retrieval monitoring effect, it was unsurprising that there was no significant correlation with behavioural reaction time.

7.4.2 Left Parietal Correlate of Recollection

The left parietal effect is widely considered to provide an index of recollection (Allan, Wilding and Rugg, 1998). Consequently, it was unsurprising that the effect did not significantly correlate with performance on any of the neuropsychological tests. Consistent with the bilateral frontal effect, the results do not speak to the recollection interpretation of the left parietal effect, however they do imply that the effect is not related to the executive functions assessed in this experiment. The size of the effect was related to behavioural accuracy, suggesting that greater activation was associated with higher accuracy on the exclusion task. As the left parietal effect is a core memory retrieval effect, as opposed to a post retrieval monitoring effect, it was unsurprising that there was no significant correlation with behavioural reaction time.

7.4.3 Left Frontal Negativity

The functional significance of the left frontal negativity is unclear, however Trott et al., 1997; Wegesin et al., 2002 and Li et al., 2004 have proposed that it reflects the engagement of additional, compensatory, processes to assist with retrieval. If this interpretation is correct, the fact that the effect did not significantly correlate with performance on any of the neuropsychological tests suggests that the compensatory processes are not related to the executive functions assessed in this experiment. The functional significance of this effect still remains unclear.

7.4.4 Bilateral Anterior Frontal Effect

The bilateral anterior frontal effect was not related to short-term memory or flexibility of thinking and responding, but was related to working memory, strategy use, planning and behavioural accuracy and reaction time. The fact that the effect did not correlate with short-term memory, which is not considered to be an executive function, but did correlate with some of the executive functions, provides support for the executive functioning account of the late right frontal effect and highlights that the effect is not related to effort per se. There was not a large task switching requirement during the test phase therefore it was not surprising that the effect was not related to flexibility of thinking and responding. In line with the post retrieval monitoring account of the late right frontal effect, the relationship between the bilateral anterior frontal effect and working memory, strategy use and planning suggests that the effect is associated with holding retrieved information in working memory, monitoring whether or not the chosen retrieval strategy is being employed and planning ahead to what button will be pressed for the recollected information. The relationship between the effect and behavioural accuracy and reaction time indicates that monitoring retrieved information increases accuracy and decision times.

7.4.5 Right Prefrontal Effect

The right prefrontal effect was not related to short-term memory, flexibility of thinking and responding or strategy use, but was related to working memory, planning and behavioural accuracy and reaction time. In accordance with the bilateral anterior frontal effect, the fact that the effect did not correlate with short-term memory, but did correlate with some of the executive functions, provides support for the executive functioning account of the late right frontal effect and highlights that the effect is not simply related to effort. As already noted, there was not a large task switching requirement during the test phase therefore it was not surprising that the effect was not related to flexibility of thinking and responding. In line with the post retrieval monitoring account of the late right frontal effect, the relationship between the right prefrontal effect and working memory and planning suggests that the effect is associated with holding retrieved information in working memory, reflecting back to monitor the accuracy of the recollected information, and planning ahead to what button they will press for the recollected information. The relationship between the effect and behavioural accuracy and reaction time indicates that monitoring retrieved information increases accuracy and leads to longer decision times.

7.4.6 Right Frontal Effect

The right frontal effect was not related to short-term memory, flexibility of thinking and responding, strategy use or working memory, but was related to planning and behavioural accuracy and reaction time. In accordance with the bilateral anterior frontal and right prefrontal effects, the fact that the effect did not correlate with short-term memory, but did correlate with some of the executive functions, provides support for the executive functioning account of the late right frontal effect and highlights that the effect is not simply related to effort. As already noted, there was not a large task switching requirement during the test phase therefore it was not surprising that the effect was not related to flexibility of thinking and responding. There was no relationship between the right frontal effect and working memory, suggesting that the distribution is not associated with holding retrieved information in working memory and reflecting back on the accuracy of this information but instead is related to planning ahead to what they need to do on the next trial. The relationship between the effect and behavioural accuracy and reaction time indicates that planning ahead increases accuracy and decision times.

Chapter 8 Experiment 2a

8.1 Introduction

As people grow older, they often report that their memory is not as good as it used to be. Behavioural studies have indicated that older individuals have impoverished recollection, while their ability to recognise something as familiar remains relatively intact (e.g. see Jennings and Jacoby, 1997; Jacoby, 1999; Benjamin and Craik, 2001). Consequently, the elderly have more difficulty remembering the source or context in which an episode happened, than in remembering the episode itself (e.g. see McIntyre and Craik, 1987; Schacter et al., 1991; Spencer and Raz, 1995). In particular, older adults have greater impairment on memory for extrinsic context than for intrinsic context (e.g. see Spencer and Raz, 1995).

As discussed in the ERPs, Memory and Ageing chapter, ERP studies have shown that the neural correlates of episodic retrieval alter with age (e.g. see Friedman, 2000). With regards to the putative bilateral frontal correlate of familiarity, Wegesin et al. (2002) reported that an early bilateral frontal effect present in young adults had an equivalent magnitude, but a more right frontal distribution, in older adults. Furthermore, Morcom and Rugg (2004) reported early frontal effects (300-500ms) in younger and older adults that were more right sided for the elderly. The authors proposed that due to changes in brain morphology with ageing, this early right frontal effect may represent the older adults’ homologue of the bilateral frontal correlate of familiarity evident in younger adults, or it may reflect the age-related engagement of different cognitive processes. If the former is the case, these ERP results would be in accordance with the dual process theory view that familiarity based remembering remains relatively intact in the elderly.

Consistent with the dual process theory view that recollection diminishes with age, some source memory studies have demonstrated a severely reduced or absent left parietal correlate of recollection in older adults (Mark and Rugg, 1998; Li et al., 2004). In contrast, other source memory studies have reported age invariance with regards to the left parietal effect (Trott et al., 1997; Wegesin et al., 2002). Similarly, the putative right frontal correlate of post retrieval/executive processes has shown an age related reduction in some studies (Trott et al., 1997; Wegesin et al., 2002), while in others it appears equivalent in magnitude and topography across young and older adults (Mark and Rugg, 1998; Li et al., 2004). Taken together, these ERP results are ambiguous with regards to the effect of ageing on recollection and post retrieval/executive processes.

Together the behavioural and ERP results provide some evidence that, in comparison to young adults, the elderly rely more on familiarity and less on recollection during episodic memory retrieval. It follows, therefore, that the strategies that the young and old employ during retrieval are likely to be different. Evidence that the young and old adopt different retrieval strategies comes from a series of studies using the exclusion task. In these studies (Dywan et al., 1998; 2001; 2002), young and older adults distinguished between target (studied) words, new (unstudied) words and non-target lures (new words repeated at test); although target accuracy was equivalent in both age groups, the elderly made more false alarms to non-targets. In addition, young adults had greater left parietal ERP positivities to targets compared to non-targets, whereas the older participants' effects were greater for non-targets than targets. These results suggest that the young focussed more on the retrieval of target information, and were better able to inhibit the recall of non-relevant non-target information. In contrast, the elderly were more reactive to recently presented information, adopting a strategy of focussing more on the retrieval of non-targets.

This experimental chapter further investigates whether young and older adults use different retrieval strategies (as indexed by behaviour) and examines differences in the engagement of the three retrieval processes (bilateral frontal correlate of familiarity, left parietal correlate of recollection and late right frontal correlate of post retrieval processing) between age groups, to further reveal the retrieval strategies used. In particular, we investigate the effect of retrieving an extrinsic context on the retrieval strategies adopted by young and older adults. Pilot studies indicated that retrieving both intrinsic and extrinsic context was too demanding for the elderly participants, therefore an ageing comparison between contexts was not possible. Consequently, as the results of Experiment 1a indicated that the retrieval of extrinsic context reduces familiarity, young and older participants were required to retrieve the extrinsic context to encourage the elderly to use recollection as well as relying on familiarity.

In the current experiment, young and older participants' EEG was recorded while they studied a series of words spoken in a male or female voice (intrinsic context). In addition, they made an action or liking judgement about the word (extrinsic context). During the test phase, participants were only required to retrieve the extrinsic context and were instructed to discriminate between target, non-target and new items (targets were old items from one judgement; non-targets were old items from the other judgement). Because the young adults from Experiment 1a retrieved both contexts, a new group of young participants was recruited for this experiment, to ensure an equivalent comparison between young and old. The key prediction was that retrieval strategies would differ for younger and older participants (as indexed by behavioural performance) and this would be associated with variation in the accompanying ERP effects, thus further elucidating the retrieval strategies employed.

8.2 Methods

8.2.1 Participants

Twenty-eight young adults (different to those in Experiment 1a) and 32 older adults participated in the experiment. The data from 12 participants was discarded: 5 due to electrode drift and alpha activity (3 older, 2 younger), 5 due to excessive eye movement (3 older, 2 younger) and 2 older participants due to fatigue. Twenty-four participants remained in each group (younger: aged 18-30, mean age 20.33, 13 female; older: aged 64-77, mean age 69.80, 12 female). All other aspects of the methods are described in the ‘General Methods’ chapter.

8.2.2 Stimulus Materials and Procedure

The ‘General Methods’ chapter describes the stimulus materials and procedure, however, this experiment differs from that described in the following ways: Stimuli consisted of 204 low frequency nouns and verbs [compared to 408 in Experiment 1a]. Stimuli were used to form 1 practice study-test block (12 randomly selected words) and 4 experimental study-test blocks (48 words randomly allocated to each block for each participant), [compared to 2 practice blocks and 8 experimental blocks in Experiment 1a]. To form the 4 experimental blocks, the stimuli were randomly allocated into 3 sets of 64 words [compared to 3 sets of 128 words in Experiment 1a]. During the test phase, judgements based on task (extrinsic context) were performed for all 4 test blocks, participants were not required to retrieve the gender the word was spoken in (intrinsic context); [in Experiment 1a the extrinsic context was retrieved for 4 blocks and the intrinsic context was retrieved for 4 blocks]. All other aspects of the stimulus materials and procedure remained the same as in Experiment 1a.

8.3 Results

8.3.1 Neuropsychological Tests

As can be seen in Table 19 (below) the groups were matched on years of education, health ratings and performance on the WMS-R Logical Memory I and II. Although the older group had marginally significantly higher BDI scores, both groups' scores were within the normal range (0-10). The older participants also had higher IQ scores.

	Young	Older	p-value
Gender	11 male/13 female	12 male/12 female	
Age (years)	20.33 (2.68)	69.80 (3.84)	<0.001
Education (years)	14.46 (2.06)	14.92 (5.43)	n.s.
BDI	3.63 (3.28)	5.38 (2.92)	0.06
Health	4.08 (0.65)	4.08 (0.50)	n.s.
IQ (NART)	116.58 (3.65)	122.33 (3.63)	<0.001
WMS-R			
Logical Memory I	*40.04 (6.26)*	*39.13 (6.55)*	*n.s.*
Logical Memory II	*31.88 (6.38)*	*28.29 (6.79)*	*n.s.*

Table 19. Mean (SD) neuropsychological test results for Experiment 2a. Both groups were matched on years of education, health ratings and performance on the WMS-R Logical Memory I and II. The older group had higher IQ scores and marginally significantly higher BDI scores, however, both groups' BDI scores were within the normal range (0-10).

8.3.2 Behaviour

The behavioural data are reported in Table 20 (below). Accuracy was generally lower for older participants than younger participants, however there was little difference in accuracy for correct rejections across age groups. An ANOVA comparing the hit and correct rejection rates (see 'General Methods' chapter for the structure of this and the other behavioural data ANOVAs) revealed a main effect of response [$F(2,92) = 72.66$, $p < 0.001$], and age [$F(1,46) = 23.61$, $p < 0.001$] and a significant interaction between

	Younger	Older
Accuracy		
Hits/Target	0.71 (0.15)	0.58 (0.19)
Hits/Non-Target	0.87 (0.12)	0.67 (0.18)
Correct Rejection	0.98 (0.02)	0.94 (0.10)
Sensitivity (Pr)		
Target vs. Non-Target	0.58 (0.20)	0.25 (0.26)
Target vs. New	0.69 (0.15)	0.52 (0.21)
Bias (Br)		
Target vs. Non-Target	0.31 (0.19)	0.44 (0.18)
Target vs. New	0.06 (0.10)	0.13 (0.16)
PDP Estimates		
Familiarity	0.31 (0.23)	0.44 (0.18)
Recollection	0.58 (0.20)	0.25 (0.26)
RT(ms)		
Hits/Target	1440 (264)	1660 (269)
Hits/Non-Target	1520 (234)	1731 (240)
Correct Rejection	1174 (237)	1314 (241)

Table 20. Mean (SD) behavioural data for Experiment 2a. Accuracy was lower for the older participants for targets and non-targets, while there was no significant difference in accuracy for correct rejections across age groups. Older adults were less sensitive than younger adults, especially when discriminating targets and non-targets. Older adults adopted a more liberal bias than the young when discriminating targets from non-targets; there was no difference in bias between groups when discriminating targets and new items. The PDP revealed that recollection was greater for younger participants than older participants, whereas familiarity was higher for older adults than younger adults. Reaction times were slower for older participants than younger participants, and for non-targets followed by targets then new items.

the factors [F(2,92) = 4.67, p = 0.02]. Subsidiary t-tests revealed lower accuracy for the older participants for target responses [t(46) = 2.56, p = 0.01] and non-target responses [t(46) = 4.85, p < 0.001]. There was no significant difference in accuracy for correct rejections across age groups.

Table 20 shows that within each age group Pr was greater than zero suggesting that participants were able to discriminate targets from non-targets and new items. This was confirmed by paired t-tests, which revealed that, for both age groups, more target responses were made to targets than to non-targets and new items [Younger: target vs. non-target: $t(23) = 14.57$, $p < 0.001$, target vs. new: $t(23) = 22.64$, $p < 0.001$; Older: target vs. non-target: $t(23) = 4.77$, $p < 0.001$, target vs. new: $t(23) = 11.98$, $p < 0.001$].

Table 20 also shows that Pr was lower for the older participants than the younger participants, and that this age difference appeared larger for target compared to non-target than for target compared to new. An ANOVA comparing sensitivity (Pr) between age groups revealed main effects of response [$F(1,46) = 126.47$, $p < 0.001$] and age [$F(1,46) = 18.42$, $p < 0.001$] and an interaction between response and age [$F(1,46) = 21.82$, $p < 0.001$]. Subsidiary t-tests revealed lower sensitivity for the older participants for target compared to non-target [$t(46) = 5.03$, $p < 0.001$] and target compared to new [$t(46) = 3.06$, $p = 0.004$]; the age difference was larger, however, for target compared to non-target than target compared to new. This result suggests that the older adults were less sensitive than the younger adults, especially when discriminating targets and non-targets.

Bias (Br) was more liberal in the older group than the younger group when discriminating targets and non-targets, while there was little difference between groups when discriminating targets and new items (see Table 20). An ANOVA comparing bias between age groups revealed a main effect of response [$F(1,46) = 151.91$, $p < 0.001$] and an interaction between age and response [$F(1,46) = 5.32$, $p = 0.03$]. Subsidiary t-tests showed that older participants adopted a more liberal bias than younger participants when discriminating targets from non-targets. There was no significant difference in bias between groups when discriminating targets and new items.

Table 20 shows that the PDP estimated that the contribution of recollection was greater in the younger group than the older group, whereas the contribution of familiarity was greater in the older group than the younger group. An ANOVA comparing the estimates of familiarity and recollection revealed a main effect of age [$F(1,46) = 5.92$, $p = 0.02$] and a significant interaction between age and estimate [$F(1,46) = 22.03$, $p < 0.001$]. Subsidiary t-tests confirmed that recollection was greater for younger participants than older participants [$t(46) = 4.87$, $p < 0.001$], while familiarity was higher for older participants than younger participants [$t(46) = -2.10$, $p = 0.04$].

Reaction times were slower for older participants than younger participants, and for non-targets followed by targets then new items (see Table 20). An ANOVA comparing the reaction times revealed main effects of age [$F(1,46) = 10.06$, $p = 0.003$] and response [$F(2,92) = 82.86$, $p < 0.001$] but no interaction between the factors. The main effect of age confirmed slower reaction times for older than younger participants, while subsidiary t-tests (collapsed across age) investigating the main effect of response revealed that reaction times to non-targets were slower than targets [$t(47) = -2.11$, $p = 0.04$] and new items [$t(47) = 12.83$, $p < 0.001$]. In turn, reaction times to targets were slower than new items [$t(47) = 8.70$, $p < 0.001$].

8.3.2.1 Summary of Behavioural Data

Although both younger and older adults were able to perform the task (as indicated by Pr being significantly above zero), older adults were less sensitive than younger adults, especially when discriminating targets from non-targets, and their accuracy for targets and non-targets was significantly reduced compared to the young. The older adults' more liberal response bias when discriminating targets and non-targets reflected their higher false alarm rate for non-targets. The process dissociation procedure estimates revealed that older adults relied more on familiarity, whereas the younger adults relied more on recollection. This finding is consistent with dual process theory that older adults show an increased reliance on familiarity as recollection becomes impaired, and also corroborates Jennings and Jacoby (1993) PDP results, that compared with young adults, older adults depend less on recollection and more on familiarity. Finally, consistent with reduced speed of processing theory, older adults had longer reaction times than younger adults during retrieval. Together, these results suggest that how the elderly and young participants performed the task was different, indicating that they may have adopted different retrieval strategies.

8.3.3 Event-Related Potentials

8.3.3.1 Younger Participants

Figure 25 and Figure 26 show the grand average target, non-target and new waveforms for the extrinsic context condition, from 36 electrode sites in Figure 25 and a close up of 6 sites in Figure 26. The mean number of trials contributing to the waveforms was 37 target, 42 non-target and 48 new. The waveforms begin to diverge over parietal sites from approximately 250ms post-stimulus onset, with target and non-target waveforms becoming more positive than new waveforms. This divergence is greater for target compared to non-target waveforms and becomes maximal at left parietal sites as the epoch progresses; although the effect begins to decline at approximately 700ms, it continues until the end of the recording epoch. A bilateral old/new positivity is also evident over fronto-central sites from approximately 300ms post stimulus onset, which appears to be of equivalent magnitude for targets and non-targets. From about 900ms, a prominent old/new effect is a bilateral negativity over parieto-centro-occipital sites, which looks to be larger for non-targets compared to targets from approximately 1400ms. An old/new positivity is also present over right frontal sites from approximately 900ms. This effect appears to be larger for targets compared to non-targets at sites F2, F4, F6 and AF4. Finally, an old/new negativity is evident from about 1000ms at sites AF7, F7 and F5.

8.3.3.2 Older Participants

Figure 27 and Figure 28 show the grand average target, non-target and new waveforms for the extrinsic context, again from 36 electrode sites in Figure 27 and a close up of 6 sites in Figure 28. The mean number of trials contributing to the waveforms was 29 target, 33 non-target and 47 new. The waveforms begin to diverge over fronto-central sites from approximately 250ms post-stimulus onset, with target and non-target waveforms becoming more positive than new waveforms. This divergence exhibits a bilateral distribution, and is greater for target compared to non-target waveforms. The parietal component evident in the young group from approximately 250ms is also present for the older group, however it appears to be reduced in magnitude. This effect is maximal at left parietal sites (continuing until approximately 900ms compared to 2000ms for the young group) and is of greater magnitude for targets compared to non-targets. The waveforms exhibit a right frontal distribution sooner for the older group compared to the young group: target and non-target waveforms become more positive than new waveforms over right frontal sites from approximately 500ms (compared to 900ms for the young group) and there appears to be little difference in magnitude between targets and non-targets. From about 900ms, a prominent old/new effect is a bilateral negativity over parieto-centro-occipital sites, which looks to be larger for targets compared to non-targets from approximately 1000ms. Finally, the old/new

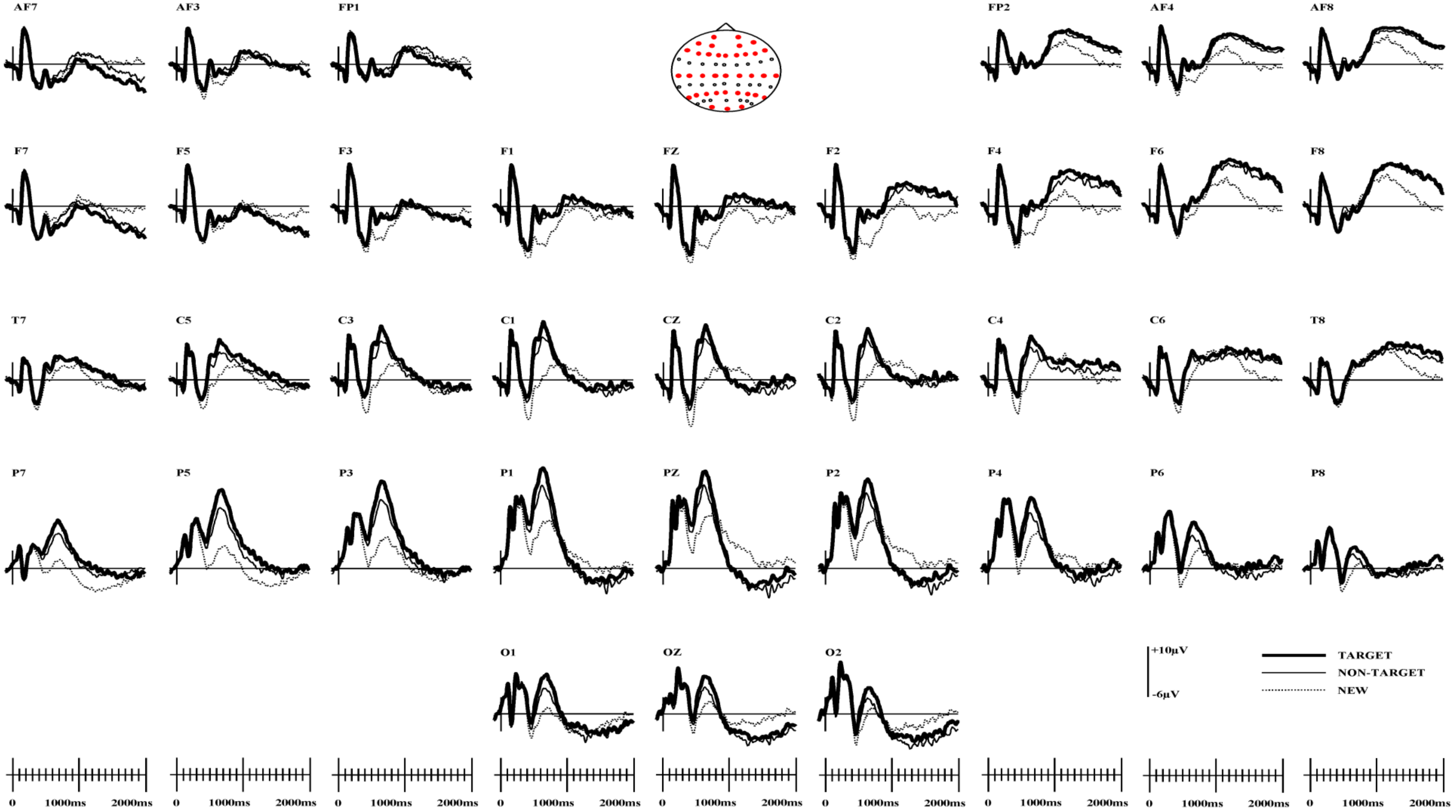

Figure 25. Grand average ERP waveforms for correctly classified target, non-target and new items for the young participants. 36 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16µV.

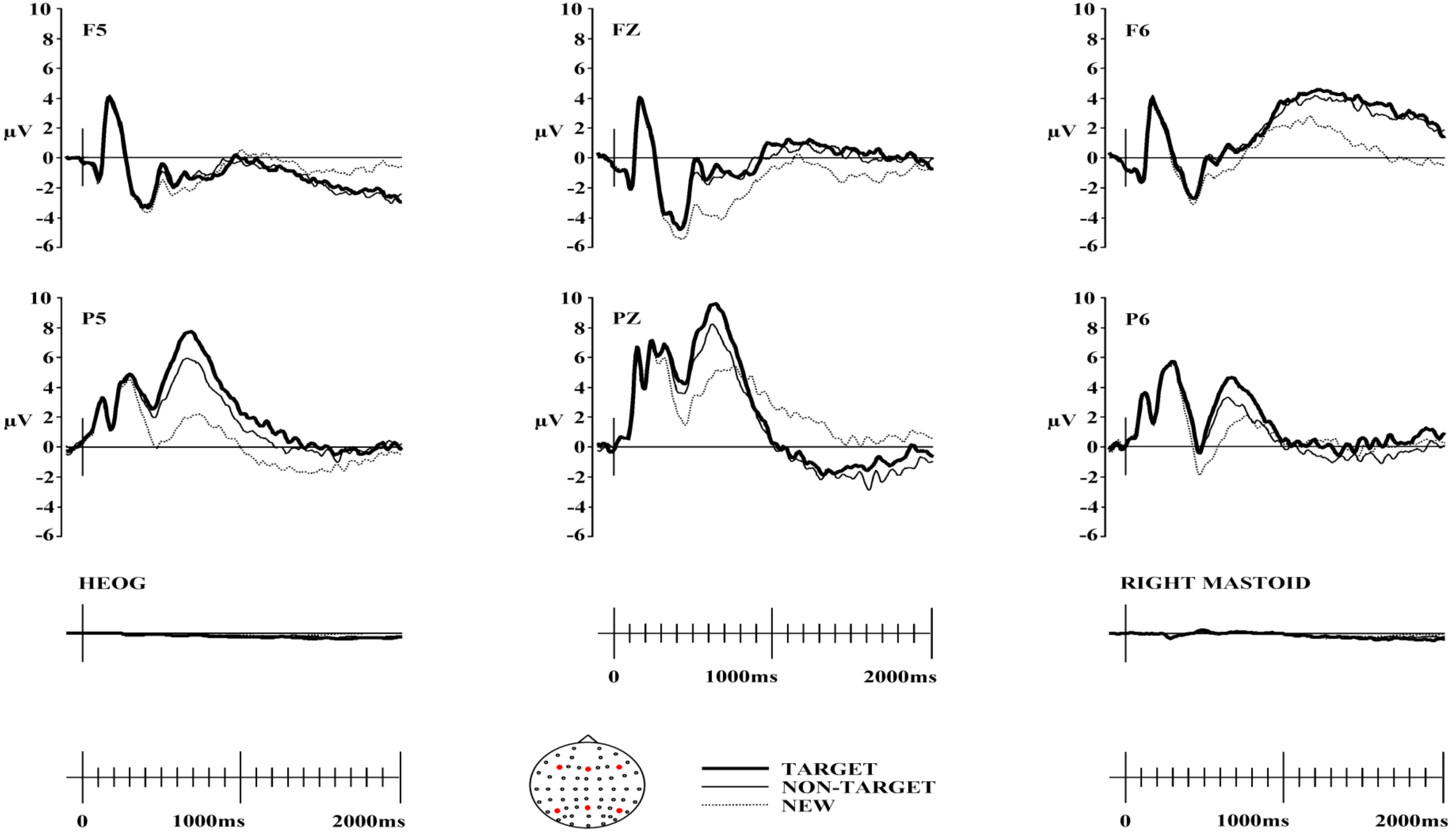

Figure 26. Grand average ERP waveforms for correctly classified target, non-target and new items for the young participants. A close up of 6 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16μV.

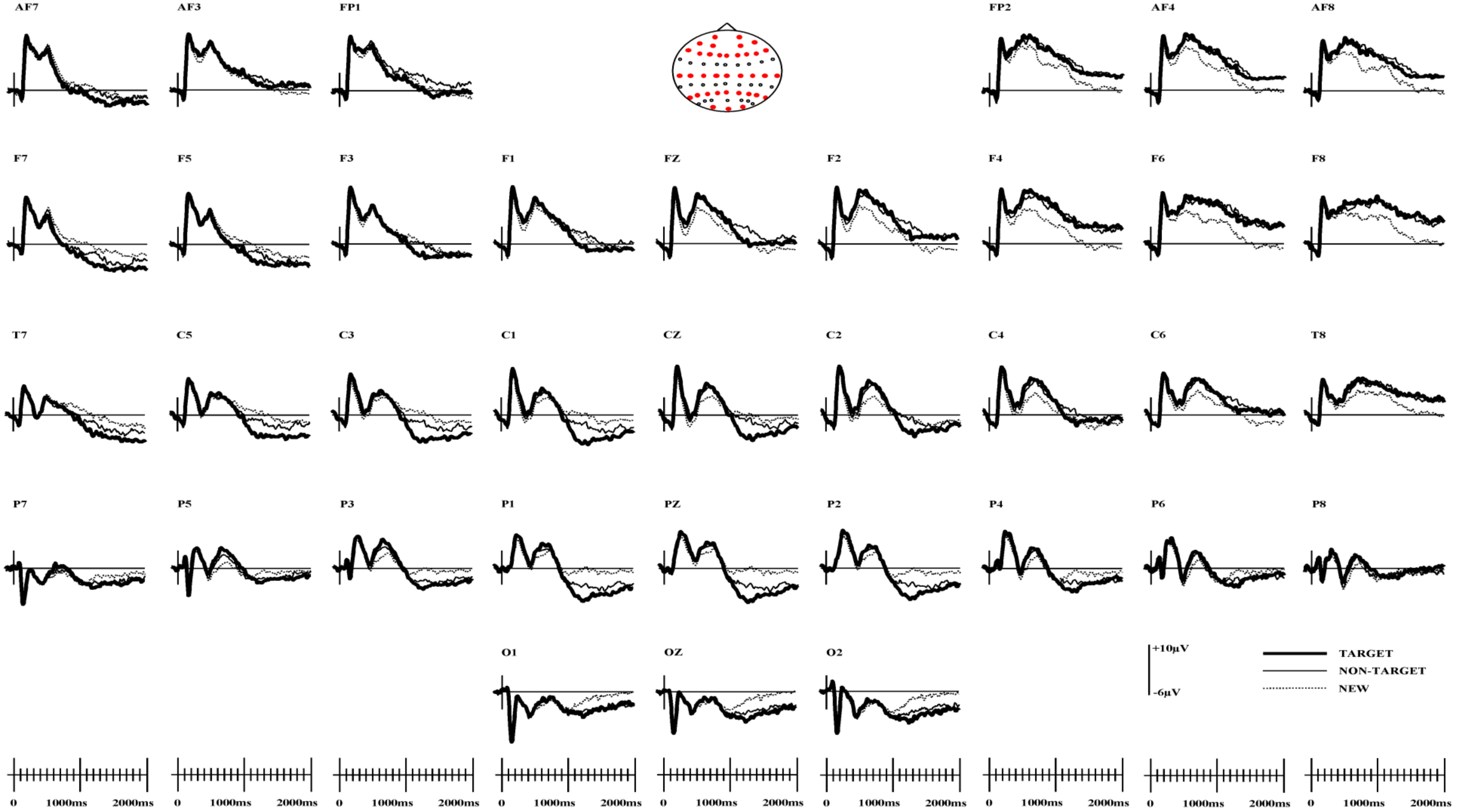

Figure 27. Grand average ERP waveforms for correctly classified target, non-target and new items for the older participants. 36 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16µV.

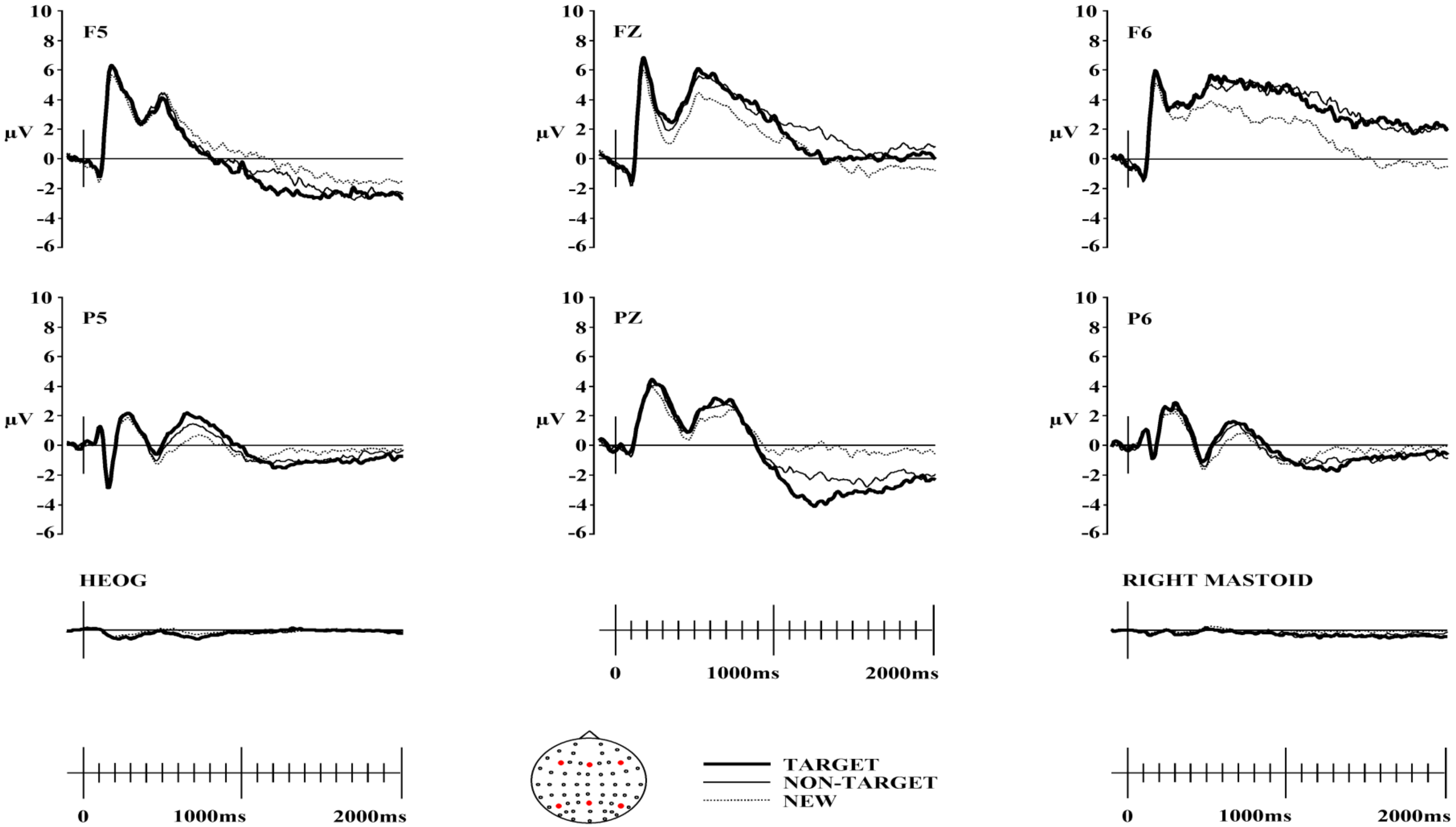

Figure 28. Grand average ERP waveforms for correctly classified target, non-target and new items for the older participants. A close up of 6 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16μV.

negativity evident in the young group from about 1000ms at sites AF7, F7 and F5 is also present for the older group, however the effect onsets earlier (approximately 600ms) and exhibits a more widespread left sided distribution, appearing greater for targets compared to non-targets.

8.3.3.3 Rationale for the ERP Analyses

The aim of the ERP analyses was to compare early bilateral frontal, left parietal and late right frontal old/new effects elicited by the retrieval of an extrinsic context for younger and older adults. Preliminary analyses (see ‘General methods’ chapter for details) showed that the following time windows best captured the evolution of the ERP effects over time for both age groups: 300-450ms, 450-900ms, 900-1300ms and 1300-2000ms. The distribution of the effects in these time windows are illustrated in the topographic maps shown in Figure 29 and Figure 30 (p216 and 217). Within-age magnitude and topographic ANOVAs were conducted to assess the presence of significant ERP modulations within each latency window, and any qualitative differences across latency windows, respectively. Due to the more widespread left sided negativity present for the older group, additional fronto-central magnitude and topographic ANOVAs were used to analyse this effect from 900-1300ms and 1300-2000ms: For the magnitude analyses, an initial global ANOVA employed factors of response (target vs. non-target vs. new), hemisphere (left vs. right) and site [inferior (FC5/FC6) vs. mid (FC3/FC4) vs. superior (FC1/FC2)]. For the topographic analyses, an initial global ANOVA included factors of epoch (latency period 3 vs. latency period 4), response (target minus new vs. non-target minus new), hemisphere (left vs. right) and site [inferior (FC5/FC6) vs. mid (FC3/FC4) vs. superior (FC1/FC2)]. The fronto-central global ANOVAs were followed up in the same way as the main global ANOVAs (see ‘General Methods’ chapter).

In addition, between-age magnitude and topographic ANOVAs were conducted to examine quantitative and qualitative differences between the ERP correlates of younger and older adults within each latency window. Again, between-age magnitude and topographic fronto-central ANOVAs were conducted, including the factor of age (younger vs. older). The magnitude analyses employed the factors of: age (younger vs. older), response (target minus new vs. non-target minus new vs. target minus non-target), hemisphere (left vs. right) and site [inferior (FC5/FC6) vs. mid (FC3/FC4) vs. superior (FC1/FC2)]. The topographic analyses included the same factors as the magnitude analyses without the response level target minus non-target. The fronto-central global ANOVAs were followed up in the same way as the main global ANOVAs (see 'General Methods' chapter).

8.3.3.4 Within Age Magnitude Analyses

8.3.3.4.1 Younger Participants

The global magnitude analyses revealed main effects and/or interactions involving the factor of response for all four latency windows (see Table 21 below). The highest order ANOVA result from 300-450ms was a two-way response by site interaction, and from 450-900ms, 900-1300ms and 1300-2000ms the highest order results were four-way response by location by hemisphere by site interactions. The highest order interaction in the additional fronto-central analyses from 1300-2000ms was a three-way response by hemisphere by site interaction. These results were further examined with subsidiary analyses investigating all possible paired comparisons (target vs. new; non-target vs. new; target vs. non-target).

Latency Window	Target vs. Non-Target vs. New
300-450ms	
R	F(1.86,42.86)=6.01,p=0.006
RxS	F(1.98,45.46)=6.93,p=0.002
450-900ms	
R	F(1.98,45.43)=12.18,p<0.001
RxL	F(1.75,40.33)=3.70,p=0.04
RxH	F(1.99,45.70)=4.26,p=0.02
RxS	F(2.11,48.46)=5.07,p=0.009
RxLxH	F(1.71,39.42)=28.14,p<0.001
RxLxS	F(2.25,51.84)=21.31,p<0.001
RxLxHxS	F(3.00,69.06)=15.84,p<0.001
900-1300ms	
RxL	F(1.99,45.81)=2.85,p=0.07
RxS	F(2.01,46.30)=8.69,p=0.001
RxLxH	F(1.99,45.69)=35.05,p<0.001
RxLxS	F(2.03,46.67)=36.78,p<0.001
RxLxHxS	F(2.94,67.58)=14.05,p<0.001
Additional fronto-central analyses	*No significant results*
1300-2000ms	
RxL	F(1.98,45.48)=3.74,p=0.03
RxH	F(1.60,36.74)=8.06,p=0.002
RxS	F(2.17,49.89)=5.72,p=0.005
RxLxH	F(1.96,45.16)=55.38,p<0.001
RxLxS	F(2.46,56.61)=20.35,p<0.001
RxHxS	F(3.22,74.02)=10.39,p<0.001
RxLxHxS	F(3.12,71.73)=17.57,p<0.001
Additional fronto-central analyses	
RxHxS	*F(2.78,63.92)=15.33,p<0.001*

Table 21. Results of the within age global magnitude analyses for the young group. R, L, H and S represent the factors of response, location, hemisphere and site respectively. Main effects and/or interactions involving the factor of response were present for all four latency windows.

Target vs. New: Subsidiary analyses investigating the global response by site interaction in the 300-450ms time window (Table 21) also gave rise to a response by site interaction [F(1.20,27.67) = 17.88, p < 0.001], indicating that while target waveforms were more positive than new waveforms at all sites [superior – t(23) = 3.26, p = 0.003; mid – t(23) = 2.94, p = 0.007; inferior – t(23) = 2.35, p = 0.03], the difference was greater at the superior site [superior site = Mean 1.29μV; mid site = Mean 1.01μV; inferior site = Mean 0.72μV]. Although the results do not reveal a significant interaction with location, inspection of the topography during this time window (Figure 29, A) shows an effect that appears maximal at the parietal location. Consequently, targeted t–tests were used to examine data from parietal sites, revealing significant differences at all sites [P1 – t(23) = 3.85, p = 0.001; P3 – t(23) = 3.61, p = 0.001; P5 – t(23) = 3.61, p = 0.0001; P2 – t(23) = 3.16, p = 0.004; P4 – t(23) = 2.54, p = 0.02; P6 – t(23) = 2.15, p = 0.04]. Importantly, targeted t-tests of data from frontal sites revealed no significant differences at any site; therefore, despite the impression given in Figure 29 (A) there was no statistically significant bilateral frontal effect in the target versus new contrast.

By 450-900ms old/new effects were present at the frontal location. Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 21) also revealed a response by location by hemisphere by site interaction in the target versus new contrast [F(1.81,41.73) = 18.14, p < 0.001]. This interaction reflected the left parietal effect and possible early bilateral onset of the late right frontal effect (Figure 29, B): significant target greater than new differences were present at frontal superior [t(23) = 3.98, p = 0.001] and mid sites [t(23) = 3.71, p = 0.001], and at all left parietal sites [superior – t(23) = 4.31, p < 0.001; mid – t(23) = 6.57, p < 0.001; inferior – t(23) = 7.73, p < 0.001], this difference was greatest, however, at mid and inferior sites [superior site = Mean 3.08μV; mid site = Mean 4.09μV; inferior site = Mean 4.21μV]. A main effect of response at the posterior right hemisphere [F(1,23) = 8.93, p = 0.007] probably reflected spread of the left parietal effect.

The late right frontal effect, continuation of the left parietal effect and presence of the late posterior negativity were evident from 900-1300ms (Figure 29, C). Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 21) also revealed a response by location by hemisphere by site interaction in the target versus new contrast [F(1.68,38.62) = 17.98, $p < 0.001$]: analysis at the posterior location revealed a significant negativity at the right hemisphere superior site and a positivity at the left hemisphere mid and inferior sites [superior – t(23) = -3.07, p = 0.005; mid – t(23) = 1.94, p = 0.07; inferior – t(23) = 3.76, p = 0.001]. Meanwhile, analysis at the frontal location revealed a significant difference at the right hemisphere only [t(23) = 2.48, p = 0.02]. Despite the appearance of a weak anterior left hemisphere negativity (Figure 29, C), this was not statistically significant in the main or additional analyses.

By 1300-2000ms the anterior left hemisphere negativity was statistically significant. Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 21) also produced a response by location by hemisphere by site interaction in the target versus new contrast [F(1.79,41.24) = 20.90, $p < 0.001$]. This interaction reflected a left frontal negativity (Figure 29, D) at the inferior site [t(23) = -2.65, p = 0.01], and a right frontal effect at all sites [superior – t(23) = 2.52, p = 0.02; mid – t(23) = 3.62, p = 0.001; inferior – t(23) = 4.34, $p < 0.001$], maximal at the inferior site [superior site = Mean 1.95μV; mid site = Mean 2.64μV; inferior site = Mean 2.94μV]. The left parietal effect was no longer robust, but the late posterior negativity was statistically significant at the posterior superior site [t(23) = -2.32, p = 0.03]. Subsidiary analyses investigating the response by hemisphere by site interaction in the global fronto-central ANOVA also revealed a response by hemisphere by site interaction [F(1.74,40.08) = 29.38, $p < 0.001$], reflecting spread of the late right frontal effect to right fronto-central mid and inferior sites [mid – t(23) = 2.14, p = 0.04; inferior

– t(23) = 3.70, p = 0.001]. The left frontal negativity was not statistically significant at fronto-central sites.

Non-Target vs. New: Subsidiary analyses investigating the response by site interaction in the global ANOVA between 300 and 450ms (Table 21) also revealed a response by site interaction [F(1.13,26.08) = 8.39, p = 0.006]. This interaction reflected a non-target greater than new difference at all sites [superior – t(23) = 3.24, p = 0.003; mid – t(23) = 2.96, p = 0.007; inferior – t(23) = 2.30, p = 0.03], but the difference was larger at the superior site [superior site = Mean 1.26μV; mid site = Mean 1.01μV; inferior site = Mean 0.73μV]. In keeping with the target versus new contrast, the results do not reveal a significant interaction with location; however, inspection of the topography during this time window (Figure 29, E) also shows an effect that appears maximal at the parietal location. Consequently, targeted t–tests were used to examine data from parietal sites, revealing significant differences at all sites [P1 – t(23) = 3.82, p = 0.001; P3 – t(23) = 3.81, p = 0.001; P5 – t(23) = 3.20, p = 0.004; P2 – t(23) = 2.37, p = 0.03; P4 – t(23) = 2.01, p = 0.05; P6 – t(23) = 1.86, p = 0.07]. Importantly, targeted t-tests of data from frontal sites revealed no significant differences at any site; therefore, despite the impression given in Figure 29 (E) there was no statistically significant bilateral frontal effect in the non-target versus new comparison.

By 450-900ms old/new effects were present at the frontal location. Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 21) also revealed a response by location by hemisphere by site interaction in the non-target versus new contrast [F(1.99,45.83) = 21.67, p < 0.001]. This interaction reflected the left parietal effect and possible early bilateral onset of the late right frontal effect (Figure 29, F): significant non-target greater than new differences were present at left frontal superior [t(23) = 3.50, p = 0.002] and mid sites [t(23) = 2.66, p = 0.01], and at all right frontal sites [superior – t(23) = 3.81, p = 0.001; mid – t(23) = 3.55, p = 0.002; inferior – t(23) = 2.97, p = 0.007]; non-targets were greater than new items at all left parietal sites [superior – t(23) = 3.05, p = 0.006; mid – t(23) = 5.60, p < 0.001; inferior – t(23) = 6.64, p < 0.001], this difference was greatest, however, at mid and inferior sites [superior site = Mean 1.71μV; mid site = Mean 2.64μV; inferior site = Mean 2.75μV]. There were no significant differences at the posterior right hemisphere.

The late right frontal effect, continuation of the left parietal effect and presence of the late posterior negativity were evident from 900-1300ms (Figure 29, G). Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 21) also revealed a response by location by hemisphere by site interaction in the non-target versus new contrast [F(1.80,41.32) = 18.30, p < 0.001]: analysis at the posterior location revealed a significant negativity at the right hemisphere superior and mid sites [superior – t(23) = -4.48, p < 0.001; mid – t(23) = -3.40, p = 0.002], and at the left hemisphere superior site [t(23) = -3.23, p = 0.004]. A positivity was also present at the posterior left hemisphere inferior site [inferior – t(23) = 3.79, p = 0.001]. Meanwhile, analysis at the frontal location revealed a significant difference at the right hemisphere only [t(23) = 2.82, p = 0.01]. Despite the appearance of a weak anterior left hemisphere negativity (Figure 29, G), this was not statistically significant in the main or additional analyses.

By 1300-2000ms the anterior left hemisphere negativity was statistically significant. Subsidiary analyses investigating the global response by location by hemisphere by site interaction from 1300-2000ms (Table 21) also produced a response by location by hemisphere by site [F(1.84,42.27) = 27.63, p < 0.001] interaction in the non-target versus new contrast. This interaction reflected a left frontal negativity (Figure 29, H) at the inferior site [t(23) = -2.90, p = 0.008], and a right frontal effect at all sites [superior

– t(23) = 3.12, p = 0.005; mid – t(23) = 4.36, p < 0.001; inferior – t(23) = 5.89, p < 0.001], maximal at the inferior site [superior site = Mean 1.80μV; mid site = Mean 2.20μV; inferior site = Mean 2.73μV]. The left parietal effect was no longer robust, but the late posterior negativity was statistically significant at the posterior left hemisphere superior site [t(23) = -3.22, p = 0.004], and at the posterior right hemisphere superior and mid sites [superior – t(23) = -3.98, p = 0.001; mid – t(23) = -2.79, p = 0.01]. Subsidiary analyses investigating the response by hemisphere by site interaction in the global fronto-central ANOVA also revealed a response by hemisphere by site interaction [F(1.61,36.97) = 18.79, p < 0.001], reflecting spread of the late right frontal effect to central mid and inferior sites [mid – t(23) = 2.85, p = 0.009; inferior – t(23) = 5.71, p < 0.001]. Consistent with the target versus new contrast, the left frontal negativity was not statistically significant at fronto-central sites.

Target vs. Non-Target: Subsidiary analyses investigating the global response by site interaction in the 300-450ms time window (Table 21) did not reveal any significant results, suggesting that there were no magnitude differences between targets and non-targets during this time window (Figure 29, A and E). Subsidiary analyses investigating the global response by location by hemisphere by site interaction between 450 and 900ms revealed a response by location interaction [F(1,23) = 4.58, p = 0.04]. This interaction reflected a target greater than non-target difference at the posterior location [t(23) = 2.12, p = 0.05], indicating the widespread difference between targets and non-targets at parietal sites (Figure 29, B and F). As the old/new contrasts showed significant left parietal effects, targeted t tests of this region were conducted, showing that the left parietal effect was greater for targets than non-targets at all left parietal sites [superior – t(23) = 2.22, p = 0.04; mid – t(23) = 2.69, p = 0.01; inferior – t(23) = 2.92, p = 0.008]. There were no significant differences at the posterior right hemisphere.

The late right frontal effect, late posterior negativity and anterior left hemisphere negativity did not differ for targets and non-targets: subsidiary analyses investigating the global response by location by hemisphere by site interactions from 900-1300ms and 1300-2000ms (Table 21) did not produce significant results involving the factor of response. In addition, no significant results including the factor of response were present in the subsidiary analyses investigating the response by hemisphere by site interaction in the global fronto-central ANOVA from 1300-2000ms (Figure 29, C,D,G and H).

8.3.3.4.2 Older Participants

The global magnitude analyses revealed main effects and/or interactions involving the factor of response for all four latency windows (see Table 22 below). The highest order ANOVA result from 300-450ms was a three-way response by location by site interaction, and from 450-900ms, 900-1300ms and 1300-2000ms the highest order results were four-way response by location by hemisphere by site interactions. The highest order interactions in the additional fronto-central analyses from 900-1300ms and 1300-2000ms were three-way response by hemisphere by site interactions. As for the younger participants, these results were further examined with subsidiary analyses investigating all possible paired comparisons (target vs. new; non-target vs. new; target vs. non-target).

Latency Window	Target vs. Non-Target vs. New
300-450ms	
R	F(1.95,44.78)=4.80,p=0.01
RxS	F(2.40,55.08)=5.02,p=0.007
RxLxS	F(2.74,63.08)=3.87,p=0.02
450-900ms	
R	F(1.95,44.91)=4.31,p=0.02
RxH	F(1.41,32.49)=9.80,p=0.001
RxLxH	F(1.80,41.41)=20.61,p<0.001
RxLxS	F(2.80,64.46)=8.40,p<0.001
Rx	F(2.10,48.24)=4.13,p=0.02
RxLxHxS	F(2.59,59.52)=9.63,p<0.001
900-1300ms	
RxL	F(1.98,45.61)=6.76,p=0.003
RxH	F(1.53,35.25)=12.37,p<0.001
RxS	F(2.45,56.45)=4.18,p=0.01
RxLxH	F(1.73,39.77)=13.60,p<0.001
RxLxS	F(2.97,68.35)=13.76,p<0.001
RxHxS	F(2.13,49.07)=4.68,p=0.01
RxLxHxS	F(2.94,67.72)=7.13,p<0.001
Additional fronto-central analyses	
RxH	*F(1.24,28.48)=10.94,p=0.001*
RxHxS	*F(2.86,65.76)=6.75,p=0.001*
1300-2000ms	
RxL	F(1.95,44.94)=10.35,p<0.001
RxH	F(1.33,30.60)=11.05,p=0.001
RxS	F(2.60,59.77)=4.42,p=0.01
RxLxH	F(1.57,36.05)=10.77,p=0.001
RxLxS	F(2.54,58.31)=4.86,p=0.007
RxHxS	F(2.02,46.51)=3.57,p=0.04
RxLxHxS	F(2.36,54.23)=5.56,p=0.004
Additional fronto- central analyses	
RxH	*F(1.24,28.50)=10.39,p=0.002*
RxHxS	*F(2.76,63.46)=9.53,p<0.001*

Table 22. Results of the within age global magnitude analyses for the older participants. R, L, H and S represent the factors of response, location, hemisphere and site respectively. Main effects and/or interactions involving the factor of response were present for all four latency windows.

Target vs. New: Subsidiary analyses investigating the global response by location by site interaction in the 300-450ms time window (Table 22) also gave rise to a response by location by site interaction [F(1.50,34.45) = 8.54, p = 0.002]. This result indicated that target waveforms were more positive than new waveforms at anterior superior and mid sites [superior – t(23) = 3.25, p = 0.004; mid – t(23) = 2.61, p = 0.02]. There were no significant differences at posterior sites. This result is consistent with the presence of a bilateral frontal effect during this time window (Figure 30, A).

The greater positivity of target waveforms compared to new waveforms continued into the 450-900ms time window (Figure 30, B). Subsidiary analysis investigating the global response by location by hemisphere by site interaction (Table 22) also revealed a response by location by hemisphere by site interaction [F(1.56,35.87) = 11.70, p < 0.001] in the target versus new contrast. This interaction reflected the presence of a left parietal effect: target waveforms were more positive than new waveforms at left and right parietal mid and inferior sites [left parietal mid – t(23) = 2.62, p = 0.02; left parietal inferior – t(23) = 3.61, p = 0.001; right parietal mid – t(23) = 2.50, p = 0.02; right parietal inferior – t(23) = 2.36, p = 0.03]. The target greater than new difference was larger, however, at left parietal sites [left parietal mid site = Mean 0.83μV; left parietal inferior site = Mean 1.07μV; right parietal mid site = Mean 0.81μV; right parietal inferior site = Mean 0.74μV]. Meanwhile, analyses at the frontal location indicated the presence of the late right frontal effect [t(23) = 4.14, p < 0.001]. Despite the appearance of a left frontal negativity (Figure 30, B), this was not statistically significant.

Subsidiary analyses investigating the global response by location by hemisphere by site interaction from 900-1300ms (Table 22) also produced a response by location by hemisphere by site interaction [F(1.48,34.07) = 8.11, p = 0.003]. In addition, subsidiary analyses investigating the global response by hemisphere by site interaction in the fronto-central ANOVA also revealed a response by hemisphere by site interaction

[F(1.71,39.34) = 8.93, p = 0.001]. These interactions demonstrated the left sided negativity and continuation of the late right frontal effect (Figure 30, C): the left sided negativity was significant at left frontal mid and inferior sites [mid – t(23) = -2.07, p = 0.05; inferior – t(23) = -2.37, p = 0.03], and extended to all left fronto-central sites [superior – t(23) = -2.23, p = 0.04; mid – t(23) = -3.13, p = 0.005; inferior – t(23) = -5.55, p < 0.001]; whereas the late right frontal effect was significant at all right frontal sites as indicated by a main effect of response [F(1,23) = 9.40, p = 0.005], and extended to the right fronto-central inferior site [t(23) = 2.03, p = 0.07]. The left sided negativity was not statistically significant at frontal or fronto-central sites during this time window in the younger participants. Finally, the late posterior negativity was significant at posterior superior and mid sites [superior – t(23) = -4.20, p < 0.001; mid – t(23) = -2.66, p = 0.01].

The late right frontal effect, late posterior negativity and left sided negativity continued throughout the 1300-2000ms epoch (Figure 30, D). Subsidiary analyses investigating the global response by location by hemisphere by site interaction (Table 22) also produced a response by location by hemisphere by site interaction [F(1.47,33.70) = 3.77, p = 0.05] in the target vs. new contrast. In addition, subsidiary analyses investigating the global response by hemisphere by site interaction in the fronto-central ANOVA also revealed a response by hemisphere by site interaction [F(1.62,37.29) = 13.16, p < 0.001]. As in the previous time window, these interactions reflected the left sided negativity and continuation of the late right frontal effect (Figure 30, D): the left sided negativity was no longer significant at left frontal sites, but was at left fronto-central mid and inferior sites [mid – t(23) = -2.13, p = 0.04; inferior – t(23) = -3.95, p = 0.001]; in contrast, the late right frontal effect was significant at all right frontal sites [superior – t(23) = 2.90, p = 0.008; mid – t(23) = 4.52, p < 0.001; inferior – t(23) = 3.67, p = 0.001], greatest at mid and inferior sites [superior site = Mean 1.42μV; mid site = Mean 2.37μV; inferior site = Mean 2.55μV], and extended to the right central inferior site [t(23) = 2.81, p = 0.01]. There was a significant negativity at left frontal sites, but not at left fronto-central sites, during this time window in the younger participants, therefore the effect was more widespread in the older participants. The late posterior negativity was significant at all sites [superior – t(23) = -5.66, p < 0.001; mid – t(23) = -4.23, p < 0.001; inferior – t(23) = -2.87, p = 0.009], maximal at the superior site [superior site = Mean -2.24μV; mid site = Mean -1.35μV; inferior site = Mean -0.53μV].

Non-Target vs. New: Subsidiary analyses investigating the global response by location by site interaction in the 300-450ms time window (Table 22) produced a main effect of response [F(1,23) = 4.42, p = 0.05], indicating that non-target waveforms were generally more positive than new waveforms. Inspection of the topography during this time window (Figure 30, E), however, shows an effect that appears maximal at frontal electrodes. Consequently, targeted t tests of data from frontal and parietal sites were conducted, revealing significant differences at frontal superior and mid sites [superior – t(23) = 2.49, p = 0.02; mid – t(23) = 2.14, p = 0.04]. There were no significant differences at posterior electrodes. As in the target versus new contrast, this result is consistent with the presence of a bilateral frontal effect during this time window.

The greater positivity of non-target waveforms compared to new waveforms continued into the 450-900ms epoch (Figure 30, F). Subsidiary analysis investigating the global response by location by hemisphere by site interaction (Table 22) also revealed a response by location by hemisphere by site interaction [F(1.36,31.25) = 6.81, p = 0.008] in the non-target versus new contrast. This interaction reflected the presence of the left parietal effect: non-target waveforms were more positive than new waveforms at the left parietal inferior site [t(23) = 2.64, p = 0.02]. Meanwhile, analyses at the frontal location indicated the presence of the late right frontal effect [t(23) = 4.11, p < 0.001]. Despite the presence of a weak left frontal negativity (Figure 30, F), this was not statistically significant.

Subsidiary analyses investigating the global response by location by hemisphere by site interaction from 900-1300ms (Table 22) produced response by location by hemisphere [F(1,23) = 17.36, p < 0.001] and response by location by site [F(1.33,30.67) = 19.16, p < 0.001] interactions in the non-target vs. new contrast. Furthermore, subsidiary analyses investigating the global response by hemisphere by site interaction in the fronto-central ANOVA gave rise to a response by hemisphere interaction [F(1,23) = 44.88, p < 0.001]. The response by location by hemisphere interaction in the main analyses and the response by hemisphere interaction in the additional analyses reflected the continuation of the late right frontal effect at right frontal sites (Figure 30, G), and extending to right fronto-central sites [main analyses: t(23) = 3.81, p = 0.001; additional analyses: t(23) = 2.74, p = 0.01]. The response by location by site interaction in the main analyses indicated the presence of the late posterior negativity at the posterior superior site [t(23) = -2.29, p = 0.03]. In contrast to the target versus new comparison, the left sided negativity was not statistically significant at left frontal or left central sites.

The late right frontal effect and late posterior negativity continued throughout the 1300-2000ms time window (Figure 30, H). Subsidiary analyses investigating the global response by location by hemisphere by site interaction between 1300 and 2000ms (Table 22) also produced a response by location by hemisphere by site interaction [F(1.79,41.20) = 19.49, p < 0.001] in the non-target vs. new contrast. Also, subsidiary analyses investigating the response by hemisphere by site interaction in the global fronto-central ANOVA gave rise to a response by hemisphere by site interaction

[F(1.39,32.03) = 12.01, $p = 0.001$]. These interactions represented the late right frontal effect, which was significant at all right frontal sites [superior – t(23) = 2.77, $p = 0.01$; mid – t(23) = 3.73, $p = 0.001$; inferior – t(23) = 3.87, $p = 0.001$], greatest at mid and inferior sites [superior site = Mean 1.70μV; mid site = Mean 2.11μV; inferior site = Mean 2.52μV], and extended to right fronto-central mid and inferior sites [mid – t(23) = 2.31, $p = 0.03$; inferior – t(23) = 4.12, $p < 0.001$]. Moreover, subsidiary analyses investigating the global response by location by hemisphere by site interaction in the main analyses showed that the late posterior negativity was significant at superior and mid sites [superior – t(23) = -3.53, $p = 0.002$; mid – t(23) = -2.70, $p = 0.01$]. Again, in contrast to the target versus new comparison, the left sided negativity was not statistically significant at left frontal or left fronto-central sites.

Target vs. Non-Target: Subsidiary analyses investigating the global response by location by site interaction in the 300-450ms time window, and the response by location by hemisphere by site interaction in the 450-900ms and 1300-2000ms time windows (Table 22) did not reveal any significant results involving the factor of response. This finding suggests that the bilateral frontal effect, left parietal effect, late right frontal effect and late posterior negativity from 1300-2000ms did not differ between targets and non-targets. The late posterior negativity, however, was greater for targets compared to non-targets from 900-1300ms (Figure 30, C and G): subsidiary analyses investigating the global response by location by hemisphere by site interaction from 900-1300ms produced a marginally significant response by site interaction [F(1.37,31.48) = 3.10, $p = 0.07$], which reflected target greater than non-target differences at superior sites. However, targeted t-tests of anterior and posterior sites revealed marginally significant differences at the posterior superior site only [t(23) = -1.89, $p = 0.07$].

Subsidiary analyses investigating the global response by hemisphere by site interaction in the additional fronto-central ANOVA from 900-1300ms and 1300-2000ms revealed main effects of response [900-1300ms: F(1,23) = 5.51, p = 0.03; 1300-2000ms: F(1,23) = 3.75, p = 0.07] indicating general target/non-target differences at fronto-central sites. As the old/new contrasts showed a significant left sided negativity, targeted t tests of this region were conducted, showing that the left sided negativity was greater for targets than non-targets at all left fronto-central sites [900-1300ms: superior – t(23) = -2.79, p = 0.01; mid – t(23) = -2.62, p = 0.02; inferior – t(23) = -2.80, p = 0.01; 1300-2000ms: superior – t(23) = -2.31, p = 0.03; mid – t(23) = -2.34, p = 0.03; inferior – t(23) = -2.88, p = 0.009]. There were no significant differences at right fronto-central sites.

8.3.3.4.3 Within Age Topographic Analyses

Figure 29 and Figure 30 illustrate the change in distribution of the old/new effects over time. Figure 29 shows the extrinsic context condition for the younger participants; there is a change in distribution over successive latency periods from a parietal effect to a left parietal effect, followed by a right frontal effect, late posterior negativity and finally a left frontal negativity. Figure 30 shows the extrinsic context condition for the older participants; there is a change in distribution over successive latency periods from a bilateral frontal effect to a left parietal effect and a right frontal effect, followed by a late posterior negativity and a left sided negativity. The change over time is similar for targets and non-targets for both age groups.

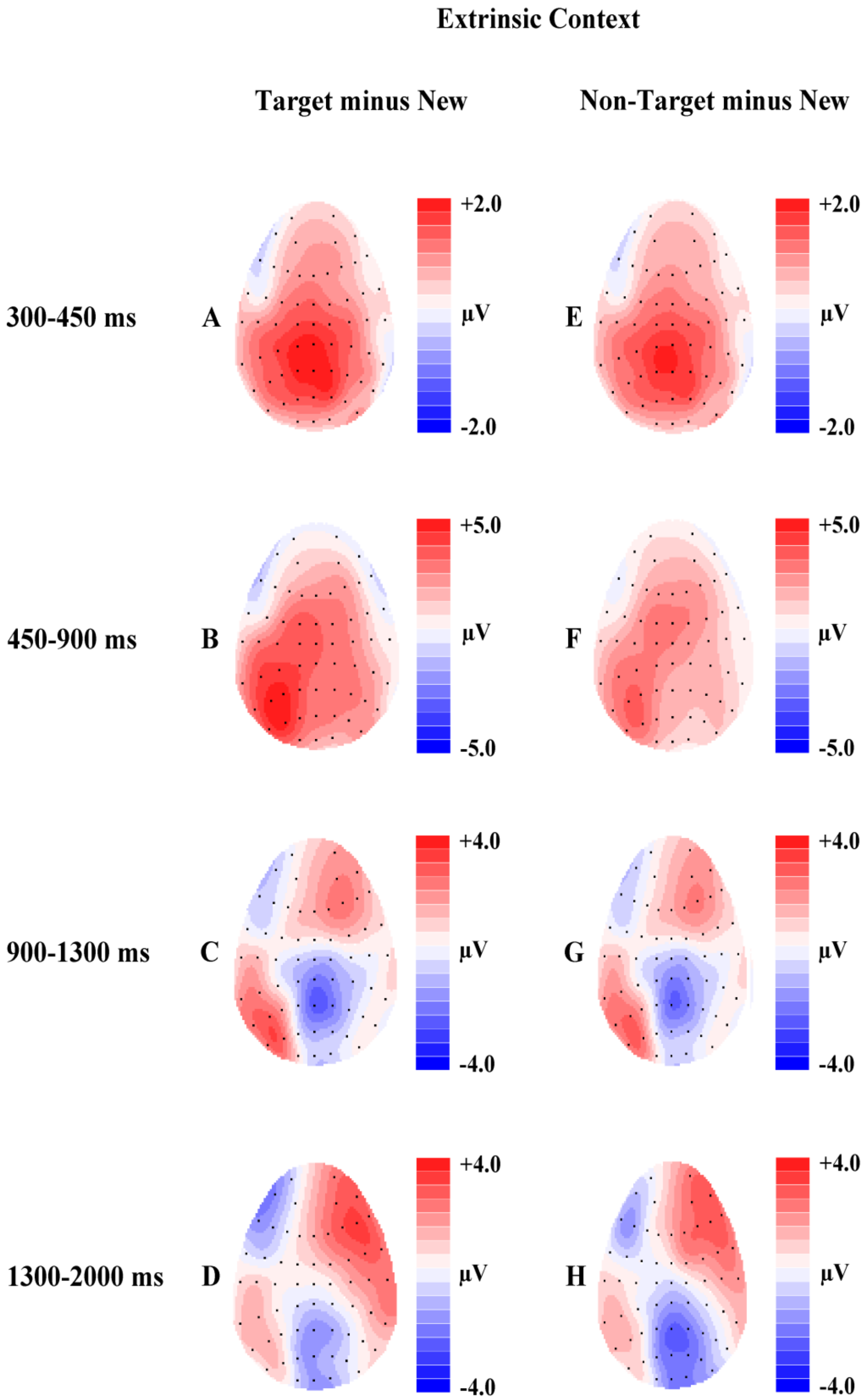

Figure 29. Topographic maps illustrating the scalp distribution of ERP effects for the younger participants. Each map is shown as if looking down onto the top of the head with frontal sites towards the top of the page. There is a change in distribution over successive latency periods from a parietal effect to a left parietal effect followed by a right frontal effect, late posterior negativity and finally a left frontal negativity. The change over time is similar for targets and non-targets.

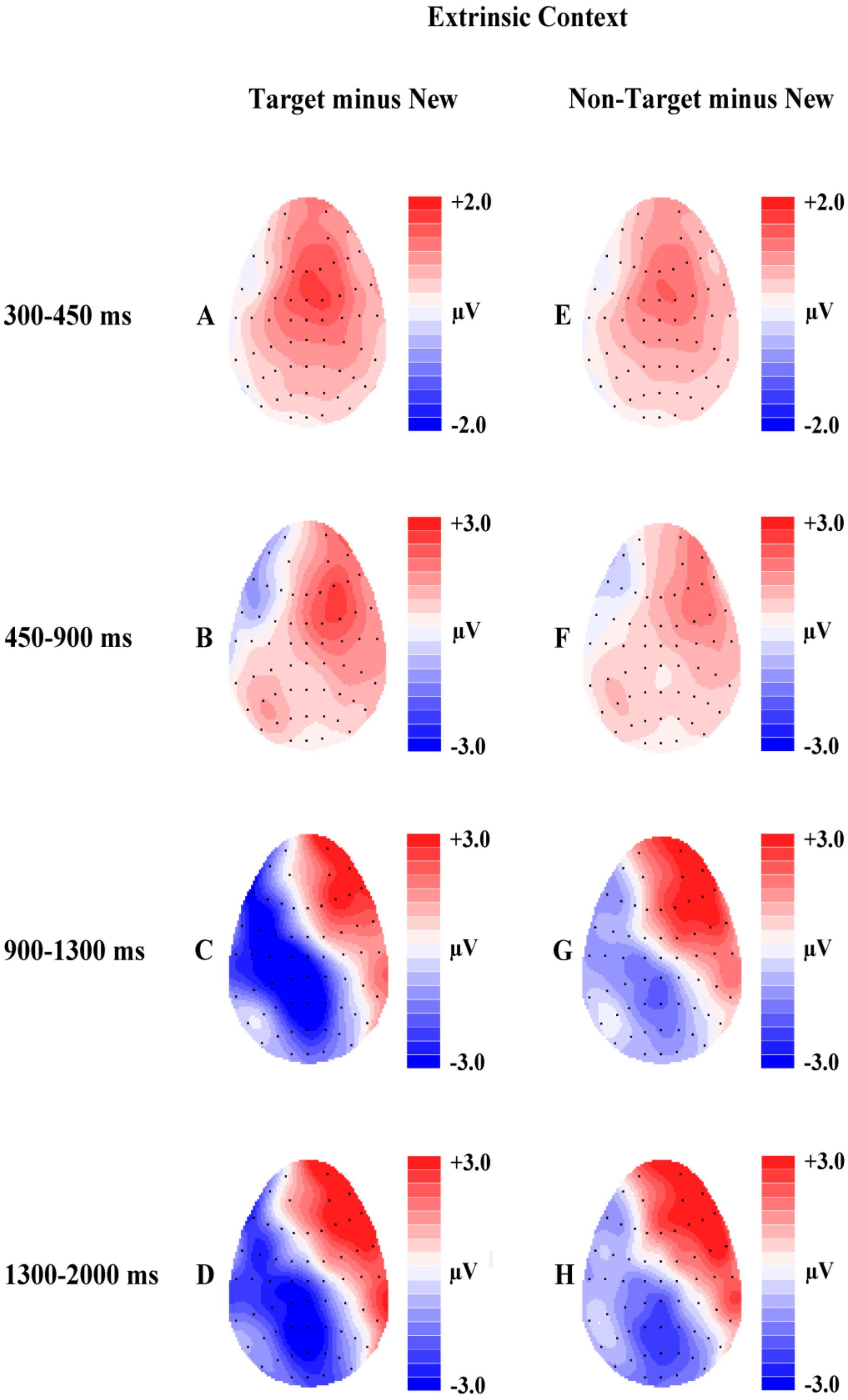

Figure 30. Topographic maps illustrating the scalp distribution of ERP effects for the older participants. There is a change in distribution over successive latency periods from a bilateral frontal effect to a left parietal effect and a right frontal effect, followed by a late posterior negativity and a left sided negativity. The change over time is similar for targets and non-targets.

For both age groups, the main global analyses revealed interactions involving the factor of epoch, but no epoch by response interactions (see Table 23, below), suggesting that there were qualitative differences in the ERP effects over time, and that these differences were similar for targets and non-targets. Consequently, subsidiary analyses were performed on data collapsed across targets and non-targets, and the factor of response was removed from the analyses. For both age groups, three subsidiary topographic comparisons were conducted (300-450 ms vs. 450-900 ms, 450-900 ms vs. 900-1300 ms, 900-1300 ms vs. 1300-2000 ms), investigating the highest order epoch by location by hemisphere by site interactions. Additional global fronto-central topographic analyses were conducted only for the elderly, (comparing 900-1300ms with 1300-2000ms) because there were no significant modulations at fronto-central sites from 900-1300ms in the younger group.

	Younger Participants	Older Participants
ExL	F(1.94,44.67)=5.80,p=0.006	
ExH	F(1.75,40.19)=6.18,p=0.006	
ExS	F(1.70,39.10)=25.45,p<0.001	F(1.44,33.00)=12.94,p<0.001
ExLxH	F(1.79,41.14)=9.19,=0.001	F(1.75,40.27)=6.08,p=0.007
ExLxS	F(1.84,42.27)=15.64,p<0.001	
ExHxS	F(2.56,58.87)=5.15,p=0.005	
ExLxHxS	F(2.14,49.13)=3.84,p=0.03	F(2.52,58.01)=2.52,p=0.05
Additional fronto-central analyses	*Not performed*	*No significant results*

Table 23. Results of the within age global topographic analyses of rescaled difference waveforms, comparing all four latency windows. The additional analyses only compared the 900-1300ms and 1300-2000ms latency windows. E, L, H and S represent the factors of epoch, location, hemisphere and site respectively. Interactions involving the factor of epoch were present for both age groups.

Younger Participants: Subsidiary analyses investigating the global epoch by location by hemisphere by site interaction (Table 23) also revealed an epoch by location by hemisphere by site interaction [F(1.37,31.50) = 3.83, p = 0.05] from 300-450ms vs. 450-900ms. This interaction reflected a progression from a bilaterally distributed parietal effect in the first latency period to a clear left parietal effect in the second latency period (Figure 29, A,B,E and F).

For the 450-900ms vs. 900-1300ms contrast, subsidiary analyses investigating the global epoch by location by hemisphere by site interaction (Table 23) revealed epoch by location by hemisphere [F(1,23) = 5.38, p = 0.03] and epoch by location by site [F(1.37,31.58) = 11.95, p = 0.001] interactions. The former interaction reflected a progression from a bilateral anterior frontal effect from 450-900ms to a right frontal effect, whereas the latter interaction indicated the appearance of the late posterior negativity in the 900-1300ms time window (Figure 29, B,C,F and G).

Finally, for the 900-1300ms vs. 1300-2000ms comparison, subsidiary analyses investigating the global epoch by location by hemisphere by site interaction (Table 23) showed an epoch by hemisphere by site interaction [F(1.14,26.15) = 12.42, p = 0.001]. This result marked the decline of the left parietal effect and the evolution of a left frontal negativity in the latter time window (Figure 29, C,D,G and H).

Older Participants: Subsidiary analyses investigating the global epoch by location by hemisphere by site interaction (Table 23) also revealed an epoch by location by hemisphere by site interaction [F(1.42,32.58) = 5.67, p = 0.01] from 300-450ms vs. 450-900ms. This interaction reflected a progression from a bilaterally distributed frontal effect in the first latency period to a right frontal effect and a clear left parietal effect in the second latency period (Figure 30, A,B,E and F).

Again, for the 450-900ms vs. 900-1300ms contrast, subsidiary analyses investigating the global epoch by location by hemisphere by site interaction (Table 23) also revealed an epoch by location by hemisphere by site [$F(1.53,35.24) = 8.06$, $p = 0.03$] interaction. This interaction indicated the evolution of the left sided negativity and the appearance of the late posterior negativity in the latter time window (Figure 30, B,C,F and G).

Finally, for the 900-1300ms vs. 1300-2000ms comparison, subsidiary analyses investigating the global epoch by location by hemisphere by site interaction (Table 23) showed an epoch by location by site interaction [$F(1.48,34.05) = 14.28$, $p < 0.001$]. This result marked the slightly more widespread distribution of the late posterior negativity in the 1300-2000ms time window (Figure 30, C,D,G and H).

8.3.3.5 Summary of the ERP Effects Elicited Separately by Younger and Older Participants

The older group produced the putative bilateral frontal correlate of familiarity from 300-450ms for targets and non-targets. This effect was of equivalent magnitude for targets and non-targets. From 450-900ms, the left parietal correlate of recollection was significant for targets and non-targets, and the putative right frontal correlate of post retrieval processing was present for targets and non-targets. These effects were statistically equivalent for targets and non-targets. The putative right frontal correlate of post retrieval processing and the late posterior negativity were present from 900-1300ms and 1300-2000ms for targets and non-targets. The late posterior negativity was larger for targets from 900-1300ms. In addition, a left sided negativity was significant for targets from 900-1300ms and 1300-2000ms, and was larger for targets compared to non-targets.

In contrast to the older group, the younger group produced no significant early bilateral frontal effects. The left parietal correlate of recollection was significant from 450-900ms and 900-1300ms for targets and non-targets, along with a bilateral anterior frontal effect from 450-900ms. The left parietal effect was greater in magnitude for targets than non-targets from 450-900ms. The right frontal effect and late posterior negativity were present for targets and non-targets from 900-1300ms and 1300-2000ms along with a left frontal negativity in the latter time window; there were no magnitude differences between targets and non-targets in either of these time windows.

8.3.3.6 Between Age Magnitude and Topographic Analyses

Significant ERP effects were present for targets and non-targets during each latency window for both age groups, therefore between age magnitude and topographic analyses were conducted for each time window. In the main within age magnitude analyses from 450-900ms, target greater than non-target differences were present in the younger group, and from 900-1300ms target greater than non-target differences were present in the older group. As a result, the main between age magnitude analyses of the second two latency windows included a third level of response (target minus new, non-target minus new and target minus non-target). The first and last time windows did not include the target minus non-target level. In the additional within age magnitude analyses from 900-1300ms and 1300-2000ms, target greater than non-target magnitude differences were present in the older group, therefore the additional between age magnitude analyses also included the target minus non-target level. As the within age additional magnitude analyses from 900-1300ms revealed no significant differences in the young, additional between age topographic analyses were only performed for 1300-2000ms.

Table 24 shows the results of the global between age magnitude and topographic analyses. Interactions involving age and response were investigated with subsidiary analyses of separate responses; when there were no interactions between age and response subsidiary analyses were performed on data collapsed across responses. Subsidiary analysis investigating the age by location interaction in the 300-450ms global magnitude ANOVA revealed significant differences over the parietal location [$t(46) = -2.51$, $p = 0.02$]. The lack of significant magnitude differences at the frontal location suggests that frontal effects did not differ between ages. Although the bilateral frontal effect was only significant in the older group, visual inspection of the data suggests that frontal effects were also present in the younger group (Figure 29, A and E). The more posterior distribution of effects in the younger group from 300-450ms was indicated by the subsidiary analyses investigating the age by location interaction in the 300-450ms global topographic ANOVA (Table 24).

The age by response by location by site interaction in the 450-900ms global magnitude ANOVA (Table 24) reflected a greater parietal effect in the younger group for both targets and non-targets: subsidiary analyses for targets revealed a main effect of age at the posterior location [$F(1,46) = 9.53$, $p = 0.003$], and a significant difference at posterior mid and inferior sites [mid – $t(46) = -2.42$, $p = 0.02$; inferior – $t(46) = -2.79$, $p = 0.008$] for non-targets. Importantly, targeted t-tests of data from left and right parietal sites revealed significant differences at left parietal sites only [targets: superior – $t(46) = -3.16$, $p = 0.003$; mid – $t(46) = -4.66$, $p < 0.001$; inferior – $t(46) = -5.07$, $p < 0.001$; non-targets: superior – $t(46) = -2.22$, $p = 0.03$; mid – $t(46) = -4.16$, $p < 0.001$; inferior – $t(46) = -4.65$, $p < 0.001$], consistent with a larger left parietal effect in the younger group

Latency Window	Magnitude	Topographic
300-450ms		
AxL	F(1,46)=4.14,p=0.05	F(1,46)=4.32,p=0.04
450-900ms		
AxH		F(1,46)=25.13,p<0.001
AxLxS		F(1.31,60.12)=4.37,p=0.03
AxHxS		F(1.53,70.56)=9.07,p=0.001
AxRxH	F(1.36,62.55)=5.72,p=0.01	
AxLxHxS		F(1.88,86.33)=4.34,p=0.04
AxRxLxS	F(1.57,72.34)=3.41,p=0.05	
900-1300ms		
AxH		F(1,46)=15.90,p<0.001
AxRxH	F(1.46,67.10)=3.66,p=0.04	
AxLxS	F(1.50,69.01)=8.92,p=0.001	F(1.37,62.83)=6.71,p=0.006
AxHxS		F(1.34,61.46)=4.26,p=0.03
AxLxHxS		F(1.71,78.69)=6.51,p=0.009
Additional fronto-central analyses		
AxH	*F(1,46)=4.74,p=0.04*	*Not performed*
1300-2000ms		
AxLxH		F(1,46)=7.99,p=0.007
AxLxS		F(1.52,69.91)=6.21,p=0.007
AxLxHxS		F(1.65,75.97)=6.91,p=0.008
AxRxLxH	F(1,46)=7.07,p=0.02	
Additional fronto-central analyses		
AxH	*F(1,46)=5.68,p=0.05*	*No significant results*

Table 24. Results of the between age global magnitude and topographic analyses of difference and rescaled difference waveforms respectively. The main between age magnitude analyses of the second two latency windows included three levels of response (target minus new, non-target minus new and target minus non-target). The first and last time windows did not include the target minus non-target level. The additional between age magnitude analyses included three levels of response. A, R, L, H and S represent the factors of age, response, location, hemisphere and site respectively.

(Figure 29, B and F; Figure 30, B and F). There were no target/non-target differences between age groups.

The age by response by hemisphere interaction in the global magnitude ANOVA from 450-900ms (Table 24) reflected greater effects in the younger group than the older group at the left hemisphere only [targets: left hemisphere – t(46) = -4.11, p < 0.001;

non-targets: left hemisphere – t(46) = -3.09, p = 0.003]; these differences were larger for targets than non-targets [targets: left hemisphere = Mean 2.22μV; non-targets: left hemisphere = Mean 1.63μV]. Again, subsidiary analyses revealed no target/non-target differences between age groups. There were no between age magnitude differences at frontal sites during the 450-900ms time window, however there were topographic differences (Figure 29, B and F; Figure 30, B and F): subsidiary analyses investigating the age by location by hemisphere by site interaction in the global topographic ANOVA (Table 24) reflected the more right sided distribution of frontal activity in the older group.

Between 900 and 1300ms, the age by location by site and age by response by hemisphere interactions in the global magnitude ANOVA (Table 24) demonstrated larger effects in the older group at the posterior inferior site [t(46) = -2.41, p = 0.02], and for targets over the left hemisphere [t(46) = -2.57, p = 0.01], respectively. The age by hemisphere interaction in the additional magnitude analyses reflected larger effects over the left hemisphere for older participants [t(46) = -2.08, p = 0.04]. Meanwhile, the age by location by hemisphere by site interaction in the main global topographic ANOVA confirmed the continued presence of the left parietal effect in the younger group but not in the older group (Figure 29, C and G; Figure 30, C and G).

The pattern of results from 1300-2000ms was similar to 900-1300ms, except for slight differences. The age by response by location by hemisphere interaction in the main global magnitude ANOVA (Table 24) reflected bigger effects for targets over the left parietal location [t(46) = -2.57, p = 0.01] in the older group. Again, the age by hemisphere interaction in the additional analyses reflected larger effects over the left hemisphere for older participants [t(46) = -2.02, p = 0.05]. Consistent with the previous time window, the age by location by hemisphere by site interaction in the main global topographic ANOVA reflected the presence of the non-significant left parietal effect in the younger group but not in the older group (Figure 29, D and H; Figure 30, D and H).

8.3.3.7 Summary of the Differences in the ERP Effects Elicited by Younger and Older Adults

The bilateral frontal effect was significant from 300-450ms for targets and non-targets, but only for older adults. By contrast, from 450-900ms, although topographically similar, the left parietal effect was significantly reduced for older adults than younger adults for targets and non-targets, and the frontal effects were right sided in the elderly compared to bilateral in the young. From 900-1300ms, an extended left parietal effect was present in the younger group for targets and non-targets. Also, the left sided negativity was significant earlier in the elderly (900-1300ms compared to 1300-2000ms in the young) and exhibited a more widespread left sided distribution. The magnitude and topography of the late posterior negativity and late right frontal effect (from 900-1300ms and 1300-2000ms) appeared equivalent in both age groups.

8.4 Discussion

The aim of Experiment 2a was to investigate the effect of retrieving an extrinsic context on the retrieval strategies adopted by young and older adults, by using behavioural performance as an indication of different retrieval strategies and examining differences in the engagement of the three retrieval processes to further reveal the retrieval strategies used. Consistent with the dual process theory view that ageing is associated with a decline in recollection while familiarity remains relatively intact, the process dissociation procedure estimates revealed that the contribution of recollection was lower for older adults compared to younger adults, whereas the contribution of familiarity was higher. This result was evident in the elderly participants' reduced hit rate to targets and increased false alarm rate to non-targets, compared to the young.

In accordance with the behavioural results, the bilateral frontal correlate of familiarity was significant only in the elderly, and the left parietal correlate of recollection was severely reduced compared to the young. The distribution of the late right frontal effect was more right sided from 450-900ms for the elderly compared to the young, whereas it was equivalent in magnitude and topography from 900-1300ms and 1300-2000ms. The right prefrontal effect, present from 900-1300ms in the young adults from Experiment 1a, was not present in the younger group from Experiment 2a. Instead, the right frontal effect was significant from 900-1300ms. Previous studies have shown that task switching can alter ERP effects (e.g. see Wilding and Nobre, 2001). The minimal task switching component in Experiment 1a was removed from Experiment 2a, making the task easier and it was therefore possibly not necessary to monitor the accuracy of retrieved information for as long as in Experiment 1a. In addition to the three retrieval processes, a left frontal negativity was also significant in the young from 1300-2000ms; this effect was significant earlier in the elderly (900-1300ms through to 1300-2000ms) and exhibited a more widespread left sided distribution. Together the behavioural and ERP findings suggest that younger and older adults adopted different retrieval strategies: the elderly relied more on familiarity and less on recollection, whereas the young relied more on recollection and less on familiarity. In addition, and of particular interest, post retrieval/evaluative processes appeared inconsistent for the young and old, and the left sided negativities were not equivalent across ages.

8.4.1 Bilateral Frontal Correlate of Familiarity

As stated previously, the bilateral frontal effect is thought to be a neural correlate of familiarity (Rugg and Curran, 2007), and it is therefore unlikely to be linked to executive/post retrieval processing. Unsurprisingly, the bilateral frontal correlate of familiarity was present for the elderly. In light of the age-related reduction in the left parietal correlate of recollection, familiarity appeared to form the older participants' primary basis for retrieval. In contrast to previous ageing studies (Wegesin et al., 2002; Morcom and Rugg, 2004) that have reported early frontal effects of equivalent magnitude in young and older subjects, but of a more right-sided distribution in the elderly, the early frontal effects exhibited here were bilateral and appeared similar to those reported in studies in the young. This finding questions whether the early right frontal effect reported in previous studies is the older adults' homologue of the bilateral frontal effect in young adults and suggests that it may reflect the age-related engagement of different cognitive processes. Also, in light of the findings from Experiment 1a, revealing no significant bilateral frontal effect in the extrinsic context condition, the absence of a robust bilateral frontal effect in the young was expected.

8.4.2 Left Parietal Correlate of Recollection

Again, unsurprisingly, the left parietal correlate of recollection was severely reduced in magnitude in the elderly. This finding is consistent with dual process theory that recollection is impoverished in older adults, and corroborates previous source memory studies (Li et al., 2004). As the elderly have particular difficulty retrieving extrinsic context (Spencer and Raz, 1995), it is not surprising that the effect was severely reduced in magnitude compared to the young. Despite being reduced in magnitude, however, the left parietal effect was significant in the elderly, suggesting retrieval of extrinsic context did encourage recollection.

8.4.3 Late Right Frontal Correlate of Post Retrieval/Executive Processing

The magnitude and distribution of the late right frontal effect in the latter two time windows appeared equivalent in younger and older participants, suggesting a common reliance on post retrieval/executive processing and corroborating previous studies (Mark and Rugg, 1998; Li et al., 2004). However, the distribution of the effect from 450-900ms was more right sided in the elderly compared to the young, indicating that different post retrieval/executive processes may have been engaged during this time window. Distributional differences in the right frontal effect of the young are not uncommon, and attest to the non-unitary interpretation of the effect. For example, Duzel et al. (1997) found right frontal effects of equivalent magnitude for remember and know responses, however, the know effect had a more widespread distribution than the remember effect. In addition, Friedman and Johnson (2000) and Mecklinger (2000) claimed that the functional significance of the late right frontal effect may be obscured by measuring the effect over extended time periods, which would obscure the presence of any temporally shorter sub components.

It therefore follows that there may be distributional differences in the right frontal effect of the elderly too, reflecting the engagement of different post retrieval/executive processes across age groups. Executive processes act in a supporting role during retrieval (Shimamura and Squire, 1987) and, according to the frontal lobe hypothesis of ageing, there is a negative correlation between executive impairment with ageing and accuracy on source memory tasks (Craik et al., 1990; Parkin and Walter, 1992; Parkin and Lawrence, 1994; Glisky et al., 1995; 2001; Fabiani and Friedman, 1997; Glisky, 2001). This proposal, along with the reduced performance and left parietal effect compared to the young suggests that the distributional difference in the right frontal effect may have reflected the engagement of less effective post retrieval processes in the elderly (the functional significance of the late right frontal effect will be investigated in Experiment 2c by correlating the magnitude of the effects in the older participants with performance on CANTAB tests of executive functioning. This approach will therefore further our understanding of the role of executive functions in the retrieval of source information from episodic memory in older adults).

8.4.4 Left Sided Negativities

The young adults produced a left frontal negativity from 1300-2000ms, an effect that onset earlier in the elderly (900-1300ms through to 1300-2000ms) and exhibited a more widespread left sided distribution. Previous source memory studies (Trott et al., 1997; Wegesin et al., 2002; Li et al., 2004) have demonstrated negative going modulations in the elderly, however these have been more centrally distributed. Although the functional significance of these effects is unclear, one interpretation is that they reflect older peoples' engagement of additional, compensatory, processes to assist with retrieval (Nolde et al., 1998; Wegesin et al., 2002). If this interpretation is correct, the fact that recollection was reduced in the elderly compared to the young is consistent with the requirement for additional processes earlier than in the young. In addition, if the elderly have greater impairment on memory for extrinsic context than for intrinsic context (e.g. see Spencer and Raz, 1995) compensatory processes may be required. The different distribution between young and old may simply reflect changes in brain morphology or the recruitment of different compensatory processes between age groups. The functional significance of these negativities will be investigated in

Experiment 2c by correlating the magnitude of the effects in the older participants with performance on CANTAB tests of executive functioning; prior to this, however, the following chapter will investigate whether the young and older participants differed in their neuropsychological functioning.

Chapter 9 Experiment 2b

9.1 Introduction

Cumulative evidence suggests that healthy older adults show a decline in executive functioning compared to healthy younger adults (for a review see Parkin, 2002). The aim of this experimental chapter is to describe the neuropsychological functioning of the 24 older adults from Experiment 2a, using the CANTAB battery, and compare this with the 24 younger adults (also from Experiment 2a). Participants completed four tests from the CANTAB battery: the non-executive Spatial Span task, and three tests of executive functioning: IDED Set Shifting task, Spatial Working Memory and the Stockings of Cambridge (see ‘General Methods’ chapter for a description of the tasks). Based on the previous literature investigating age related changes in executive functioning, it is predicted that, in comparison to the younger adults, older adults will show reduced performance on the neuropsychological tests.

9.2 Methods

9.2.1 Participants

Participants were those that took part in Experiment 2a. Twenty-four young and 24 older adults took part in the experiment (younger: aged 18-30, mean age 20.33, 13 female; older: aged 64-77, mean age 69.80, 12 female). All other aspects of the methods are described in the ‘General Methods’ chapter.

9.2.2 Stimulus Materials and Procedure

A description of the CANTAB tests and implementation procedure are provided in the 'General Methods' chapter.

9.3 Results

Spatial Span: Figure 31 and Figure 32 show the spatial span score and the total errors respectively, for both age groups. As can be seen in Figure 31 older adults had lower spatial span scores than younger adults, which was confirmed by an independent t-test [t(46) = 6.51, p < 0.001].

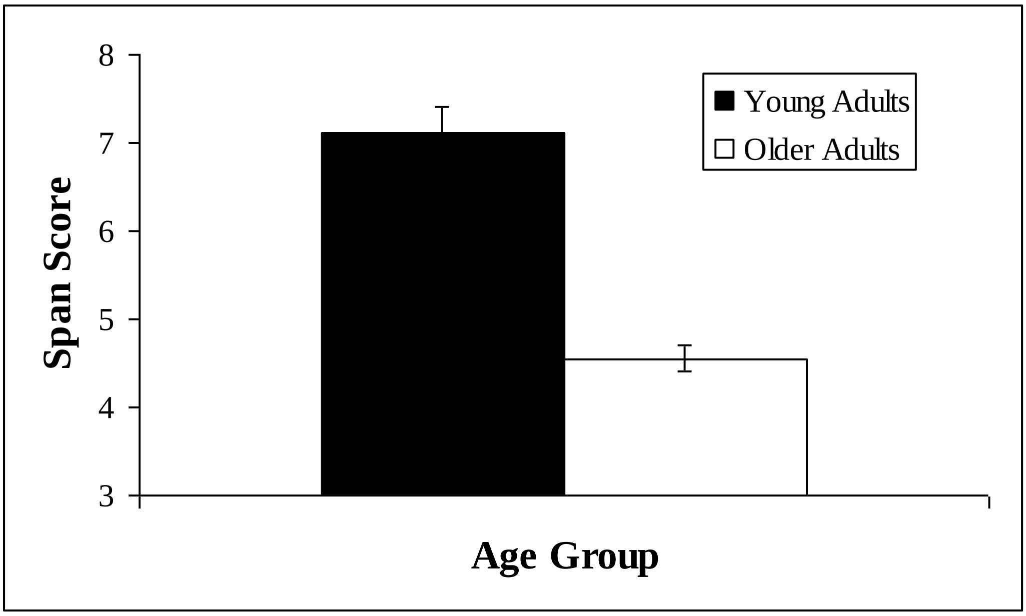

Figure 31. Spatial Span Score for young and older adults. Older adults had a significantly lower span score than younger adults. Error bars represent the standard error.

Although Figure 32 suggests that the total number of errors made was greater for young adults than older adults, an independent t-test failed to reveal any significant difference between the age groups [t(46) = 1.61, p = 0.12].

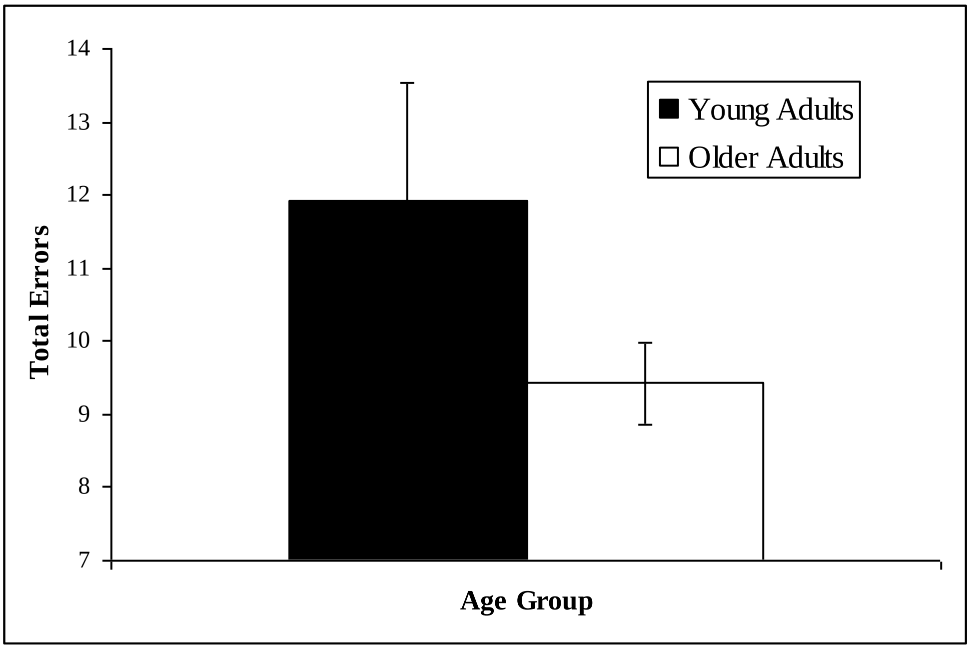

Figure 32. Spatial Span Total Errors for young and older adults. There was no significant difference between the age groups. Error bars represent the standard error.

ID/ED Attentional Set-Shifting Task: Figure 33, Figure 34, Figure 35 and Figure 36 show the stage reached, the proportion that successfully completed each stage, errors at each stage and response time at each stage, respectively, for both age groups. Figure 33 suggests that older adults completed fewer stages successfully, however, an independent t-test failed to reach significance [t(46) = 1.74, p = 0.10].

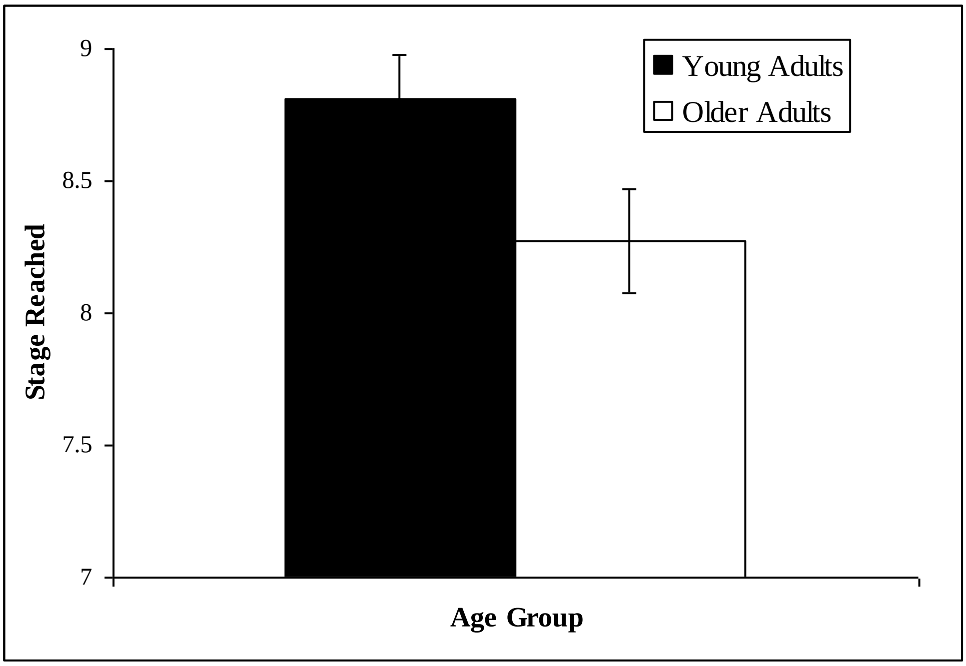

Figure 33. Stage reached by young and older adults on the ID/ED task. There are 9 stages on this task: (1) simple discrimination, (2) simple reversal, (3) compound discrimination 1, (4) compound discrimination 2, (5) compound reversal, (6) intradimensional (ID) shift, (7) intradimensional (ID) reversal, (8) extradimensional (ED) shift, and (9) extradimensional (ED) reversal. There was no significant difference between age groups in the stage reached. Error bars represent the standard error.

Although Figure 34 indicates that older adults were less likely to complete the ED shift (EDS) and ED reversal (EDR) stages, an ANOVA with one between participants factor (Age Group) and one within participants factor (Stage: 1-9) failed to reveal main effects of age group [F(1,45) = 0.85, p = 0.30] or stage [F(1,45) = 0.93, p = 0.29] or interaction between the factors [F(1,45) = 0.63, p = 0.42].

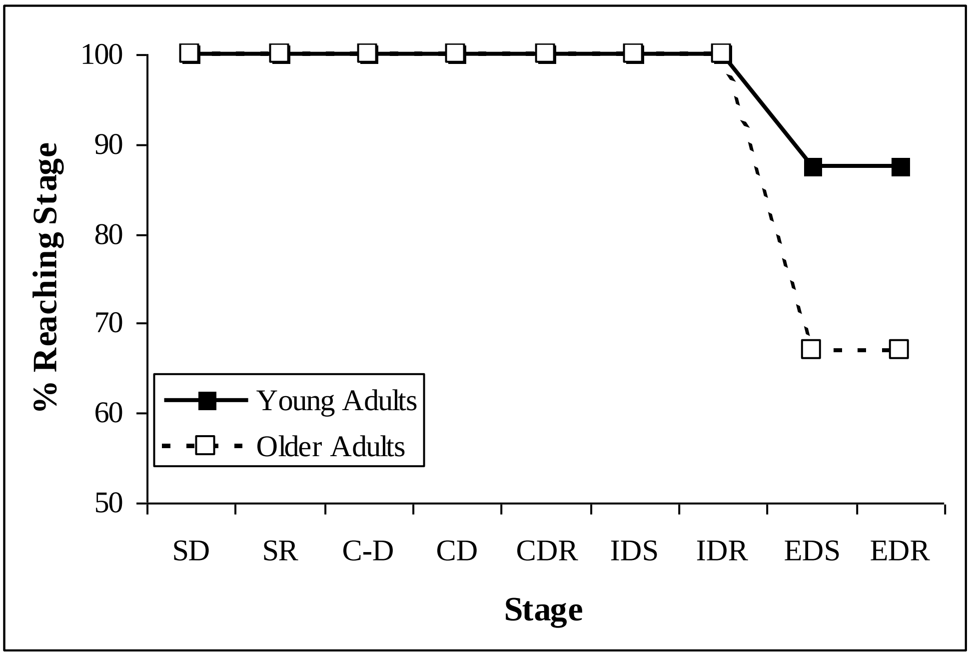

Figure 34. The percentage of young and older adults reaching criterion at each stage of the ID/ED task. See Figure 33 for a definition of each of the 9 stages. There was no significant difference between the age groups at any stage. Error bars are too small to be seen.

As can be seen in Figure 35, there is little difference between the age groups in the errors made during the first 7 stages, however older adults appeared to make more errors than younger adults at the EDS and EDR stages. An ANOVA with one between participants factor (Age Group) and one within participants factor (Stage: 1-9) produced a significant main effect of age group [F(1,402) = 13.49, p < 0.001] and stage [F(8,402) = 23.33, p < 0.001] and a significant interaction between the factors [F(8,402) = 3.60, p < 0.001]. Subsidiary independent t-tests investigating the interaction confirmed that older adults made more errors than younger adults at the EDS [t(46) = -3.43, p < 0.001] and EDR [t(46) = -2.78, p < 0.001] stages only.

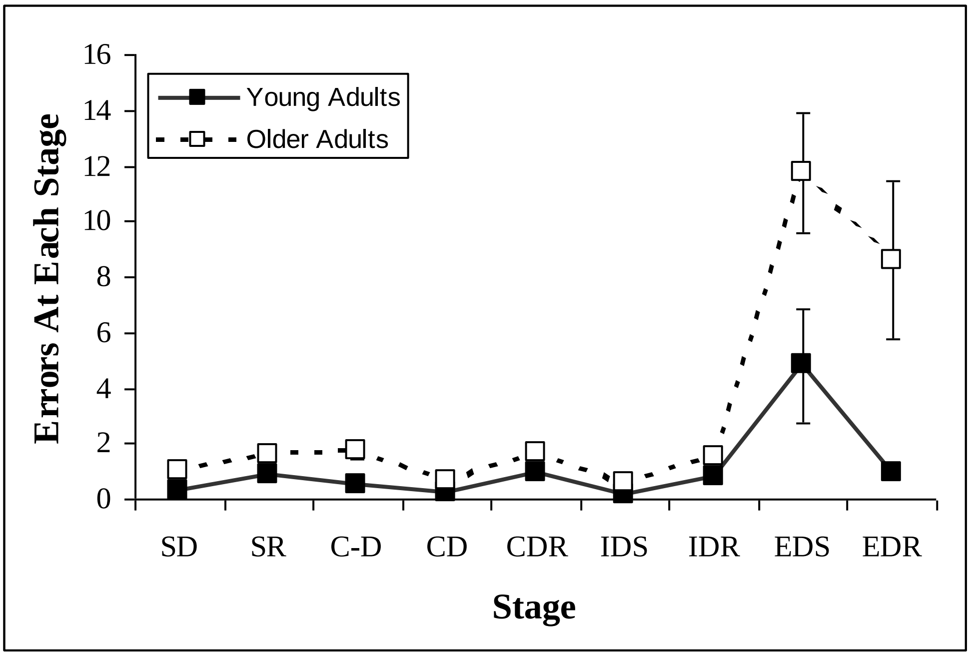

Figure 35. Number of errors at each stage made by young and older adults on the ID/ED task. See Figure 33 for a definition of each of the 9 stages. Older adults produced significantly more errors than young adults at the EDS and EDR stages only. Error bars represent the standard error and are too small to be seen on some stages.

Response times were slower at each stage for older adults than younger adults; this difference was greatest at stage SD (see Figure 36). An ANOVA with one between participants factor (Age Group) and one within participants factor (Stage: 1-9) revealed a significant main effect of age group [F(1,402) = 45.05, p < 0.001] and stage [F(8,402) = 115.77, p < 0.001] and a significant interaction between the factors [F(8,402) = 6.34, p < 0.001]. Subsidiary independent t-tests investigating the interaction verified that older adults had slower response times than younger adults at all stages [SD - t(46) = 3.69, p = 0.001; SR - t(46) = 2.75, p = 0.008; C-D - t(46) = 4.45, p < 0.001; CD - t(46) = 5.37, p < 0.001; CDR - t(46) = 4.68, p < 0.001; IDS - t(46) = 5.58, p < 0.001; IDR - t(46) = 4.28, p < 0.001; EDS - t(46) = 4.88, p < 0.001; EDR - t(46) = 3.73, p = 0.01]. The age difference was greatest, however, at the SD stage [SD = 4590msec; SR = 937msec; C-D = 1808msec; CD = 1004msec; CDR = 925msec; IDS = 1057msec; IDR = 795msec; EDS = 1095msec; EDR = 920msec].

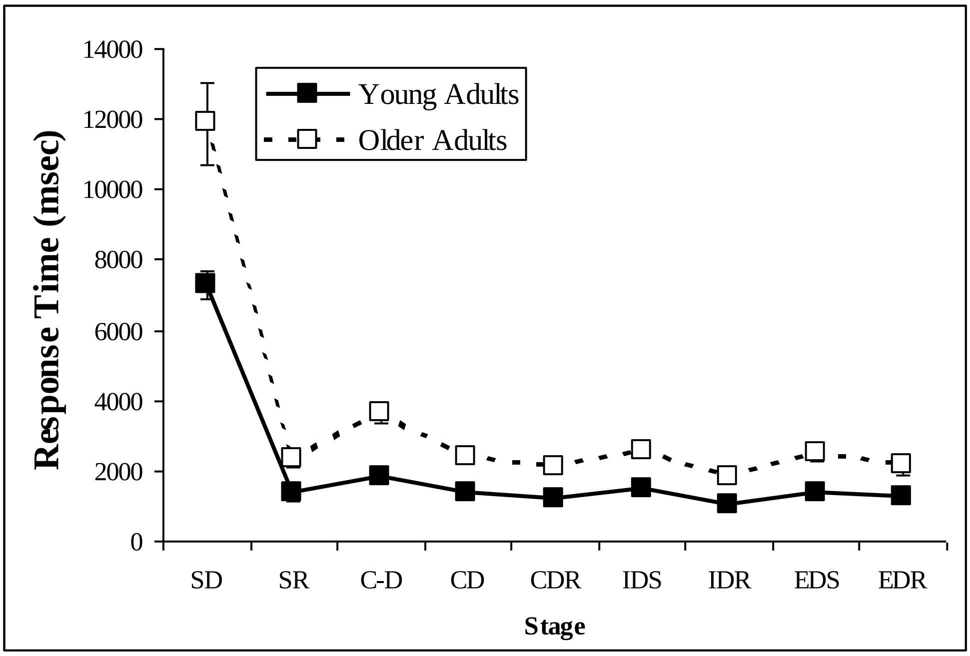

Figure 36. Response time (msec) of young and older adults at each stage on the ID/ED task. See Figure 33 for a definition of each of the 9 stages. Response times were significantly slower at each stage for older adults than young adults; this difference was greatest at stage SD. Error bars represent the standard error and are too small to be seen on some stages.

Spatial Working Memory: Figure 37, Figure 38 and Figure 39 show the between search errors at each stage, the strategy score and the total time to complete each stage respectively, for both age groups. As can be seen in Figure 37, there is little difference between the age groups in the between search errors made at the 3 and 4 box stages, however older adults appeared to make more errors than younger adults at the 6 and 8 box stages. An ANOVA with one between participants factor (Age Group) and one within participants factor (Box Stage: 3,4,6 and 8) produced a significant main effect of age group [F(1,183) = 23.89, p < 0.001] and stage [F(3,183) = 61.75, p < 0.001] and a significant interaction between the factors [F(3,183) = 28.83, p < 0.001]. Subsidiary independent t-tests investigating the interaction confirmed that older adults made more between search errors than younger adults at the 6 [t(46) = 3.20, p = 0.003] and 8 [t(46) = 6.56, p < 0.001] box stages only.

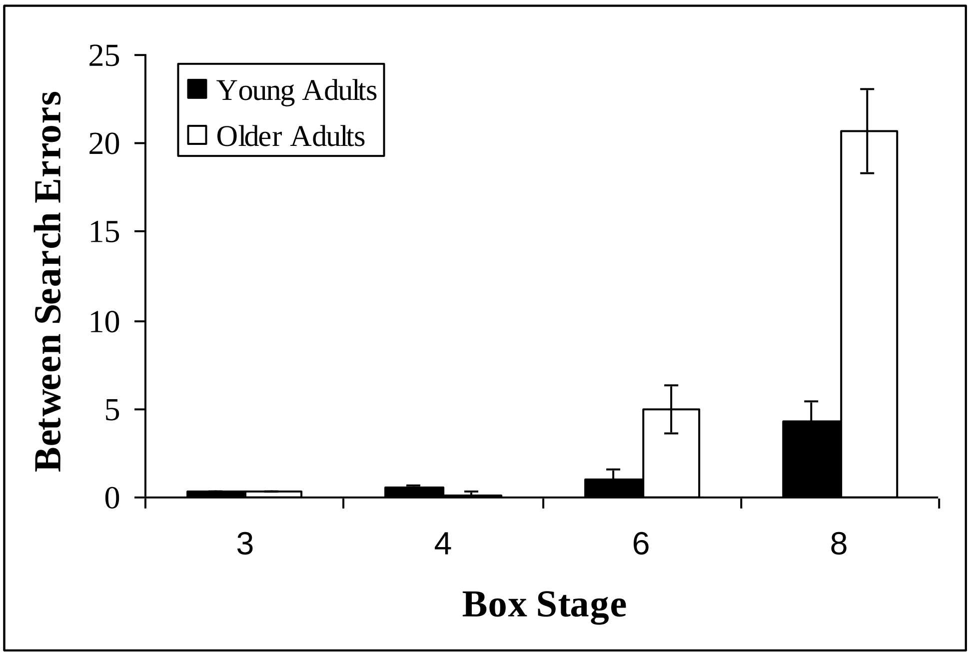

Figure 37. Number of between search errors made by young and older adults at each stage of the Spatial Working Memory Task. Older adults made significantly more between search errors than young adults at the 6 and 8 box stages only. Error bars represent the standard error.

Older adults had a higher Strategy Score than young adults, indicating a lower use of strategy (see Figure 38). This result was confirmed by an independent t-test [t(46) = -4.57, p < 0.001].

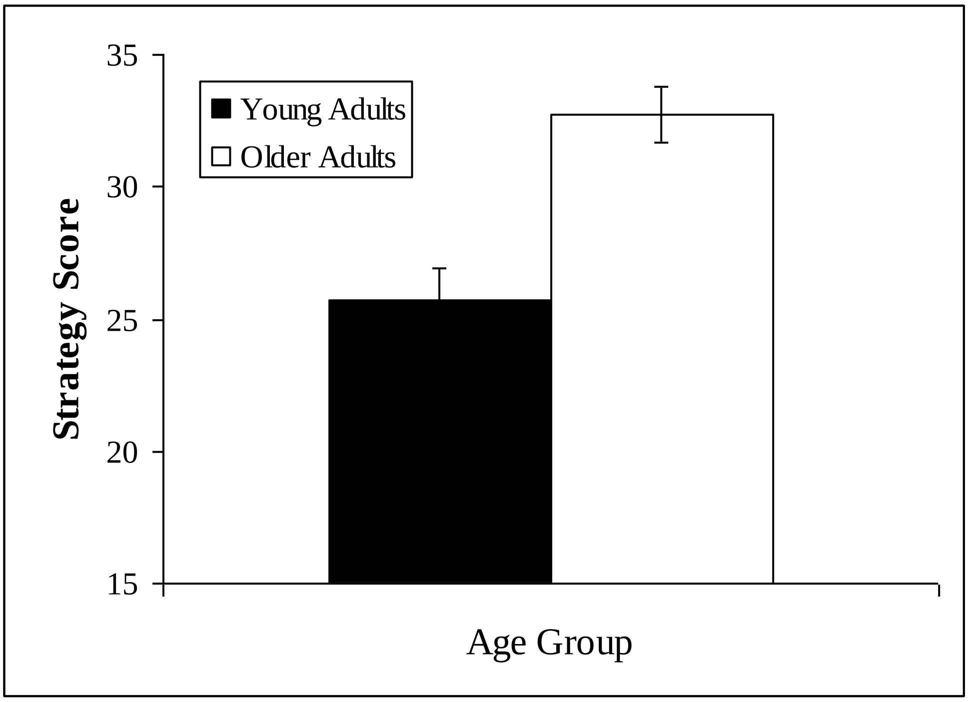

Figure 38. Young and older adults strategy score on the Spatial Working Memory task. Older adults had a significantly higher strategy score than young adults indicating a lower use of strategy. Error bars represent the standard error.

It is evident from Figure 39 that the total time to complete each stage was longer for older adults than younger adults; this difference was greatest at the 6 and 8 box stages. An ANOVA with one between participants factor (Age Group) and one within participants factor (Box Stage: 3,4,6 and 8) revealed a significant main effect of age group [F(1,183) = 67.02, p < 0.001] and stage [F(3,183) = 224.74, p < 0.001] and a significant interaction between the factors [F(3,183) = 31.52, p < 0.001]. Subsidiary independent t-tests investigating the interaction verified that older adults took longer to complete each box stage than young adults [3 - t(46) = 3.45, p = 0.001; 4 - t(46) = 4.24, p < 0.001; 6 - t(46) = 7.24, p < 0.001; 8 - t(46) = 8.63, p < 0.001]. The age difference was greatest, however, at the 6 and 8 box stages [3 = 20991msec; 4 = 28909msec; 6 = 61556msec; 8 = 132115msec].

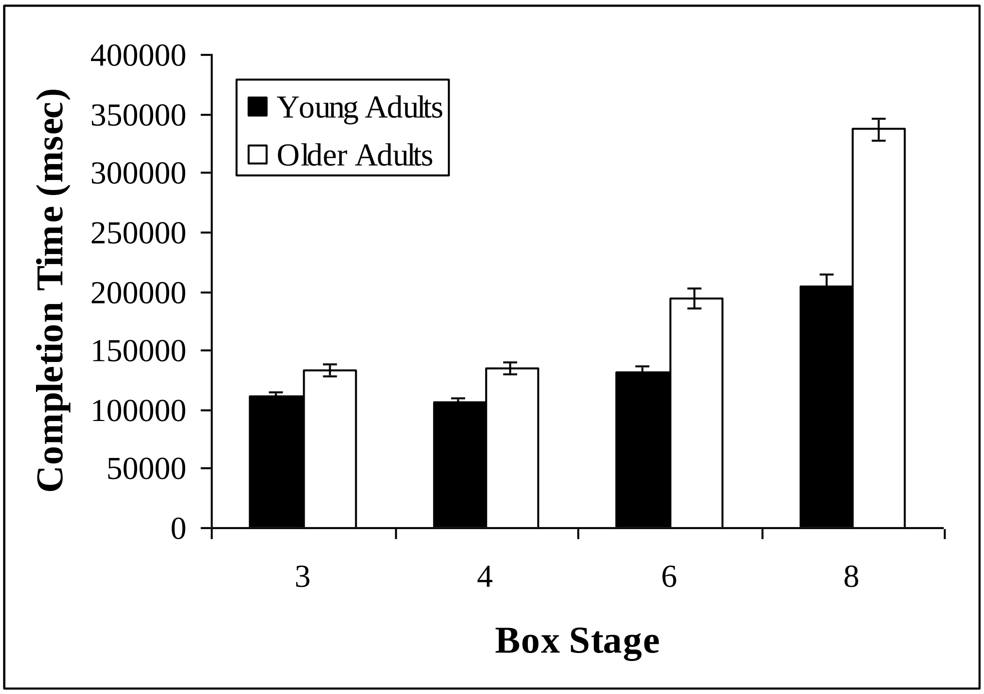

Figure 39. Young and older adults total time to complete each stage of the Spatial Working Memory Task. Older adults took significantly longer to complete each stage than young adults. The age difference was greater at the 6 and 8 box stages. Error bars represent the standard error.

Stockings of Cambridge: Figure 40, Figure 41, Figure 42 and Figure 43 show the problems solved in the minimum number of moves, initial thinking time at each stage, subsequent thinking time at each stage and number of excess moves at each stage, respectively, for both age groups. There is little difference between the young and older adults in the problems solved in the minimum number of moves (see Figure 40). This result was confirmed by an independent t-test [t(46) = 1.23, p = 0.15].

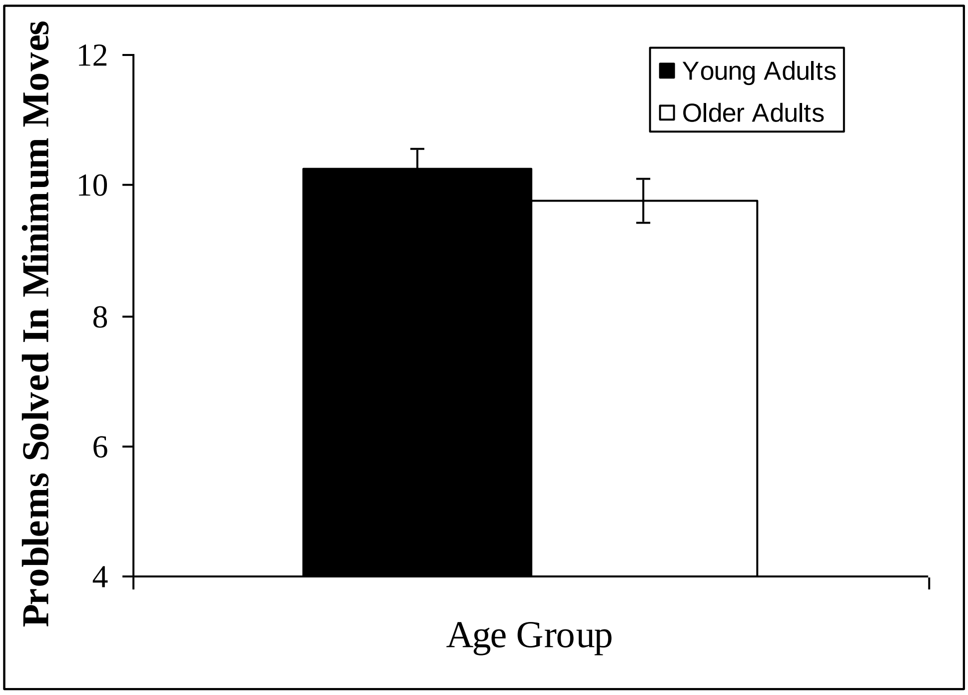

Figure 40. The number of problems solved in the minimum number of moves on the Stockings of Cambridge task, for young and older adults. There was no significant difference between the age groups. Error bars represent the standard error.

It is evident from Figure 41 that older adults had longer initial thinking times than young adults at all stages, and thinking times were longest at the 5 move stage followed by the 4 move stage, then 3 move stage and were shortest at the 2 move stage.

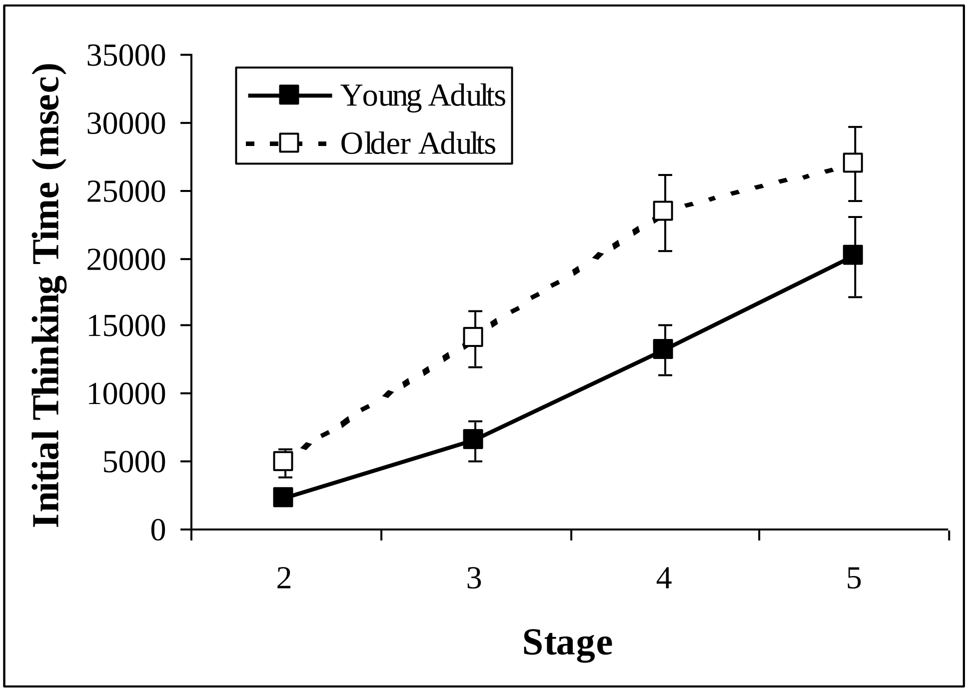

Figure 41. Young and older adults' initial thinking time at each stage of the Stockings of Cambridge task. Initial thinking is the time spent deliberating prior to initiating a first move. It is calculated by subtracting initial movement times made in the 'yoked' control condition from response times (thinking and movement time). This calculation is automatic within the test results. Older adults had significantly longer initial thinking times than young adults at all stages, and thinking times were longest at the 5 move stage followed by the 4 moves stage, then 3 move stage and were shortest at the 2 move stage. Error bars represent the standard error.

An ANOVA with one between participants factor (Age Group) and one within participants factor (Stage: 2,3,4 and 5) revealed a significant main effect of age group [F(1,183) = 12.03, p = 0.001] and stage [F(3,183) = 35.05, p < 0.001] but no significant interaction between the factors [F(3,183) = 1.07, p = 0.36]. The main effect of age confirmed that generally older adults showed longer initial thinking times compared to young adults, while subsidiary independent t-tests investigating the main effect of stage verified that initial thinking times increased as the number of moves increased [stage 2 vs. 3 - t(47) = 4.84, p < 0.001; stage 3 vs. 4 - t(47) = 4.81, p < 0.001; stage 4 vs. 5 - t(47) = 3.37, p = 0.001].

As can be seen in Figure 42, there is little difference between the age groups in subsequent thinking time at the 2 and 3 move stages, however older adults exhibit longer subsequent thinking times compared to young adults at the 4 and 5 move stages.

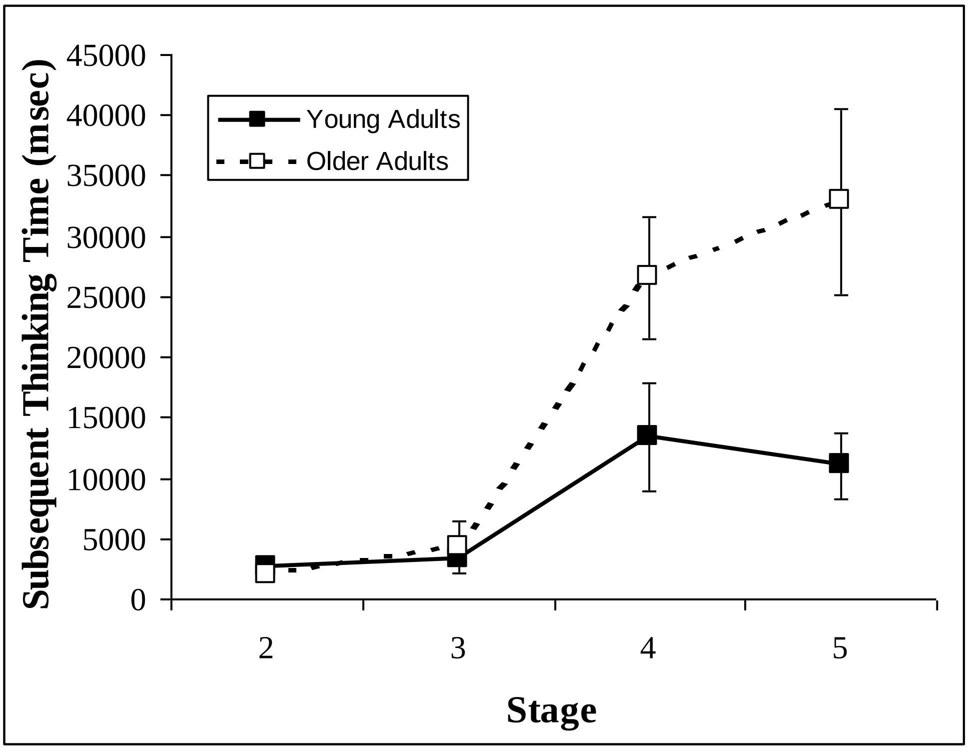

Figure 42. Young and older adults' subsequent thinking time at each stage of the Stockings of Cambridge task. Subsequent thinking is the time spent deliberating subsequent to an initial move. It is calculated by subtracting subsequent movement times made in the 'yoked' control condition from response times (thinking and movement time). This calculation is automatic within the test results. Older adults had significantly longer subsequent thinking times compared to young adults at the 4 and 5 move stages only. Error bars represent the standard error.

An ANOVA with one between participants factor (Age Group) and one within participants factor (Stage: 2,3,4 and 5) revealed significant main effects of age group [F(1,183) = 5.19, p = 0.02] and stage [F(3,183) = 16.39, p < 0.001] and a significant interaction between the factors [F(3,183) = 4.63, p = 0.004]. Subsidiary independent t-tests investigating the interaction confirmed that older adults had longer subsequent thinking times compared to young adults at the 4 [t(46) = 2.50, p = 0.02] and 5 [t(46) = 3.11, p = 0.003] move stages only.

There is little difference between the age groups in the number of excess moves at the 2 and 3 move stages, however older adults exhibit a greater number of excess moves compared to young adults at the 4 and 5 move stages (see Figure 43). An ANOVA with one between participants factor (Age Group) and one within participants factor (Stage: 2,3,4 and 5) revealed a significant main effect of stage [F(3,183) = 24.85, p < 0.001] but no significant main effect of age group [F(1,183) = 2.38, p = 0.13] and a significant interaction between the factors [F(3,183) = 3.85, p = 0.01]. Subsidiary independent t-tests investigating the interaction confirmed that older adults made more excess moves compared to young adults at the 4 [t(46) = 1.77, p = 0.03] and 5 [t(46) = 2.62, p = 0.01] move stages only.

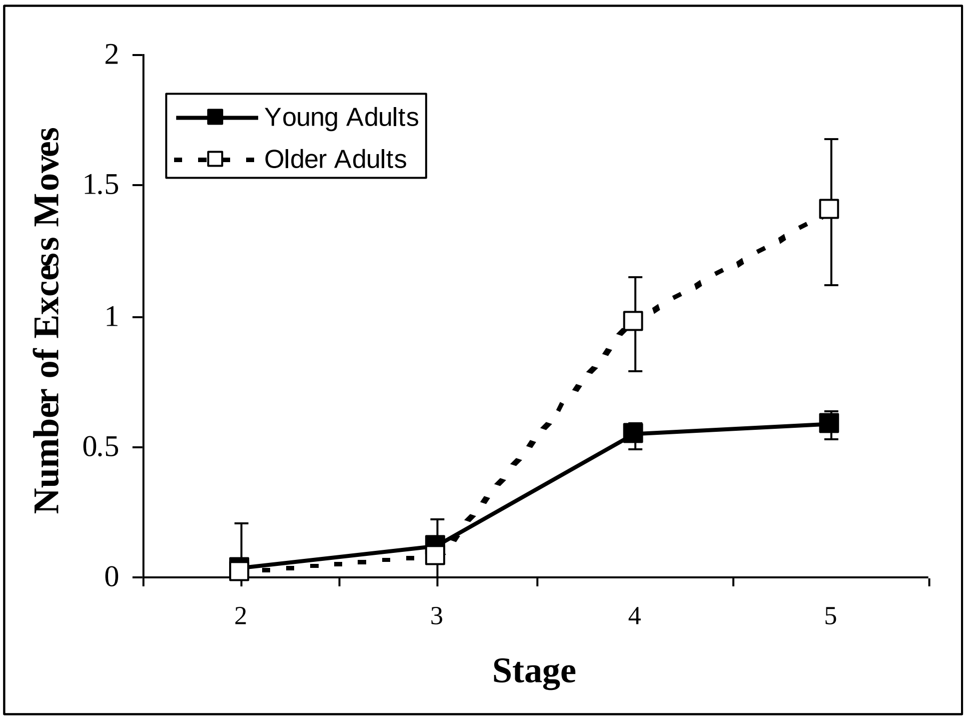

Figure 43. Number of excess moves made by young and older adults at each stage of the Stockings of Cambridge task. Older adults made more excess moves than young adults at the 4 and 5 move stages only. Error bars represent the standard error.

Inter-Relationship Between Cognitive Tests: Correlations were performed between the spatial span score and the between search errors at each stage of the Spatial Working Memory task, to assess the role of short-term memory capacity on working memory performance. There were no significant correlations between the spatial span score and the between search errors at any stage of the Spatial Working Memory task for young or older adults, therefore there was no relationship between short-term memory capacity and working memory performance.

In addition, to assess the relationship between strategy use and working memory performance, correlations were performed between the strategy score and the total number of between search errors across all stages, revealing a positive correlation for young ($r = 0.34$, $p = 0.07$) and older ($r = 0.72$, $p < 0.001$) adults. For both age groups, greater use of strategy was associated with reduced errors, therefore better working memory performance, on the Spatial Working Memory task.

Neuropsychological Test	Measure	Findings: Young vs. Old
Spatial Span	Span Score Total Errors	**Old had lower Span Score** No significant difference between young and old
ID/ED Attention Set-Shifting	Stage Reached Proportion completing each stage Errors at each stage Response time at each stage	No significant difference between young and old No significant difference between young and old **Old greater than young at EDS and EDR stages** **Old greater than young at all stages, especially SD stage**
Spatial Working Memory	Between Search Errors Strategy Score Total Time	**Old greater than young at 6 and 8 box stages** **Old had lower use of strategy** **Old greater than young at all stages, especially 6 and 8 box stages**
Stockings of Cambridge	Solved in Minimum Moves Initial Thinking Time Subsequent Thinking Time Excess Moves	No significant difference between young and old **Old greater than young at all stages** **Old greater than young at 4 and 5 move stages** **Old greater than young at 4 and 5 move stages**

Table 25. Summary of young and older adults' results from the CANTAB tests.

9.4 Discussion

The aim of Experiment 2b was to describe the neuropsychological functioning of the 24 older adults from Experiment 2a using the CANTAB battery and compare this with the

24 younger adults also from Experiment 2a. As predicted, in comparison to young adults, older adults showed reduced performance on the neuropsychological tests without a prominent executive component (Spatial Span task) and those with a prominent executive component (ID/ED Attentional Set-Shifting task, Spatial Working Memory task and the Stockings of Cambridge task).

Before discussing each of the tasks in turn, we briefly outline the overall pattern of performance. On the Spatial Span task, older adults had a lower span score compared to the young group, but showed no difference in the total errors made. The young and older adults did not differ in the stage reached or proportion completing each stage of the ID/ED task, however older adults made more errors than the young at the extra-dimensional shift and reversal stages, and had longer response times at all stages particularly the simple discrimination stage. Older adults had a greater number of between search errors than their younger counterparts at the harder 6 and 8 box stages of the Spatial Working Memory task, and had a higher strategy score - indicating a lower use of a strategy when performing the task. The older group also took longer to complete each stage, especially the 6 and 8 box stages. On the Stockings of Cambridge task, there was no group difference in the number of problems solved in the minimum number of moves, however the older group made more excess moves at the more difficult 4 and 5 move stages. Older adults also showed longer initial thinking times at all stages and greater subsequent thinking times at the 4 and 5 moves stages only.

9.4.1 Spatial Span Task

The elderly had lower span scores than the young indicating that spatial short-term memory performance was poorer in older adults. This finding is consistent with previous ageing studies that have demonstrated an age-related deficit in short-term memory (for a meta-analysis see Verhaeghen et al., 1993). However, despite the age-related decline, both young and old scores were in line with normative data using the CANTAB (see Robbins et al., 1998; De Luca et al., 2003).

9.4.2 ID/ED Attention Set-Shifting Task

The young and older adults did not differ in the stage reached or proportion completing each stage of the ID/ED task, indicating that the older group's ability to form an attentional set and then shift attention to a different set was comparatively intact. However, the elderly made more errors when shifting attention to a different set (the extra-dimensional shift and reversal stages) suggesting that when both age groups had a failed attempt to identify the correct rule at the hardest stages (extra-dimensional shift and reversal stages) the elderly were disproportionately affected by the initial failure resulting in greater errors to identify the correct rule. Importantly, both age groups attained greater than stage 8 (extra-dimensional shift stage) suggesting that, as expected in the normal population, neither group had an executive impairment in flexibility of thinking and responding. The longer response times for the older adults can be explained by a reduced speed of information processing; their response times were especially slow at the first stage because they took longer to initiate the task. The results were in accordance with normative data using the CANTAB (see Robbins et al., 1998; De Luca et al., 2003).

9.4.3 Spatial Working Memory Task

The age difference in the number of between search errors at the 6 and 8 box stages suggests that as working memory load increased, the elderly group's working memory was not as good as the young. The between search errors were low and did not differ for both groups at the easier 3 and 4 box stages, indicating that both age groups understood task rules and requirements. Longer completion times can be attributed to reduced speed of processing in the elderly. Adopting a repetitive search strategy can aid performance on this task by reducing working memory load. The optimal strategy involves searching through the boxes in the same order on each trial, while remembering not to search in boxes containing tokens on previous trials (e.g. Fray et al., 1996; Owen et al., 1990). The older group's lower use of a repetitive search strategy when performing the task meant that they lost the benefit of reducing working memory load; this indicates that they had a reduced ability to formulate an effective strategy when problem solving compared to younger adults. The results were in accordance with normative data using the CANTAB (see Robbins et al., 1998; De Luca et al., 2003).

9.4.4 Stockings of Cambridge Task

There was no age difference in the number of problems solved in the minimum number of moves therefore planning was relatively intact in the elderly. The older adult's longer initial thinking times suggested that, in accordance with reduced speed of processing theory, they took longer to 'think out' a plan. Interestingly, however, the elderly group's longer subsequent thinking times and greater excess moves at the harder 4 and 5 move stages suggested that when both age groups had a failed attempt at the harder stages, the elderly were disproportionately affected by the initial failure resulting in longer time to re-think the plan and more errors to produce the correct pattern. This finding implies that planning ability only deteriorates in the elderly after a failure. Similar results have been reported for depressed elderly compared to normal elderly controls (Beats et al., 1996) but, to our knowledge, this pattern of results has not been demonstrated in normal elderly compared to young adults. The results were in accordance with normative data using the CANTAB (see Robbins et al., 1998; De Luca et al., 2003).

9.4.5 Inter-Relationship Between Cognitive Tests

There were no significant correlations between the spatial span score and the between search errors at any stage of the Spatial Working Memory task for younger or older adults, therefore there was no relationship between short-term memory capacity and working memory performance. This result suggests that the older group's reduced performance on the Spatial Working Memory task was related to a decreased ability to manipulate information in short-term memory (an executive aspects of neuropsychological functioning) rather than holding information in short-term memory (a non-executive aspect of neuropsychological functioning). In addition, for both age groups, greater use of strategy was associated with reduced between search errors on the Spatial Working Memory task, confirming that a repetitive search strategy aided working memory performance.

9.5 Conclusion

The elderly were impaired compared to the young in spatial short-term memory, spatial working memory and strategy use but relatively intact in flexibility of thinking and responding, and spatial planning. Interestingly, planning ability and flexibility of thinking and responding only deteriorated in the elderly after an initial failure. Any age related decline in performance on any of the tasks occurred at the harder stages indicating that cognitive tests need to be difficult to observe the effects of normal ageing. The findings from this chapter form the basis for interpreting the outcomes of the correlation analyses in the following chapter, where the magnitude of the late right frontal effect recorded for the elderly in Experiment 2a was correlated with performance on the CANTAB tests presented in this chapter.

Chapter 10 Experiment 2c

10.1 Introduction

Experiment 1a identified the presence of three temporally and topographically distinct frontal old/new effects in the young adults, which were qualitatively similar for the retrieval of intrinsic and extrinsic contexts: a bilateral anterior frontal effect from 450-900ms, a right prefrontal effect from 900-1300ms and a right frontal effect from 1300-2000ms. Significant correlations between the magnitude of these effects and performance on the CANTAB tests (Experiment 1b) suggested that the bilateral anterior frontal effect was related to working memory, strategy use and planning, the right prefrontal effect was related to working memory and planning and the right frontal effect was related to planning.

Experiment 2a revealed three topographically similar right frontal effects across all three time windows (450-900ms, 900-1300ms and 1300-2000ms) for the retrieval of the extrinsic context in older adults. The right frontal effect from 450-900ms was topographically different to a bilateral anterior frontal effect present in the new group of young participants, but the right frontal effects from 900-1300ms and 1300-2000ms were topographically similar to right frontal effects evident in the young. The findings from Experiment 2a suggested that not entirely the same post-retrieval processes were adopted by young and older adults. The findings from Experiment 2b indicated that the older adults had reduced performance on tests of neuropsychological functioning, providing a possible explanation for why the age groups recruited different post-retrieval processes.

The aim of Experiment 2c is to investigate the functional significance of the right frontal effects present in the elderly from Experiment 2a, by assessing whether the magnitude of the effects correlates with performance on tests of executive functioning taken from the CANTAB. The participants were the 24 older adults from Experiment 2a. An additional 18 data sets were collected so that correlation analyses could be performed between the magnitude of the right frontal effects and performance on the CANTAB tests. Consistent with the predictions from Experiment 1b, if the current interpretation of the late right frontal effect as being an index of executive/post retrieval control, or general decision making processes, is correct, it is predicted that the magnitude of the right frontal effect will correlate with performance on the CANTAB tests, thus resolving conflict in the literature over the functional significance of the effect.

10.2 Methods

10.2.1 Participants

Participants were the 24 older adults from Experiment 2a, along with a further 21 older volunteers. Three data sets from the additional 21 participants were discarded due to insufficient behavioural trial numbers. Of the 42 participants (24 plus the additional 18) 20 were female, and all were aged between 64 and 80 (mean age 70.10). All other aspects of the methods are described in the ‘General Methods’ chapter.

10.3 Results

The within age topographic analyses from Experiment 2a demonstrated that three topographically similar right frontal effects were present across all three time windows (450-900ms, 900-1300ms and 1300-2000ms). These effects were also topographically similar for target and non-target responses within each time window. Consequently, all following behavioural, ERP and correlation analyses for the elderly were performed using data collapsed across target and non-target responses and included the further 18 elderly participants that were necessary to increase statistical power to perform correlation analyses.

10.3.1 Behaviour

The behavioural data are reported in Table 26 (below). Hits represent data collapsed across target and non-target responses. Accuracy was greater for correct rejections than hits and reaction times were faster for correct rejections compared to hits. These results were confirmed by paired t-tests [Accuracy: $t(41) = -17.65$, $p < 0.001$; RT: $t(41) = 12.66$, $p < 0.001$].

Accuracy	
Hits	0.64 (0.15)
Correct Rejection	0.94 (0.10)
RT(ms)	
Hits	1745 (268)
Correct Rejection	1350 (241)

Table 26. Mean (SD) behavioural data for the 42 elderly participants in Experiment 2c. Hits represent data collapsed across target and non-target responses. Accuracy was greater for correct rejections than hits, and reaction times were faster for correct rejections compared to hits.

10.3.2 Rationale for the ERP and Correlation Analyses

Consistent with Experiment 1b, the aim of the ERP magnitude analyses was firstly to demonstrate that significant frontal and left parietal old/new effects were present when data was collapsed across target and non-target responses, and secondly to determine at which electrodes the effects were maximal. The global magnitude ANOVA included factors of response ‘R’ [old (collapsed across target and non-target responses) vs. new], hemisphere ‘H’ (left vs. right) and site (F1, F3, F5, F7, AF3, AF7, FP1, F2, F4, F6, F8, AF4, AF8, FP2). Figure 44 shows the grand average old and new waveforms from 36 electrode sites. The mean number of trials contributing to the waveforms was 32 old and 48 new.

The purpose of the ERP topographic analyses was to confirm that topographically similar right frontal old/new effects were present across time windows when data was collapsed across responses. The global topographic analyses included factors of epoch ‘E’ (300-450 ms vs. 450-900 ms vs. 900-1300 ms vs. 1300-2000 ms), hemisphere ‘H’ (left vs. right) and site ‘S’ (F1, F3, F5, F7, AF3, AF7, FP1, F2, F4, F6, F8, AF4, AF8, FP2). The distributions of the old/new effects are illustrated in the topographic map shown in Figure 45.

Subsequent correlation analyses were then conducted to assess if the magnitude of the effects (collapsed across the two electrode sites where the effects were maximal) correlated with performance on tests of executive functioning, to investigate the functional significance of the right frontal effects present in the elderly participants.

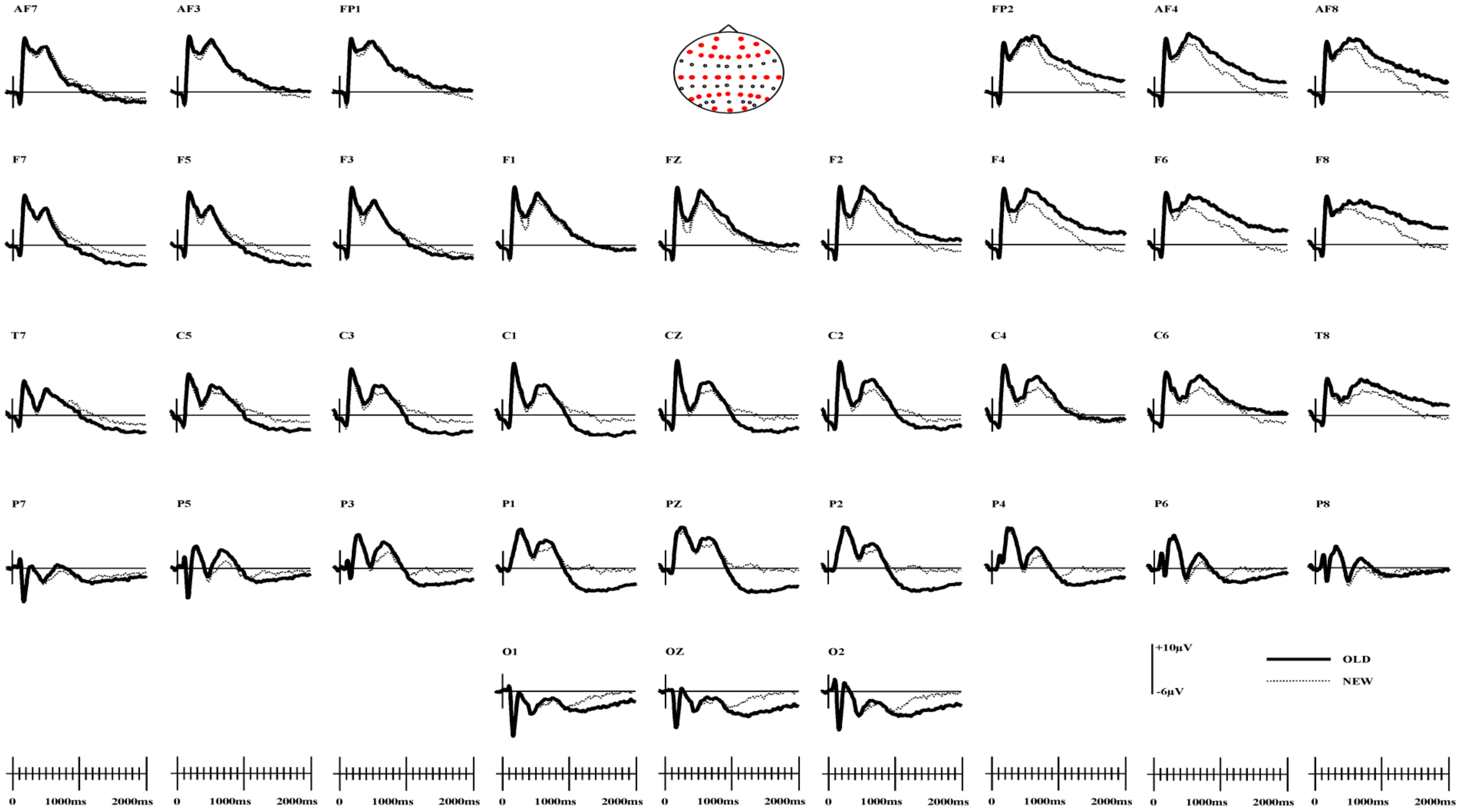

Figure 44. Grand average ERP waveforms for correctly classified old (collapsed across target and non-target responses) and new items. 36 electrode sites are shown, arranged as if looking down onto the top of the head. The total range of effects shown is 16μV.

The global magnitude analyses revealed main effects and interactions involving the factor of response for all four latency windows (see Table 27). The highest order ANOVA result from 300-450ms was a two-way response by site interaction, and three-way response by hemisphere by site interactions from 450-900ms, 900-1300ms and 1300-2000ms. These interactions were further examined with subsidiary analyses.

Latency Window	Old vs. New
300-450ms	
R	F(1,41)=8.49,p=0.006
RxS	F(2.71,111.09)=2.83,p=0.05
450-900ms	
R	F(1,41)=8.09,p=0.007
RxH	F(1,41)=47.88,p<0.001
RxS	F(2.67,109.38)=5.23,p=0.003
RxHxS	F(3.79,155.45)=9.95,p<0.001
900-1300ms	
R	F(1,41)=4.37,p=0.04
RxH	F(1,41)=33.72,p<0.001
RxS	F(2.34,96.12)=5.67,p=0.003
RxHxS	F(2.73,111.72)=7.72,p<0.001
1300-2000ms	
R	F(1,41)=7.73,p=0.008
RxH	F(1,41)=38.72,p<0.001
RxS	F(2.37,97.12)=5.59,p=0.003
RxHxS	F(3.23,132.36)=12.20,p<0.001

Table 27. Results of the global magnitude analyses. Old items are collapsed across target and non-target responses. R, H and S represent the factors of response, hemisphere and site respectively. Main effects and interactions were present for all four latency windows.

Subsidiary paired t-tests investigating the global response by site interaction from 300-450ms (Table 27) confirmed the presence of a significant bilateral frontal effect at all frontal sites (Figure 45, A), except F7/F8 [F1/F2 – t(41) = 3.51, p = 0.001; F3/F4 – t(41) = 3.17, p = 0.003; F5/F6 – t(41) = 2.63, p = 0.01; AF3/AF4– t(41) = 3.20, p = 0.003; AF7/AF8– t(41) = 2.31, p = 0.03; FP1/FP2– t(41) = 2.56, p = 0.01]. The effect was maximal at F1/F2 [Mean 0.79μV].

The positivity of old waveforms compared to new waveforms at frontal sites continued into the 450-900ms latency window (Figure 45, B). Subsidiary analyses investigating the global response by hemisphere by site interaction (Table 27) revealed that the right frontal effect was significant at all right frontal sites [F2 – $t(41) = 5.26$, $p < 0.001$; F4 – $t(41) = 6.41$, $p < 0.001$; F6 – $t(41) = 5.71$, $p < 0.001$; F8 – $t(41) = 3.68$, $p = 0.001$; AF4 – $t(41) = 5.31$, $p < 0.001$; AF8 – $t(41) = 4.11$, $p < 0.001$; FP2 – $t(41) = 3.81$, $p < 0.001$]. The effect was maximal at F4 [Mean 1.63μV] and F6 [Mean 1.57μV]. Despite the appearance of a left frontal negativity, this was not statistically significant. To assess the significance of the left parietal effect from 450-900ms, targeted t-tests at left parietal sites (P1, P3 and P5) were conducted, revealing significant differences at sites P3 [$t(41) = 3.35$, $p = 0.002$] and P5 [$t(41) = 4.70$, $p < 0.001$].

From 900-1300ms, old/new differences persisted (Figure 45, C). Subsidiary analyses investigating the global response by hemisphere by site interaction (Table 27) revealed that the right frontal effect was significant at all right frontal sites [F2 – $t(41) = 3.19$, $p = 0.003$; F4 – $t(41) = 4.75$, $p < 0.001$; F6 – $t(41) = 4.77$, $p < 0.001$; F8 – $t(41) = 3.61$, $p = 0.001$; AF4 – $t(41) = 4.81$, $p < 0.001$; AF8 – $t(41) = 4.30$, $p < 0.001$; FP2 – $t(41) = 5.07$, $p < 0.001$]. The effect was maximal at F4 [Mean 1.99μV] and F6 [Mean 1.98μV]. Moreover, the left sided negativity was significant at left frontal sites F5 [$t(41) = -2.82$, $p = 0.01$] and F7 [$t(41) = -2.93$, $p = 0.01$]. Because the magnitude analyses in Experiment 2a revealed that, for the elderly participants, the left frontal negativity extended to left fronto-central sites, targeted t tests of left fronto-central sites were conducted, revealing significant negativities at all left fronto-central sites [FC1 – $t(41) = -1.89$, $p = 0.07$; FC3 – $t(41) = -2.63$, $p = 0.01$; FC5 – $t(41) = -3.95$, $p = 0.01$; FT7 – $t(41) = -2.94$, $p = 0.01$]. However, the left sided negativity was still maximal at sites F5 [Mean -1.11μV] and F7 [Mean -1.03μV].

The right frontal effect and left sided negativity continued into the 1300-2000ms time window (Figure 45, D). Subsidiary analyses investigating the global response by hemisphere by site interaction (Table 27) revealed significant new greater than old negativities at left hemisphere sites F5 and F7 [F5 – t(41) = -2.13, p = 0.04; F7 – t(41) = -2.41, p = 0.02]. Again, targeted t tests of left fronto-central sites were performed, showing significant negativities at all left fronto-central sites, except FC1 [FC3 – t(41) = -1.86, p = 0.07; FC5 – t(41) = -3.02, p = 0.04; FT7 – t(41) = -2.40, p = 0.02]. The effect was maximal at F5 [-1.05μV] and F7 [-1.14μV]. Old greater than new positivities were also present at all right frontal sites [F2 – t(41) = 3.29, p = 0.002; F4 – t(41) = 6.13, p < 0.001; F6 – t(41) = 5.50, p < 0.001; F8 – t(41) = 5.34, p < 0.001; AF4 – t(41) = 5.50, p < 0.001; AF8 – t(41) = 5.41, p < 0.001; FP2 – t(41) = 5.99, p < 0.001]. The right frontal effect was maximal at F6 [Mean 2.80μV] and F8 [Mean 2.59μV].

10.3.2.1 ERP Topographic Analyses

Figure 45 illustrates the change in distribution of the old/new effects over time. The description and topographic analyses will only focus on the frontal and left parietal effects. There is a change in distribution over successive latency periods from a bilateral frontal effect to a left parietal effect, late right frontal effect and left frontal negativity.

The global topographic analyses revealed main effects and interactions involving the factor of epoch (Table 28). Consequently, three subsidiary topographic comparisons were conducted (300-450 ms vs. 450-900 ms, 450-900 ms vs. 900-1300 ms, 900-1300 ms vs. 1300-2000 ms), investigating the highest order epoch by hemisphere by site interaction.

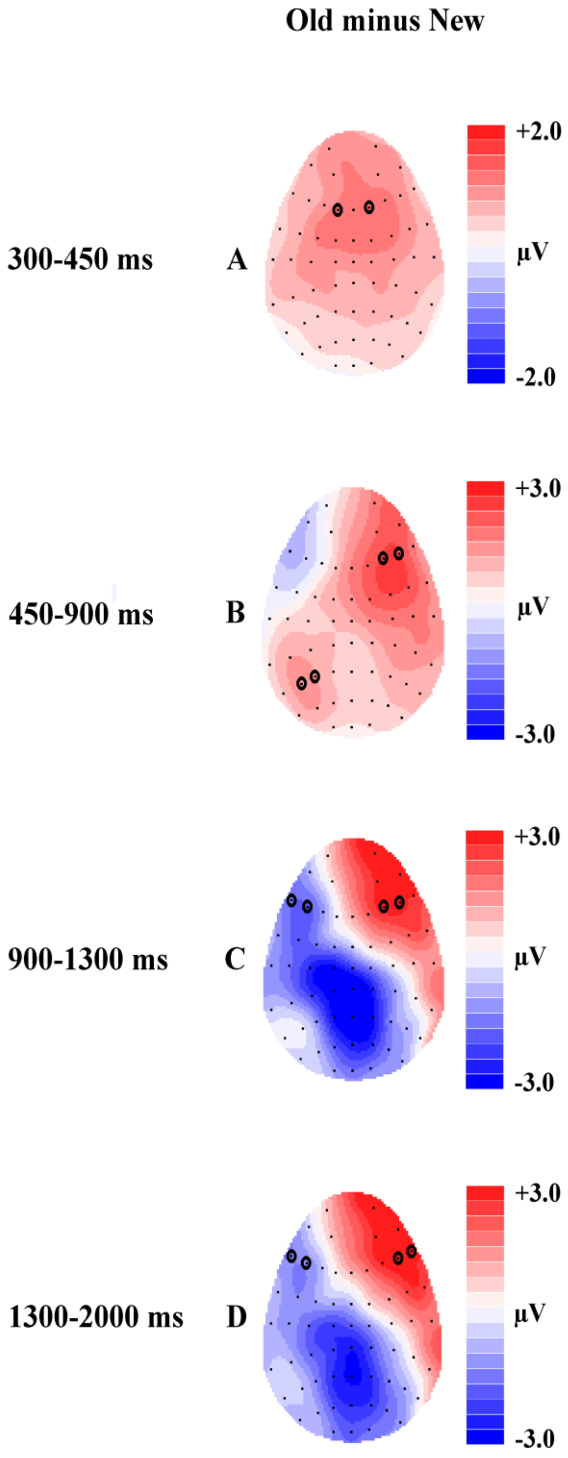

Figure 45. Topographic maps illustrating the scalp distribution of ERP effects for the 42 elderly participants. Each map is shown as if looking down onto the top of the head with frontal sites towards the top of the page. Old items are collapsed across target and non-target responses. The electrodes highlighted in black are those used in the correlation analyses. There is a change in distribution over successive latency periods from a bilateral frontal effect to a left parietal effect and a right frontal effect, and finally a left sided negativity.

	Old minus New
ExH	F(1.76,72.33)=11.11,p<0.001
ExS	F(3.57,146.19)=3.51,p=0.01
ExHxS	F(5.14,210.90)=3.54,p=0.004

Table 28. Results of the global topographic analyses of rescaled difference waveforms, comparing all four latency windows. Old items are collapsed across target and non-target responses. E, H and S represent the factors of epoch, hemisphere and site respectively. Main effects and interactions involving the factor of epoch were present.

Subsidiary analyses, from 300-450 ms vs. 450-900ms, investigating the global epoch by hemisphere by site interaction (Table 28) also revealed an epoch by hemisphere by site interaction [F(2.79,114.32) = 5.60, p = 0.002]. This interaction reflected a change in distribution over time from a bilateral frontal effect in the first latency period to a right frontal effect in the second latency period (Figure 45, A and B).

For the 450-900 ms vs. 900-1300 ms comparison, subsidiary analyses investigating the global epoch by hemisphere by site interaction (Table 28) also revealed an epoch by hemisphere by site interaction [F(2.99,122.44) = 3.24, p = 0.03]. This interaction demonstrated the evolution of the left sided negativity in the latter time window. There was no topographic difference between the right frontal effects from 450-900 ms and 900-1300 ms (Figure 45, B and C).

Subsidiary analyses, from 900-1300ms vs. 1300-2000ms, investigating the global epoch by hemisphere by site interaction (Table 28) produced no significant results involving the factor of epoch. Therefore, the left sided negativity and right frontal effect from 900-1300ms and 1300-2000ms were qualitatively similar (Figure 45, C and D).

10.3.2.2 ERP and Neuropsychological Correlation Analyses

Consistent with Experiment 1b, correlations were performed on the old minus new data, collapsed across the two sites where the frontal and left parietal effects were maximal

(300-450ms: F1 and F2; 450-900ms: F4 and F6, P3 and P5; 900-1300ms: F5 and F7, F4 and F6; 1300-2000ms: F5 and F7, F6 and F8). The sites used in the correlation analyses are highlighted on Figure 45. Correlations involving behavioural accuracy and reaction time on the exclusion task were performed using data collapsed across hits and correct rejections (see Table 26).

<u>300-450ms</u>: There were no significant correlations between the magnitude of the putative bilateral frontal correlate of familiarity (Figure 45, A) and performance on any of the neuropsychological tests (see Table 29). However, there was a significant positive correlation between the magnitude of the effect and behavioural accuracy (r = 0.55, $p < 0.001$), but not reaction time (Figure 46).

CANTAB Task and Main Measures	r	r square	p value
Spatial Span Task			
Span Score	0.01	0.00	0.94
Total Errors	-0.10	0.01	0.52
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	-0.04	0.00	0.82
Mean Errors at ED Shift	0.06	0.00	0.73
Mean Errors up to ED Shift	-0.11	0.01	0.49
Mean Response Time Across All Stages (msec)	0.11	0.01	0.49
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	0.05	0.00	0.76
Strategy Score	0.06	0.00	0.69
Mean Time Across All Stages (msec)	0.05	0.00	0.78
Stockings of Cambridge Task			
Stages Solved in Minimum Moves	-0.09	0.01	0.55
Mean Initial Thinking Time Across All Stages (msec)	0.12	0.01	0.44
Mean Subsequent Thinking Time Across All Stages (msec)	0.08	0.01	0.61
Mean Number of Excess Moves Across All Stages	0.07	0.00	0.64

Table 29. Results of the correlation analyses between the magnitude of the putative Bilateral Frontal Correlate of Familiarity from 300-450ms and performance on the CANTAB tests. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F1 and F2, where the Bilateral Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on any of the CANTAB tests.

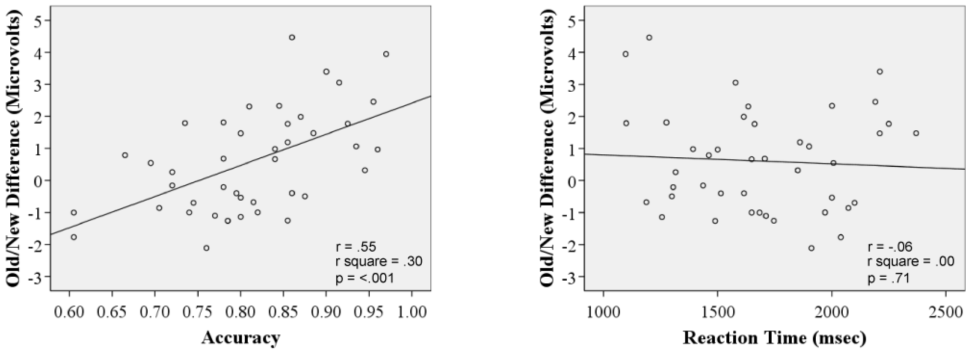

Figure 46. Scatterplots depicting the relationship between the magnitude of the putative Bilateral Frontal Correlate of Familiarity from 300-450ms and behavioural performance on the exclusion task. Accuracy and reaction time are data from Table 26 collapsed across hits and correct rejections. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There was a significant positive correlation between the magnitude of the effect and accuracy, but not reaction time.

450-900ms: There were no significant correlations between the magnitude of the left parietal correlate of recollection (Figure 45, B) and performance on any of the neuropsychological tests (see Table 30). However, there was a significant positive correlation between the magnitude of the effect and behavioural accuracy (r = 0.40, p = 0.01), but not reaction time (Figure 47).

CANTAB Task and Main Measures	r	r square	P value
Spatial Span Task			
Span Score	0.26	0.07	0.10
Total Errors	0.20	0.04	0.21
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	0.26	0.07	0.09
Mean Errors at ED Shift	0.22	0.05	0.17
Mean Errors up to ED Shift	0.14	0.02	0.38
Mean Response Time Across All Stages (msec)	0.15	0.02	0.33
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	0.03	0.00	0.83
Strategy Score	0.02	0.00	0.86
Mean Time Across All Stages (msec)	0.03	0.00	0.86
Stockings of Cambridge Task			
Stages Solved in Minimum Moves	-0.01	0.00	0.96
Mean Initial Thinking Time Across All Stages (msec)	0.27	0.07	0.08
Mean Subsequent Thinking Time Across All Stages (msec)	0.03	0.00	0.87
Mean Number of Excess Moves Across All Stages	0.09	0.01	0.58

Table 30. Results of the correlation analyses between the magnitude of the Left Parietal Correlate of Recollection from 450-900ms and performance on the CANTAB tests. Correlations were performed using the ERP old minus new data (microvolts), collapsed across sites P3 and P5, where the Left Parietal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on any of the CANTAB tests.

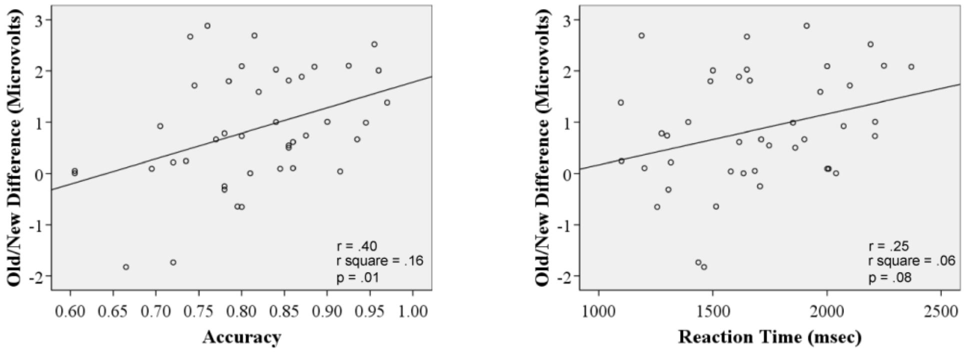

Figure 47. Scatterplots depicting the relationship between the magnitude of the Left Parietal Correlate of Recollection from 450-900ms and behavioural performance on the exclusion task. Accuracy and reaction time are data from Table 26 collapsed across hits and correct rejections. Correlations were performed using the ERP old minus new data (microvolts), collapsed across sites P3 and P5, where the Left Parietal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There was a significant positive correlation between the magnitude of the effect and accuracy, but not reaction time.

In addition, there were no significant correlations between the magnitude of the right frontal effect (Figure 45, B) and performance on the spatial span task, the ID/ED set-shifting task or the spatial working memory task (Table 31). As can be seen in Figure 48, however, significant positive correlations were present between the magnitude of the effect and the Stockings of Cambridge Sets Solved in Minimum Moves ($r = 0.30$, $p = 0.05$), Mean Initial Thinking Time ($r = 0.49$, $p = 0.001$), and significant negative correlations with Mean Subsequent Thinking Time ($r = -0.28$, $p = 0.07$) and Mean Number of Excess Moves ($r = -0.33$, $p = 0.03$). The magnitude of the effect also correlated positively (Figure 49) with behavioural accuracy ($r = 0.52$, $p < 0.001$) and reaction time ($r = 0.49$, $p = 0.001$).

CANTAB Task and Main Measures	R	r square	p value
Spatial Span Task			
Span Score	0.09	0.01	0.55
Total Errors	-0.13	0.02	0.41
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	0.04	0.00	0.83
Mean Errors at ED Shift	0.13	0.02	0.42
Mean Errors up to ED Shift	-0.13	0.02	0.40
Mean Response Time Across All Stages (msec)	0.09	0.01	0.59
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	-0.15	0.02	0.34
Strategy Score	-0.13	0.02	0.41
Mean Time Across All Stages (msec)	-0.05	0.00	0.75

Table 31. Results of the correlation analyses between the magnitude of the Right Frontal Effect from 450-900ms and performance on the Spatial Span Task, ID/ED Attention Set-Shifting Task and the Spatial Working Memory Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F4 and F6, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on the Spatial Span Task, ID/ED Attention Set-Shifting Task or the Spatial Working Memory Task.

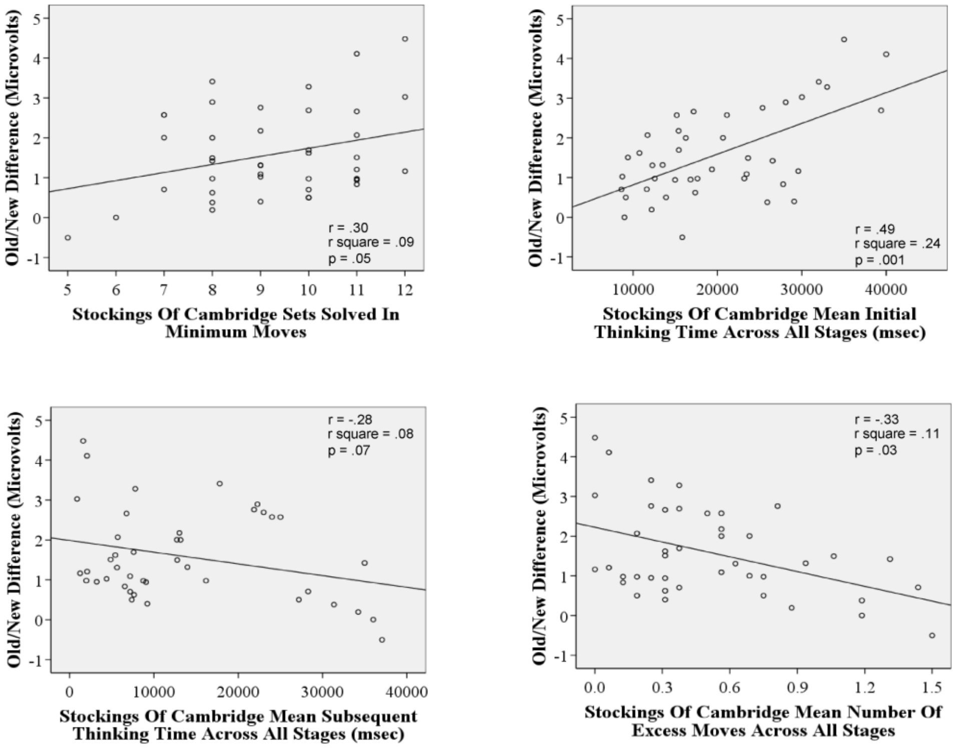

Figure 48. Scatterplots depicting the relationship between the magnitude of the Right Frontal Effect from 450-900ms and performance on the Stockings Of Cambridge Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F4 and F6, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the task. There were significant positive correlations between the magnitude of the effect and the Sets Solved In Minimum Moves, Mean Initial Thinking Time, and significant negative correlations with Mean Subsequent Thinking Time and the Mean Number Of Excess Moves.

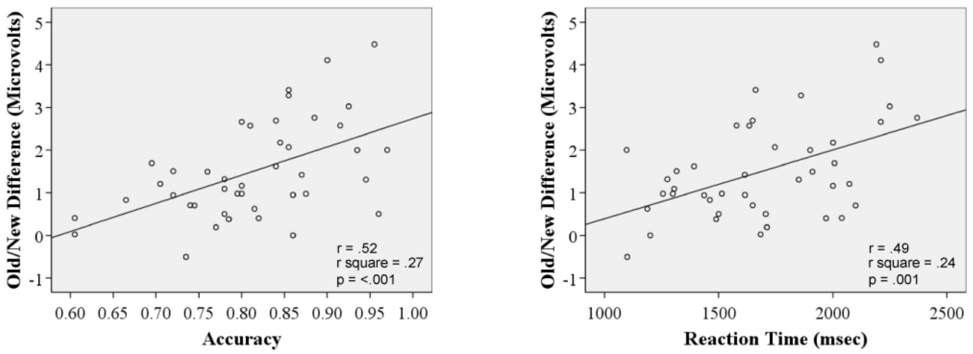

Figure 49. Scatterplots depicting the relationship between the magnitude of the Right Frontal Effect from 450-900ms and behavioural performance on the exclusion task. Accuracy and reaction time are data from Table 26 collapsed across hits and correct rejections. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F4 and F6, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There were significant positive correlations between the magnitude of the effect and accuracy and reaction time.

900-1300ms: There were no significant correlations between the magnitude of the left sided negativity (Figure 45, C) and performance on any of the neuropsychological tests, or behavioural performance on the exclusion task (see Table 32). In line with the right frontal effect in the previous time window, there were no significant correlations between the magnitude of the right frontal effect (Figure 45, C) and performance on the spatial span task, the ID/ED set-shifting task or the spatial working memory task (see Table 33). However, and again in accordance with the right frontal effect in the previous time window, there were significant correlations (Figure 50) between the magnitude of the right frontal effect and the Stockings of Cambridge Sets Solved in Minimum Moves (r = 0.47, p = 0.002), Mean Initial Thinking Time (r = 0.28, p = 0.07), and significant negative correlations with Mean Subsequent Thinking Time (r = -0.40, p = 0.009) and Mean Number of Excess Moves (r = -0.44, p = 0.004). The magnitude of the effect also correlated positively (Figure 51) with behavioural accuracy (r = 0.32, p = 0.04) and reaction time (r = 0.46, p = 0.002).

CANTAB Task and Main Measures	r	r square	p value
Spatial Span Task			
Span Score	0.06	0.00	0.70
Total Errors	0.24	0.06	0.13
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	0.23	0.05	0.15
Mean Errors at ED Shift	0.05	0.00	0.74
Mean Errors up to ED Shift	0.11	0.01	0.48
Mean Response Time Across All Stages (msec)	-0.15	0.02	0.34
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	0.12	0.01	0.47
Strategy Score	0.15	0.02	0.35
Mean Time Across All Stages (msec)	0.07	0.00	0.65
Stockings of Cambridge Task			
Stages Solved in Minimum Moves	-0.02	0.00	0.92
Mean Initial Thinking Time Across All Stages (msec)	-0.14	0.02	0.39
Mean Subsequent Thinking Time Across All Stages (msec)	0.07	0.00	0.66
Mean Number of Excess Moves Across All Stages	0.04	0.00	0.80
Exclusion Task Behavioural Performance			
Accuracy	-0.19	0.04	0.22
Reaction Time (msec)	0.03	0.00	0.87

Table 32. Results of the correlation analyses between the magnitude of the Left Sided Negativity from 900-1300ms and performance on the CANTAB tests and behavioural performance on the exclusion task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F5 and F7, where the Left Frontal Negativity was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on any of the Neuropsychological tasks or behavioural performance on the exclusion task.

CANTAB Task and Main Measures	R	r square	p value
Spatial Span Task			
Span Score	0.14	0.02	0.38
Total Errors	0.04	0.00	0.81
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	0.02	0.00	0.88
Mean Errors at ED Shift	-0.08	0.01	0.60
Mean Errors up to ED Shift	0.05	0.00	0.77
Mean Response Time Across All Stages (msec)	-0.16	0.03	0.32
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	-0.17	0.03	0.27
Strategy Score	-0.20	0.04	0.20
Mean Time Across All Stages (msec)	-0.17	0.03	0.27

Table 33. Results of the correlation analyses between the magnitude of the Right Frontal Effect from 900-1300ms and performance on the Spatial Span Task, ID/ED Attention Set-Shifting Task and the Spatial Working Memory Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F4 and F6, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on the Spatial Span Task, ID/ED Attention Set-Shifting Task or the Spatial Working Memory Task.

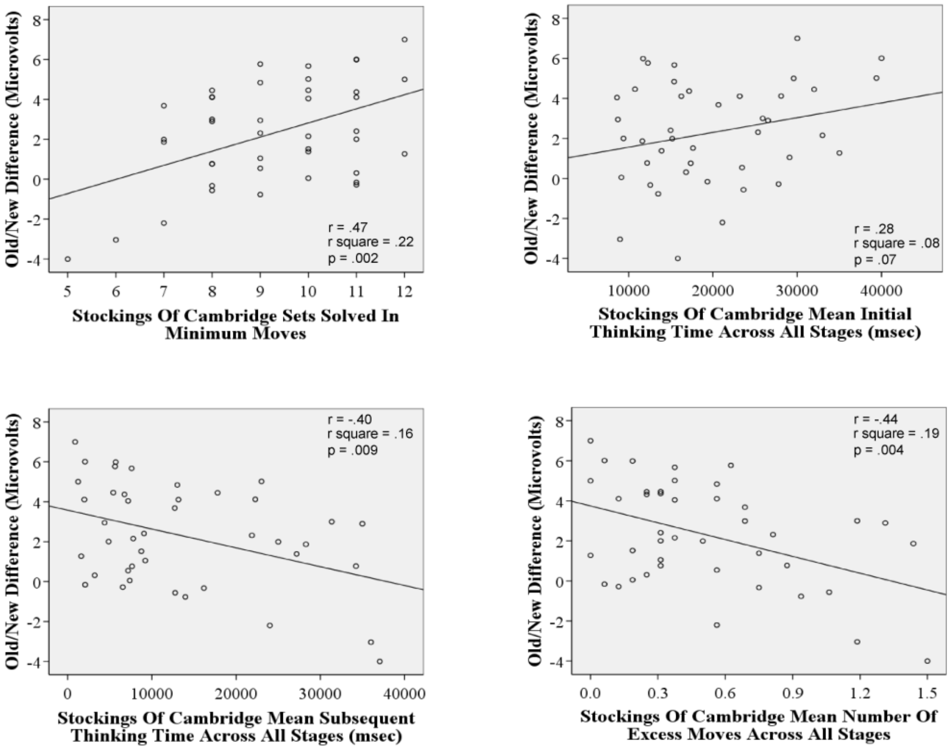

Figure 50. Scatterplots depicting the relationship between the magnitude of the Right Frontal Effect from 900-1300ms and performance on the Stockings Of Cambridge Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F4 and F6, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the task. There were significant positive correlations between the magnitude of the effect and the Sets Solved In Minimum Moves, Mean Initial Thinking Time, and significant negative correlations with Mean Subsequent Thinking Time and the Mean Number Of Excess Moves.

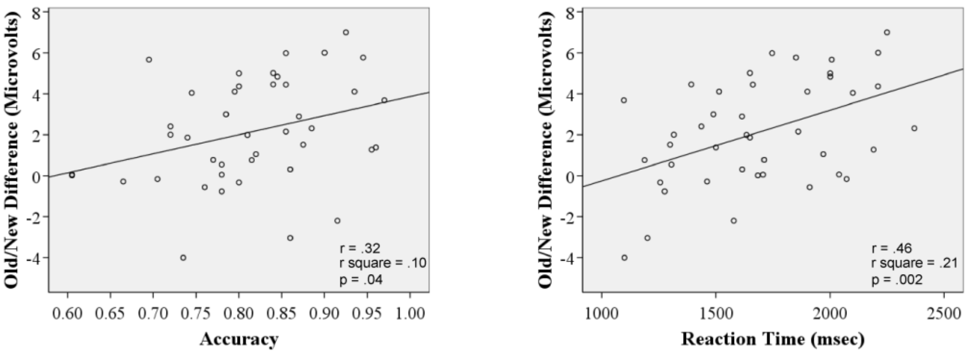

Figure 51. Scatterplots depicting the relationship between the magnitude of the Right Frontal Effect from 900-1300ms and behavioural performance on the exclusion task. Accuracy and reaction time are data from Table 26 collapsed across hits and correct rejections. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F4 and F6, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There were significant positive correlations between the magnitude of the effect and accuracy and reaction time.

<u>1300-2000ms</u>: The left sided negativity (Figure 45, D) did not correlate significantly with performance on any of the neuropsychological tests, or behavioural performance (see Table 34). In line with the right frontal effect in the previous two time windows, there were no significant correlations between the magnitude of the right frontal effect (Figure 45, D) and performance on the spatial span task, the ID/ED set-shifting task or the spatial working memory task (see Table 35). However, and again in accordance with the previous two time windows, there were significant correlations (Figure 52) between the magnitude of the right frontal effect and the Stockings of Cambridge Sets Solved in Minimum Moves (r = 0.32, p = 0.04), Mean Initial Thinking Time (r = 0.31, p = 0.04), and significant negative correlations with Mean Subsequent Thinking Time (r = -0.33, p = 0.03) and Mean Number of Excess Moves (r = -0.32, p = 0.04). The magnitude of the effect also correlated positively (Figure 53) with behavioural accuracy (r = 0.31, p = 0.04) and reaction time (r = 0.44, p = 0.003).

CANTAB Task and Main Measures	r	r square	p value
Spatial Span Task			
Span Score	0.09	0.01	0.57
Total Errors	0.22	0.05	0.15
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	0.25	0.06	0.11
Mean Errors at ED Shift	0.10	0.01	0.52
Mean Errors up to ED Shift	0.22	0.05	0.16
Mean Response Time Across All Stages (msec)	-0.09	0.01	0.58
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	0.21	0.04	0.18
Strategy Score	0.24	0.06	0.13
Mean Time Across All Stages (msec)	0.24	0.06	0.12
Stockings of Cambridge Task			
Stages Solved in Minimum Moves	0.05	0.00	0.78
Mean Initial Thinking Time Across All Stages (msec)	-0.14	0.02	0.36
Mean Subsequent Thinking Time Across All Stages (msec)	0.01	0.00	0.93
Mean Number of Excess Moves Across All Stages	0.01	0.00	0.95
Exclusion Task Behavioural Performance			
Accuracy	-0.26	0.07	0.08
Reaction Time (msec)	0.06	0.00	0.71

Table 34. Results of the correlation analyses between the magnitude of the Left Sided Negativity from 1300-2000ms and performance on the CANTAB tests and behavioural performance on the exclusion task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F5 and F7, where the Left Frontal Negativity was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on any of the Neuropsychological tasks or behavioural performance on the exclusion task.

CANTAB Task and Main Measures	R	r square	p value
Spatial Span Task			
Span Score	0.27	0.07	0.09
Total Errors	0.21	0.04	0.18
ID/ED Attention Set-Shifting Task			
Mean Errors Across All Stages	0.08	0.01	0.62
Mean Errors at ED Shift	-0.07	0.00	0.64
Mean Errors up to ED Shift	-0.04	0.00	0.78
Mean Response Time Across All Stages (msec)	-0.02	0.00	0.91
Spatial Working Memory Task			
Mean Between Search Errors Across All Stages	-0.09	0.01	0.55
Strategy Score	-0.12	0.01	0.44
Mean Time Across All Stages (msec)	-0.06	0.00	0.71

Table 35. Results of the correlation analyses between the magnitude of the Right Frontal Effect from 1300-2000ms and performance on the Spatial Span Task, ID/ED Attention Set-Shifting Task and the Spatial Working Memory Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F6 and F8, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the tasks. There were no significant correlations between the magnitude of the effect and performance on the Spatial Span Task, ID/ED Attention Set-Shifting Task or the Spatial Working Memory Task.

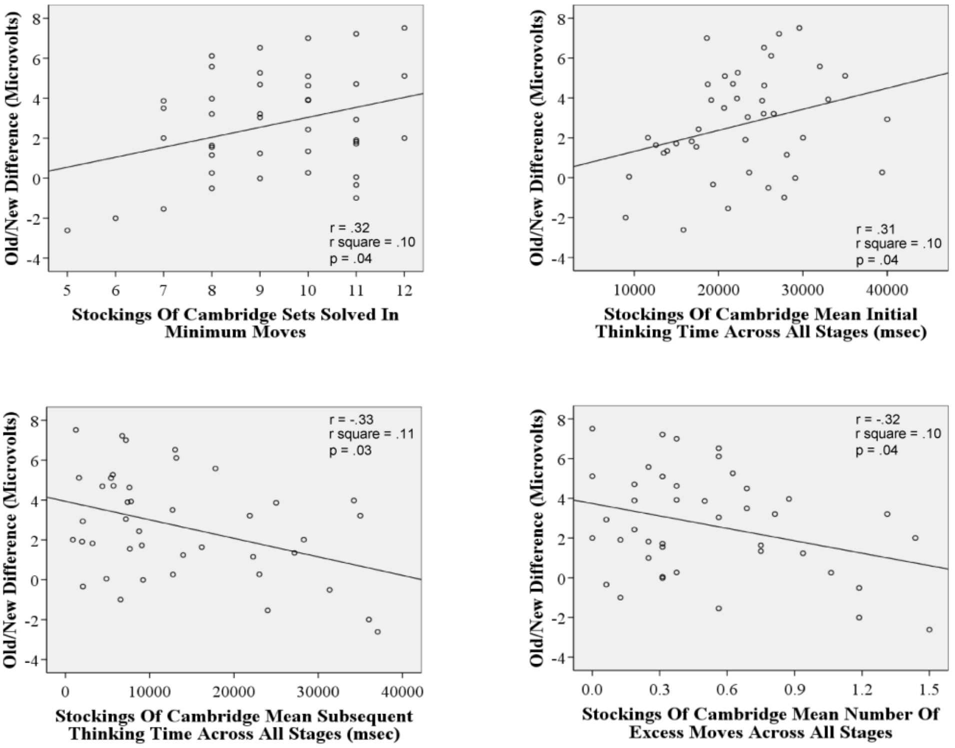

Figure 52. Scatterplots depicting the relationship between the magnitude of the Right Frontal Effect from 1300-2000ms and performance on the Stockings Of Cambridge Task. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F6 and F8, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to performance on the task. There were significant positive correlations between the magnitude of the effect and the Sets Solved In Minimum Moves, Mean Initial Thinking Time, and significant negative correlations with Mean Subsequent Thinking Time and the Mean Number Of Excess Moves.

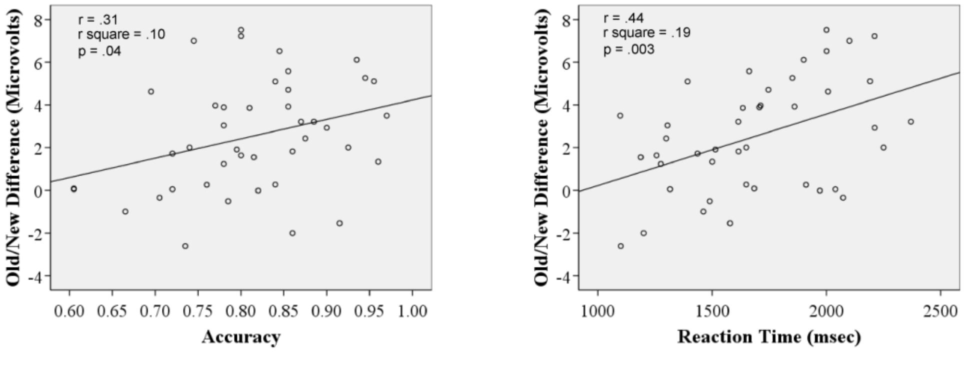

Figure 53. Scatterplots depicting the relationship between the magnitude of the Right Frontal Effect from 1300-2000ms and behavioural performance on the exclusion task. Accuracy and reaction time are data from Table 26 collapsed across hits and correct rejections. Correlations were performed on the ERP old minus new data (microvolts), collapsed across sites F6 and F8, where the Right Frontal Effect was maximal. r square (x 100) shows how much variance (%) in the magnitude of the effect is related to behavioural performance. There were significant positive correlations between the magnitude of the effect and accuracy and reaction time.

10.3.2.2.1 Summary of Results

The magnitude of the putative bilateral frontal correlate of familiarity and the left parietal correlate of recollection did not significantly correlate with performance on any of the neuropsychological tests. The effects did, however, significantly increase as behavioural accuracy improved, but did not significantly correlate with behavioural reaction time. This result suggests that these old/new effects are not related to the non-executive function of short-term memory, the executive functions of attentional set shifting (or flexibility of thinking and responding), working memory, strategy use, planning or behavioural reaction time, but are related to behavioural accuracy.

The magnitude of the left sided negativity, from 900-1300ms and 1300-2000ms, did not significantly correlate with performance on any of the neuropsychological tests or behavioural performance, suggesting that this effect is not related to the above non-executive or executive functions, or to behavioural accuracy and reaction time.

The magnitude of the right frontal effect, from 450-900ms, 900-1300ms and 1300-2000ms, did not significantly correlate with performance on any part of the Spatial Span task, the Attentional Set Shifting task or the Spatial Working Memory task. The magnitude of the effects did increase, however, as the Stockings of Cambridge number of sets solved in minimum moves and initial thinking time increased, and decreased as subsequent thinking time and number of excess moves increased. The magnitude of the effects increased as behavioural accuracy and reaction time increased. These results suggest that the right frontal effects are not related to short-term memory, flexibility of thinking and responding, strategy use or working memory, but are related to planning and behavioural accuracy and reaction time.

10.4 Discussion

The aim of Experiment 2c was to further investigate the functional significance of the late right frontal effect in the elderly from Experiment 2a, by assessing whether the magnitude of the effect correlated with performance on neuropsychological tests taken from the CANTAB. The late right frontal effect was fractionated into three topographically similar right frontal effects from 450-900ms, 900-1300ms and 1300-2000ms. The right frontal effects were not related to short-term memory, flexibility of thinking and responding, strategy use or working memory, but were related to planning and behavioural accuracy and reaction time. Furthermore, the putative bilateral frontal correlate of familiarity, the left parietal correlate of recollection and the left sided negativity were not related to short-term memory, flexibility of thinking and responding, strategy use, working memory, planning or behavioural reaction time. However, the bilateral frontal and left parietal effects were related to behavioural accuracy.

10.4.1 Bilateral Frontal Correlate of Familiarity

The majority of evidence suggests that the bilateral frontal effect provides an index of familiarity (Rugg and Curran, 2007). Consistent with the results from Experiment 1b, it is therefore unsurprising that the effect did not significantly correlate with performance on any of the neuropsychological tests. While the results cannot speak to the familiarity interpretation of the effect, they do imply that it is not related to the executive functions assessed in this experiment. The effect was related to behavioural accuracy suggesting that greater activation was associated with higher accuracy on the exclusion task. As the bilateral frontal effect is a core memory retrieval effect, as opposed to a post retrieval monitoring effect, it is unsurprising that there was no significant correlation with behavioural reaction time.

10.4.2 Left Parietal Correlate of Recollection

The left parietal effect is widely considered to provide an index of recollection (Allan et al., 1998). Consequently, and in accordance with the findings from Experiment 1b, it is unsurprising that the effect did not significantly correlate with performance on any of the neuropsychological tests. While the results do not speak to the recollection interpretation of the left parietal effect, they do imply that the effect is not related to the executive functions assessed in this experiment. The effect was related to behavioural accuracy suggesting that greater activation was associated with higher accuracy on the exclusion task. As the left parietal effect is a core memory retrieval effect, as opposed to a post retrieval monitoring effect, it is unsurprising that there was no significant correlation with behavioural reaction time.

10.4.3 Left Sided Negativity

The functional significance of the left sided negativity is unclear, however Trott et al., 1997; Wegesin et al., 2002 and Li et al., 2004 have proposed that it reflects the engagement of additional, compensatory, processes to assist with retrieval. If this interpretation is correct, the fact that the effect did not significantly correlate with performance on any of the neuropsychological tests suggests that the compensatory processes are not related to the executive functions assessed in this experiment. The functional significance of this effect still remains unclear.

10.4.4 Right Frontal Effect

The right frontal effects were not related to short-term memory, flexibility of thinking and responding, strategy use or working memory, but were related to planning and behavioural accuracy and reaction time. The fact that the effects did not correlate with short-term memory, but did correlate with some of the executive functions, provides support for the executive functioning account of the late right frontal effect and highlights that the effect is not simply related to effort. There was not a large task switching requirement during the test phase therefore it is not surprising that the effect was not related to flexibility of thinking and responding. There was no relationship between the right frontal effects and working memory, suggesting that the effects are not associated with holding retrieved information in working memory and instead are related to planning ahead, possibly to the next trial. Post retrieval monitoring in the elderly therefore appears to be associated with planning ahead, rather than reflecting back on the information just retrieved. The relationship between the effect and behavioural accuracy and reaction time indicates that planning ahead increases accuracy and decision times.

Chapter 11 General Discussion

The aim of the research reported in this thesis was to combine neuropsychological and event-related potential (ERP) approaches to investigate the effects of ageing on strategic retrieval in episodic memory. This chapter will integrate the results from the five experimental chapters into the wider literature by providing a discussion of strategic retrieval in young adults, followed by the effects of ageing on strategic retrieval, then the hypothesis of ageing and memory will be revisited and finally future directions will be considered. Prior to this, the chapter will begin by summarising the results of the research reported in this thesis.

11.1   Summary of Results

11.1.1   Younger Adults

The putative bilateral frontal correlate of familiarity (300-450ms) was significant in Experiment 1a for the retrieval of the intrinsic context, but not for the retrieval of the extrinsic context in Experiment 1a or Experiment 2a. The effect was significant for targets and non-targets in the intrinsic context condition and was of equivalent magnitude for each response. The left parietal correlate of recollection (450-900ms) was significant for the retrieval of the intrinsic and the extrinsic context in Experiment 1a and the extrinsic context in Experiment 2a. This correlate, while significant for targets and non-targets, was greater in magnitude for targets. The late posterior negativity (900-1300ms and 1300-2000ms) was significant for targets and non-targets for the intrinsic and extrinsic contexts in Experiment 1a and the extrinsic context in Experiment 2a. The magnitude of the effect did not differ for targets and non-targets.

A left frontal negativity (1300-2000ms) was significant, and of equal magnitude, for targets and non-targets in the extrinsic context of Experiment 1a and Experiment 2a.

Three temporally and topographically distinct frontal old/new effects were present for the intrinsic and extrinsic contexts in Experiment 1a: a bilateral anterior frontal effect (450-900ms), a right prefrontal effect (900-1300ms) and a right frontal effect (1300-2000ms). These frontal effects were of equivalent magnitude and topography for target and non-target responses across both contexts. Significant correlations between the magnitude of theses three effects and performance on the CANTAB tests of executive functioning in Experiment 1b suggested that the bilateral anterior frontal effect was related to working memory, strategy use and planning; the right prefrontal effect was related to working memory and planning, while the right frontal effect was related to planning. In Experiment 2a there were two topographically distinct frontal old/new effects: a bilateral anterior frontal effect (450-900ms) and a right frontal effect (900-1300ms and 1300-2000ms). These effects were of equivalent magnitude and topography for targets and non-targets. There was no evidence of a right prefrontal old/new effect from 900-1300ms in Experiment 2a.

11.1.2 Older Adults

The putative bilateral frontal correlate of familiarity (300-450ms) was significant for the retrieval of the extrinsic context in Experiment 2a. This effect was of equivalent magnitude for targets and non-targets. As stated above, this effect was not significant for the young in Experiment 2a. The left parietal correlate of recollection (450-900ms) was significant for targets and non-targets and was of equal magnitude for each response, in contrast to it being greater for targets than non-targets for the younger adults. The effect was also significantly reduced for older adults than younger adults for targets and non-targets.

The late posterior negativity (900-1300ms and 1300-2000ms) was significant for targets and non-targets, but was statistically larger for targets from 900-1300ms; the magnitude of the effect did not differ for targets and non-targets in the younger adults of Experiment 2a. The magnitude of the effect appeared equivalent in both age groups. A left sided negativity was significant for targets only from 900-1300ms and 1300-2000ms. This effect was significant later in the younger group (1300-2000ms only), was more left frontally distributed and was significant for targets and non-targets.

Three topographically similar right frontal effects were present from 450-900ms, 900-1300ms and 1300-2000ms. These frontal effects were of equivalent magnitude and topography for target and non-target responses. While the magnitude and topography of the right frontal effects from 900-1300ms and 1300-2000ms appeared equivalent across both age groups in Experiment 2a, a bilateral anterior frontal effect was present in the younger adults from 450-900ms compared to the right frontal effect evident in the older adults. Significant correlations between the magnitude of the three right frontal effects in the older adults and performance on the CANTAB tests of executive functioning in Experiment 2c suggested that all three effects were related to planning. Experiment 2b highlighted that the older adults' spatial working memory performance and strategy use was reduced compared to the young, whereas spatial planning and flexibility of thinking and responding was relatively intact, providing an explanation for the differences in post retrieval processing across age groups.

11.2 Strategic Retrieval in Young Adults

11.2.1 Bilateral Frontal Correlate of Familiarity

Experiment 1a permitted the ERP correlates of intrinsic and extrinsic contexts to be compared without confounds of different experimental designs and separate participant groups. The findings implied that context influenced strategic retrieval via familiarity: familiarity based remembering occurred only for the retrieval of intrinsic context, whereas there was as a common reliance on recollection and executive/post retrieval monitoring across contexts.

The evidence of a significant bilateral frontal effect only for the intrinsic context in Experiment 1a suggested that because the gender the word was spoken in was an inherent part of the word, the gender and the word became unitised during encoding, enhancing familiarity based remembering at retrieval and resulting in faster identification of target and non-target items. The fact that the effect was not significant in the extrinsic contexts of Experiment 1a and 2a, where the judgement made was not an inherent part of the word, provides support for this unitisation claim. Unitisation enhancing familiarity based remembering is also supported by ERP studies of associative recognition (Jager et al., 2006; Opitz and Cornell, 2006; Rhodes and Donaldson, 2007; Ecker and Zimmer, 2007), behavioural studies of associative recognition (Giovanello et al., 2006; Quamme et al., 2007) a behavioural study of recognition memory for faces (Yonelinas et al., 1999), an fMRI study of source memory retrieval (Staresina and Davachi, 2006) and finally a behavioural study of source memory retrieval (Diana et al., 2008).

The claim that, compared to extrinsic context, intrinsic context becomes unitised with the word and promotes familiarity based remembering does remain tentative, and needs to be tested by comparing the waveforms elicited by intrinsic and extrinsic contexts after varying the encoding instructions given to participants. For example, in support of the above claim, asking participants to encode both contexts under item imagery (imagine the word and context separately) and interactive imagery (imagine the word and context interacting) conditions should produce the bilateral frontal effect following item and interactive imagery for the intrinsic context, but only after interactive imagery for the extrinsic context. However, previous ERP studies investigating strategic retrieval have used either intrinsic or extrinsic contexts without any consideration of whether this influences their findings; the results from this thesis highlight the importance of considering the context of information used in source memory tasks.

Based on the evidence that the bilateral frontal effect was equivalent in magnitude following a deep and a shallow encoding condition (Rugg et al., 1998), for studied words and plurality reversed lures given an ‘old’ response (Curran, 2000), for studied pictures and mirror reversed lures given an ‘old’ response (Curran and Cleary, 2003) and for studied words and semantically related lures given an ‘old’ response (Geng et al., 2007), the most influential interpretation of the functional significance of the bilateral frontal effect is that it represents familiarity (Rugg and Curran, 2007). It was therefore unsurprising that the magnitude of the effect did not significantly correlate with any of the neuropsychological tests in Experiment 1b. The effect did increase, however, as behavioural accuracy on the exclusion task increased, suggesting that familiarity increases accuracy. The magnitude of the effect did not significantly correlate with behavioural reaction time on the exclusion task which appears surprising given the claim that unitisation during encoding enhances familiarity based remembering at retrieval and results in faster identification of target and non-target items. However, the correlations in Experiment 1b were performed on the behavioural and ERP data from Experiment 1a collapsed across intrinsic and extrinsic contexts and target, non-target and new responses, possibly masking a significant negative correlation between the magnitude of the effect and reaction time in the intrinsic context alone.

11.2.2 Left Parietal Correlate of Recollection

The left parietal correlate of recollection was significant for targets and non-targets in the intrinsic and extrinsic contexts of Experiment 1a and the extrinsic context of Experiment 2a. These results indicate that the young participants adopted the retrieval strategy of recollecting target and non-target items for both contexts. While left parietal effects for targets and non-targets are consistent with the majority of previous studies employing an intrinsic context (Wilding and Rugg, 1997b; Cycowicz et al., 2001; Wilding and Sharpe, 2004; Wilding et al., 2005), the majority of previous studies employing an extrinsic context have reported left parietal effects for targets only (Herron and Rugg, 2003a; 2003b; Herron and Wilding, 2005; Dzulkifli and Wilding, 2005). Although the behavioural evidence is very mixed, in general higher accuracy is evident for the retrieval of extrinsic context compared to intrinsic context, and Herron and Wilding (2005) proposed that when the likelihood of target recollection is high, participants focus solely on the recollection of target information as this strategy gives rise to accurate task performance. One exclusion study by Dzulkifli et al. (2005) employed an extrinsic context (a function or drawing judgement about words) and found that after a 40-minute delay between study and test, left parietal effects were present for targets and non-targets. Consistent with the fact that this delay increased task demands, lowered target accuracy and resulted in the recollection of target and non-target items, it may be the case that combining intrinsic and extrinsic in one paradigm also increased task demands and made recollection of only target items an insufficient strategy for good performance. Even when the task was simplified slightly in Experiment 2a, by removing the retrieval of the intrinsic context, target accuracy was not high enough to adopt a target specific strategy.

Based on the evidence that the left parietal effect has been observed for items studied under a deep encoding condition but not a shallow encoding condition (Rugg et al., 1998), its magnitude is greater for correct source judgements compared to incorrect source judgements (Wilding et al., 1995; 1996; Trott et al., 1997; Mark and Rugg, 1998; Senkfor and Van Petten, 1998) and is larger for remember responses than know responses (e.g. Smith, 1993; Duzel et al., 1997; Mark and Rugg, 1998; Duarte et al., 2004; Vilberg et al., 2006) it is widely considered to be a neural correlate of recollection. It was therefore unsurprising that the magnitude of the effect did not significantly correlate with any of the neuropsychological tests in Experiment 1b. The effect did increase, however, as behavioural accuracy on the exclusion task increased, suggesting that recollection increases accuracy. As the left parietal effect is a core memory retrieval effect, as opposed to a post retrieval monitoring effect, it was unsurprising that there was no significant correlation with behavioural reaction time.

11.2.3 Late Right Frontal Correlate of Post Retrieval/Executive Processing

The late right frontal effect was significant for targets and non-targets in the intrinsic and extrinsic contexts of Experiment 1a, and the extrinsic context of Experiment 2a. These results suggest that the young participants adopted the retrieval strategy of monitoring target and non-target items for both contexts. While late right frontal effects for targets and non-targets are consistent with the majority of previous studies employing an extrinsic context (Herron and Rugg, 2003a; Dzulkifli and Wilding, 2005;

Dzulkifli et al., 2005), the majority of previous studies employing an intrinsic context have reported late right frontal effects for targets only (Wilding and Rugg, 1997b; Cycowicz et al., 2001; Wilding and Sharpe, 2004). The previous studies using an intrinsic context employed a simple study task (e.g. repeating the gender the word was spoken in or the colour in which the word was presented), whereas the studies using an extrinsic context adopted more complex study tasks (e.g. making a function or drawing judgement about the object), therefore the greater complexity of the study task required post retrieval processing for all studied items. Accordingly, combining intrinsic and extrinsic contexts in the current experiments may have made the study task more complex and hence post retrieval processing was required for all items in both intrinsic and extrinsic contexts.

The current, most influential, interpretation of the functional significance of the late right frontal effect is that it reflects post retrieval monitoring processes. Support for this interpretation came from a false memory study that revealed greater right frontal effects for good performers who also had longer RTs than poor performers, indicating that they were more careful in their decision making (Curran et al., 2001). Further support came from the finding that, during a levels of processing manipulation, the right frontal effect was larger following a shallow encoding task compared to a deep encoding task (Rugg et al., 2000). According to this view, test items that were shallowly encoded will be harder to remember than those that were encoded under deep conditions, resulting in more post-retrieval monitoring following shallow encoding. However, following the finding that the late right frontal effect was significant during a semantic judgement task as well as a source memory task, Hayama et al. (2008) questioned the current interpretation in favour of a general decision making processes account. Therefore the debate over the functional significance of the effect is still ongoing.

Experiment 1a and 1b further investigated the functional significance of the late right frontal effect in young adults. Three temporally and topographically distinct late frontal old/new effects were evident for the intrinsic and extrinsic contexts in Experiment 1a: a bilateral anterior frontal effect (450-900ms), a right prefrontal effect (900-1300ms) and a right frontal effect (1300-2000ms). These frontal effects were of equivalent magnitude and topography for target and non-target responses across both contexts.

Studies of frontal lesion patients have shown source memory deficits and no right frontal effects, therefore the generators of the right frontal effect are thought to be located in the prefrontal cortex (Janowsky et al., 1999; Schacter et al., 1994; Stuss et al., 1994). The prefrontal cortex is associated with our executive functions (Aron et al., 2004), which are a set of higher order cognitive processes (e.g. working memory, planning and strategy use). Neuroimaging studies have identified different regions of the prefrontal cortex that are associated with these executive functions: PET scanning studies have shown that performance on working memory tasks and strategy use activate dorsal and ventral prefrontal regions (Mehta et al., 2000; Owen et al., 1996; Robbins et al., 1998), while performance on planning tasks activate the right dorsolateral prefrontal cortex (Baker, et al., 1996; Morris et al., 1993; Owen et al., 1996).

The identification of three temporally and topographically distinct late frontal effects in Experiment 1a follows suggestions that determining the functional significance of the late right frontal effect may be obscured by measuring it over long time periods that mask other qualitatively distinct late frontal effects associated with the engagement of various executive functions (Friedman and Johnson, 2000; Mecklinger, 2000; Hayama et al., 2008). Experiment 1b revealed that each effect correlated with the neuropsychological tests of working memory, strategy use and planning in different ways, highlighting that the three late frontal effects may indeed reflect the engagement of various executive functions over time.

The relationship between working memory and episodic memory retrieval has been well established: as working memory involves the temporary storage and manipulation of information, it is important for monitoring the retrieval of information from episodic memory (Moscovitch, 1994; Verhaeghen and Salthouse, 1997). The link between strategy use, which according to Baddeley (2007) involves seeking out a range of solutions to solve problems and choosing the most appropriate for the situation, and episodic memory retrieval is also clear from exclusion studies showing that young adults can restrict their recollection (Herron and Rugg, 2003a; Herron and Rugg, 2003b; Herron and Wilding, 2005; Dzulkifli and Wilding, 2005) and post retrieval monitoring (Wilding and Rugg, 1997b; Cycowicz et al., 2001; Wilding and Sharpe, 2004) to target information only. The relationship between planning and episodic memory retrieval is less clear however. According to Lezak et al. (2004) planning involves the identification and organisation of steps needed to carry out an intention or achieve a goal; in order to plan it is necessary to look ahead, conceive of alternatives and weigh and make choices. However, there is no literature that we are aware of that has related episodic memory retrieval with planning.

11.2.3.1 Bilateral Anterior Frontal Effect

The bilateral anterior frontal effect was related to working memory, strategy use and planning. Based on the current knowledge regarding the role of working memory and strategy use in episodic memory retrieval, the definition of planning, the requirements of the exclusion task, the fact that the effect occurred in the same time window as the left parietal correlate of recollection, and was also present prior to a behavioural response being made (RTs were around 1460ms), the following functional interpretation of the effect is proposed: the bilateral anterior frontal effect is associated with holding the recollected information in working memory and monitoring whether or not the strategy chosen to be the best to maximise performance is being employed. For example, in Experiment 1a, target accuracy was not high enough to adopt a target specific strategy, therefore a better strategy was to recollect target and non-target items. The bilateral anterior frontal effect may reflect monitoring of whether this strategy is being employed. The relationship with planning suggests that the participant is looking ahead and planning what button they will press for the recollected information, while the association with behavioural accuracy and reaction time on the exclusion task indicates that monitoring retrieved information increases accuracy and leads to longer decision times.

11.2.3.2 Right Prefrontal Effect

The right prefrontal effect was related to working memory and planning. Again, based on the current knowledge regarding the role of working memory and strategy use in episodic memory retrieval, the definition of planning, the requirements of the exclusion task, the fact that the effect occurred after the time window where the left parietal correlate of recollection was maximal, and was also present prior to a behavioural response being made (RTs were around 1460ms), the following functional interpretation of the effect is proposed: the right prefrontal effect is associated with holding the recollected information in working memory and reflecting back to monitor the accuracy of the recollected information. The absence of a relationship with strategy use indicates that as the time from recollection increases, the need to monitor the strategy at recollection decreases. The relationship with planning suggests that the participant is looking ahead and planning what button they will press for the recollected information, while the association with behavioural accuracy and reaction time on the exclusion task indicates that monitoring retrieved information increases accuracy and leads to longer decision times.

11.2.3.3 Right Frontal Effect

The right frontal effect was related to planning. Again, based on the current knowledge regarding the role of working memory and strategy use in episodic memory retrieval, the definition of planning, the requirements of the exclusion task, the fact that the effect occurred after the left parietal correlate of recollection, and was also present (mostly) after a behavioural response was made (RTs were around 1460ms), the following functional interpretation of the effect is proposed: although there is some overlap between the effect and RT (the effect was significant from 1300-2000ms and RTs were around 1460ms) the majority of the effect occurred after the behavioural response. Consequently, the relationship with planning, and absence of a relationship with working memory or strategy use, suggests that once the response is made the participant no longer reflects back to monitor the accuracy of the recollected information or the strategy employed and instead looks ahead to plan what they need to do on the next trial. The association with behavioural accuracy and reaction time on the exclusion task indicates that planning ahead to the next trial increases accuracy and leads to longer decision times.

11.2.4 Task Switching

The ERP effects in the young adults appeared larger for the extrinsic context in Experiment 2a than the intrinsic or extrinsic contexts of Experiment 1a. As the encoding tasks were held constant across experiments, it is therefore highly probable that the answer to these apparent differences are due to the minimal task switching requirement at retrieval in Experiment 1a. In Experiment 1a, participants were switching between retrieving intrinsic and extrinsic contexts between blocks whereas in Experiment 2a only the extrinsic context was retrieved, removing the task switching requirement. In support of this proposal, previous studies have also shown attenuation of ERP effects following task switching (e.g. Wilding and Nobre, 2001).

Removal of task switching in Experiment 2a might also explain why the young did not show the late right prefrontal effect from 900-1300ms. Because the task was easier than Experiment 1a, it was not necessary to monitor the accuracy of retrieved information for as long as in Experiment 1a.

11.3 The Effects of Ageing on Strategic Retrieval

11.3.1 Bilateral Frontal Correlate of Familiarity and Left Parietal Correlate of Recollection

Consistent with the dual process theory prediction that recollection becomes impaired with ageing whereas familiarity remains relatively spared (Dywan and Jacoby, 1990; Jennings and Jacoby, 1993; Jacoby et al., 1996; Hay and Jacoby, 1996; Jennings and Jacoby, 1997; Jacoby, 1999; Benjamin and Craik, 2001), the bilateral frontal effect was significant for target and non-target items in the elderly group in Experiment 2a, but the left parietal correlate of recollection, while significant, was severely reduced for targets and non-targets compared to the young. This finding is also in accordance with previous source memory studies that found an age-related reduction in the left parietal effect (Mark and Rugg, 1998; Li et al., 2004) and highlights that the elderly adopt the strategy of relying more on familiarity and less on recollection, which is reflected in their higher false alarm rate.

Interestingly, the finding that the left parietal effect was of equal magnitude for targets and non-targets in the elderly, in contrast to it being greater for targets than non-targets for the younger adults, is consistent with a series of exclusion studies (Dywan et al., 1998; 2001; 2002) that found that only younger adults were able to use the strategy of reducing recollection of non-target information. This interpretation is supported by the inhibition deficit hypothesis of cognitive ageing which states that the inhibitory mechanism that suppresses the activation of goal irrelevant information becomes deficient with ageing (Hasher and Zacks, 1988; Zacks and Hasher, 1994; Zacks, 1996; Hasher et al., 1999). In further support of this interpretation, the older group adopted a more liberal response bias than the young when discriminating targets and non-targets in Experiment 2a, suggesting that the elderly were more reactive to non-targets than the young. As stated previously, although the majority of previous studies employing an extrinsic context in the young have reported left parietal effects for targets only, the young adults in Experiment 2a did not completely inhibit recollection of non-targets because target accuracy was too low.

11.3.2 Late Right Frontal Correlate of Post Retrieval/Executive Processing

The magnitude and topography of the right frontal effects in Experiment 2a from 900-1300ms and 1300-2000ms were similar across age groups suggesting a common reliance on post-retrieval processing and replicating results of previous ERP ageing studies (Mark and Rugg, 1998; Li et al., 2004; Morcom and Rugg, 2004) and is also consistent with fMRI evidence that right frontal cortex activation in episodic retrieval is frequently age-equivalent, or increased in older adults (Daselaar et al., 2003; Cabeza, 2002; Park and Gutchess, 2004). However, the young adults exhibited a bilateral anterior frontal effect from 450-900ms, compared to the right frontal effect in the elderly. These findings suggest that qualitatively different post-retrieval processes are engaged across young and older adults.

Significant correlations between the magnitude of the three right frontal effects in the older adults and performance on the CANTAB tests of executive functioning in Experiment 2c suggested that all three effects were related to planning. The association with planning along with the absence of a relationship with working memory or strategy use suggests that post-retrieval processing in the elderly involves planning ahead to the response key used, or what they need to do on the next trial, rather than monitoring the strategy employed or reflecting back on the accuracy of retrieved information. In support of this suggestion, the elderly were impaired compared to the young in spatial working memory and strategy use but relatively intact in spatial planning (Experiment 2b). Interestingly, planning ability only deteriorated in the elderly after an initial failure.

According to the frontal lobe hypothesis the pattern of frontal activity observed in the elderly, whether epitomized by lower frontal activation or more widespread and higher levels of activation, could reflect a reduction in executive functioning associated with the neuroanatomical or neurochemical changes in the ageing frontal lobes (Stafford et al., 1998; Raz, 2000; Madden et al., 2002). Alternatively the age-related differences in frontal activity could reflect compensatory processes to help counteract the decline in executive functioning related to changes in the frontal lobes (Morcom et al., 2003; Jonides et al., 1997; Cabeza et al., 2002). The elderly showed reduced accuracy for targets and non-targets compared to the young in Experiment 2a therefore it is unlikely that post retrieval monitoring in the elderly reflected compensatory processes. The elderly group’s working memory performance and strategy use was reduced compared to the young (Experiment 2b) and the right frontal effect only correlated with planning, which was relatively intact in the elderly. Accordingly, a reduction in executive functioning resulting in less efficient retrieval strategies provides a better account of post retrieval monitoring in the elderly.

11.4 Theories of Ageing and Memory Revisited

11.4.1 Speed of Processing

Whilst a reduction in the speed at which cognitive processes operate in the elderly is a major contributing factor to age-related memory decline (Salthouse, 1996; Verghaeghen and Salthouse, 1997) it does not provide a full account for the results in this thesis. Increased reaction times were evident in the elderly in Experiment 2a, however there was no delay in the onset of significant ERP effects, which would be expected if cognitive slowing fully accounted for the data.

11.4.2 Reduced Processing Resources

The findings are difficult to reconcile with the reduced processing resources hypothesis (Craik and Simon, 1980; Craik and Byrd, 1982; Craik, 1983). According to this hypothesis, retrieval tasks that require a great deal of self initiated processing, or strategic retrieval, should be most susceptible to ageing because strategies are effortful and demand attentional resources. Consistent with this proposal, the elderly showed reduced performance on the exclusion task in Experiment 2a. However, to fully test this proposal a comparison with item recognition, which is simpler and requires less attentional resources, would be required. In addition, the presence of left frontal/sided negativites in older, as well as younger adults, in Experiment 2a, are inconsistent with there being less attentional resources available to the elderly.

11.4.3 Dual Process Theory, Inhibition Deficit Hypothesis and The Frontal Lobe Theory

The findings clearly fit with dual process theory, the inhibition deficit hypothesis and the frontal lobe theory of cognitive ageing. The severe reduction of the left parietal effect for targets and non-targets in Experiment 2a and the significance of the bilateral frontal effect is consistent with the dual process theory prediction that recollection is reduced in the elderly, whereas familiarity remains intact.

However, dual process theory does not fully account for age-related changes in episodic memory. A reduction in working memory performance and strategy use in the elderly, along with a right frontal effect that was only related to planning is highly consistent with the frontal lobe theory of cognitive ageing. Furthermore, a left parietal effect of equivalent magnitude for targets and non-targets in the elderly suggests that, in line with the inhibition deficit hypothesis (Hasher and Zacks, 1988; see also Zacks and Hasher, 1994; Zacks et al., 1996; Hasher et al., 1999), they were less able to reduce activation of goal irrelevant non-target information.

11.5 Left Frontal/Sided Negativities in Younger and Older Adults

The left sided negativity in the elderly is consistent with PET reports that during episodic retrieval older adults can produce both left and right sided prefrontal cortex activation (Backman et al., 1997; Madden et al., 1999; Grady et al., 2002). In particular, in a PET study, Cabeza et al (2002) grouped older adults according to their performance on neuropsychological memory tests. During a source recognition task, high performers on the memory tests showed bilateral prefrontal cortex activation, compared to right prefrontal activation only in the low performers. It has therefore been proposed that additional left sided activation during source memory retrieval is thought to reflect compensatory processes engaged to reduce age-related memory deficits. Further support for the proposal that older adults engage additional compensatory processes comes from ERP source memory studies that have noted central negativities in older adults who show no or reduced late right frontal effects compared to the young (Trott et al., 1997; Wegesin et al., 2002).

The magnitude of the left sided negativities did not significantly correlate with any of the neuropsychological tests (Experiment 2b). Importantly, the absence of a relationship with behaviour on the exclusion task is difficult to reconcile with the compensatory proposal. If the modulation is associated with the engagement of compensatory processes to aid performance, regardless of what these processes are, a relationship with behavioural performance would be expected.

The current data provides tentative support for the alternative account that additional negative activation reflects older adults greater need to retrieve visually based information (Li et al., 2004). In the source memory study by Li et al. (2004) participants studied pictures in an extrinsic context (making an animacy or size judgement) and noted a left sided negativity only for older adults. Although the judgements were made about pictures, which are visually based, the extrinsic context used in this thesis may have encouraged the encoding of visually based information. In support of this proposal, the young adults in Experiment 1a and 2a also produced left negativities (although these were more frontally distributed than those in the elderly), but these were only significant in the extrinsic context. This interpretation is highly speculative and requires testing by asking participants whether they found images coming to mind at encoding, and if this was more so for the extrinsic context than the intrinsic context.

11.6 Future Directions

The research presented in this thesis suggests that the late right frontal effect can be fractionated into qualitatively distinct late frontal effects that are associated with various executive functions post retrieval. The r square values, which indicate how much variance (in percentage) in the magnitude of the effects are related to performance on the neuropsychological tasks, show that the executive functions assessed in this thesis cannot account for all the variance in the magnitude of the late frontal effects. To fully understand what cognitive processes are engaged post retrieval, future research must focus on accounting for the remainder of the variance in the magnitude of the effects.

Volition, which is the motivation to initiate behaviour, is an executive function that is likely to be important during episodic memory retrieval. It should therefore be assessed whether performance on tests of volition correlate with the magnitude of the late frontal effects. Patients with damage to frontal/subcortical or frontolimbic circuitry, may be perfectly capable of performing complex activities, but cannot initiate them unless prompted to do so (Stuss et al., 2000). However the main drawback in investigating the relationship between volition and post retrieval processes is that there are no formal tests for examining volitional capacity. Volition has been investigated by requiring patients to initiate activity. Heilman and Watson (1991) scattered pennies on the table in front of patients, blindfolded them and told them to pick up as many pennies as they could. The task therefore required exploratory behaviour, which was lacking in patients whose capacity to initiate responses was impaired. A similar approach could be used across young and older healthy adults.

The reliability of these findings regarding the functional significant of the late right frontal effect must be assessed by obtaining supporting data from closely related paradigms. Generalising the findings to associative recognition and item recognition for example, will provide further support for the engagement of various executive functions post retrieval.

Future research should also focus on determining the functional significance of the left frontal/sided negativities. The absence of a relationship between the magnitude of the modulation and behavioural performance on the exclusion task does not fit with the compensatory account of its functional significance. The current data provides tentative support for the alternative account that additional negative activation reflects older adults greater need to retrieve visually based information. This interpretation is highly speculative, however, and requires testing by asking participants whether they found images coming to mind at encoding, and if this was more so for the extrinsic context than the intrinsic context.

11.7 Conclusion

The aim of the research reported in this thesis was to combine neuropsychological and event-related potential (ERP) approaches to investigate the effects of ageing on strategic retrieval in episodic memory. The findings have highlighted the necessity to consider the effects of context on the retrieval processes engaged by young and older adults. Furthermore, in order to fully understand the role of the prefrontal cortex and our executive functions in strategic retrieval, it is vital that the focus of future ERP research moves away from measuring the late right frontal effect over extended time periods and instead investigates the functional significance of various shorter duration late frontal effects. This approach will not only further our understanding of post retrieval processes in young adults, but will also help to understand how these processes change in the ageing brain.

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Appendix

This table lists the stimuli used in the source memory exclusion task. The stimuli consist of 408 low frequency nouns and verbs (range 1-7 per million, word length 3-9 letters) taken from Kucera and Francis (1967).

ACID
ADJACENT
ADULTERY
ALCOHOL
ALPHABET
ANTLER
ANVIL
APATHY
APEX
APPLAUSE
APPOINT
ATTIC
AWKWARD
BACHELOR
BAGGAGE
BANDAGE
BANG
BANGLE
BARGAIN
BARGE
BEAD
BEAKER
BEAST
BEE
BISON
BITE
BLADE
BLAST
BLAZE
BLAZER
BLEAT
BLOOM
BRANDISH
BRIBE
BRONZE
BRUISE
BUDGE
BULL
BURGLAR
BURLY
BUST
CABLE
CAMEL
CANINE
CARGO
CASUALTY
CHANT
CHAP
CHAPLAIN
CHECK
CHEESE
CHIMNEY
CHOKE
CHORD
CIGAR
CLAM
CLAW
CLIFF
CLING
CLOAK
CLOG
COARSE
COIL
COMET
COMPLY
CONTOUR
COPIOUS
COUGH
COVE
CRANK
CRATE
CRATER
CRESCENT
CRIMSON
CROOK
CROW
CRYPTIC
CUBE
CULPRIT
CUPBOARD
DEER
DENTIST
DIGITAL
DISCIPLE
DISCOUNT
DISSOLVE
DISTRUST
DIVERT
DOGMA
DONOR
DOVE
DRAGON
DUCK
DUNG
DUNGEON
DURABLE
EASEL
ELDER
ENGAGE
ENZYME
ETHNIC
EVOKE
EXPLORE
FANTASY
FERN
FETCH
FEUD
FIGMENT
FLASK
FLEA
FLOCK
FLOOD
FLUSH
FLUTE
FOAL
FORCE
FORTRESS
FRAGILE
FROST
FUR
GASP
GAUGE
GAUNT
GAUNTLET
GERM
GHETTO
GLOSS
GLUM
GOSSIP
GRANARY
GRAPE
GRAVE
GRAVY
GROAN
GROPE
GROWL
GYPSY
HALT
HALTER
HAMMER
HARSH
HATCH
HATCHET
HAVEN
HAWK
HELMET
HIVE
HOST
HOUND
HUMP
INSTINCT
INSULIN
INSULT
INTACT
JANITOR
JEWEL
JUICE
KIN
KINDLE
LACE
LAD
LANCE
LANTERN
LARD
LARDER
LATCH
LAYOUT
LEGACY
LIGAMENT
LILAC
LIMB
LION
LISTENER
LOBSTER
LUNAR
LUNATIC

LUNGE
LURE
LURID
MAJESTIC
MARITAL
MARSH
MASK
MASSAGE
MATRIX
MATRON
MAZE
MELON
MESH
METRE
MILD
MILL
MINERAL
MINK
MINT
MISTRESS
MOLE
MOLECULE
MONKEY
MONSTER
MORTAL
MOUND
MOUSE
MUCK
MUTANT
MUTE
NEWT
NUDGE
ORACLE
OTTER
PADLOCK
PAGAN
PARASITE
PARCEL
PASSPORT
PASTEL
PATIO
PATRIOT
PEACH
PELVIS
PENDANT
PENSION
PICKLE
PIG
PIVOT
PLANK
PLIERS
PLUM
PLUME
PODIUM
POISE
POISON
PONY
POUCH
PRAM
PRANK
PRAWN
PREMIUM
PRETENSE
PROSE
PROXY
PULPIT
PUPPY
PURGE
QUACK
QUAINT
RAFT
RAFTER
RAISIN
RAMBLE
RAMPAGE
RASH
RAT
RATE
RAVE
RAVEN
RECRUIT
REMEDY
RENTAL
RETINA
REVERE
REVERSAL
RINSE
ROAM
ROAR
ROBIN
ROBOT
ROCKY
ROGUE
RUBBER
RUM
RUMBLE
RUSK
RUST
SAINT
SAPLING
SAUCEPAN
SCAN
SCANDAL
SCARE
SCARF
SCREAM
SCUFFLE
SCULPTOR
SEAL
SECTOR
SENTRY
SEQUEL
SERMON
SHARK
SHAWL
SHEEP
SHILL
SHIN
SHRAPNEL
SHRIMP
SHRINK
SHUFFLE
SICKNESS
SIGH
SILK
SKEWER
SKIP
SLEDGE
SLEET
SLIM
SLOG
SLOT
SLUMBER
SMOG
SNAIL
SNAKE
SNARE
SNORE
SNORKEL
SOLAR
SOLVENT
SONATA
SOPRANO
SPACE
SPADE
SPARSE
SPASM
SPEAR
SPICE
SPIDER
SPIN
SPINACH
SQUADRON
SQUID
STAG
STAPLE
STARVE
STEEPLE
STING
STINK
STOAT
STOCKADE
STROLL
STUMBLE
SUPERB
SURGE
SWAN
SWARM
SWINDLE
SWINE
SWOLLEN
SYMPTOM
TABLET
TABOO
TAILOR
TAVERN
TENTACLE
TESTIFY
THAW
THORN
THRONE
THUD
TICKLE
TICKET
TIGER
TIGHT
TOAD
TONGUE
TONIC
TORMENT
TORSO
TOWEL
TOWER
TRAIT
TRAITOR
TRAM
TRAMP
TRICKLE
TROUT
TUNIC

TURMOIL
TWIN
TWINGE
TYPHOON
TYRANT
VEAL
VENOM
VERGE
VESSEL
VICAR
VILLA
VILLAIN
VINTAGE
VOCAL
WALTZ
WASP
WEALTHY
WEDGE
WEIRD
WHIM
WHISK
WHISKER
WHISPER
WICK
WICKET
WINCH
WOLF
WOMB
WORM
YAWN
YEAST
ZEBRA