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**Ageing and Episodic Retrieval: Using
Event-Related Potentials to Compare the
Neural Correlates of Item and Associative
Recognition in Young and Older Adults**

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Submitted as requirement for the degree of Doctor
of Philosophy at the University of Stirling in
December 2005

05/01

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Acknowledgements

Firstly, I would like to thank all the older volunteers who took part, both in the experiments reported in this thesis and in various pilot studies. People travelled from as far afield as Aberdeen, Dundee, Edinburgh and Glasgow to attend the laboratory; many on two or three occasions. All showed amazing patience and stoicism as they submitted to the ordeal of ERP capping. Most were incredibly supportive and interested in my research, and many waived their payment, being happy to donate their time towards what they considered to be a very worthwhile project. Thanks also to the young volunteers, very few of whom failed to show up at the arranged time, thus allowing the experimental phase to proceed smoothly and to schedule.

Next, I would like to thank my supervisor Dr. David I. Donaldson. David thanks for all your help, support, encouragement and guidance. I feel privileged to have had such a rigorous training, to have been allowed to develop as an independent researcher, and to have been given numerous opportunities to meet many of the leading players in the field of episodic memory over the course of the last four years.

Thanks also to the other members, past and present, of the Psychological Imaging Laboratory at Stirling University. It has been a great experience to see the lab grow from its humble beginnings to what has now become a thriving academic community allowing the exchange of ideas, critiques and (on occasion) alcoholic beverages. A special mention must go to Catriona Bruce whose friendship and technical support proved particularly invaluable during the latter stages of the research.

This project was funded by an ESRC studentship, and I am extremely appreciative of this funding. I am also grateful to my friends, both my journeymen at Stirling and those outside the academic enclave, who have given me encouragement, motivation, and much needed distraction.

Most importantly, my heartfelt gratitude must go to Richard, Kiefer, Oliver and Ella, who have allowed me the freedom to pursue this goal. I hope that you will all be proud of this achievement; it is as much yours as it is mine. I couldn't have done it without your immense patience and loving support (both emotional and practical). Thanks for being there when I needed you, and for putting up with me on the many occasions when research took priority over family life. And finally, thanks to Madeleine, whose recent, somewhat surprising, arrival has allowed me to re-experience life beyond a PhD.

Abstract

Older people commonly report problems with remembering, and behavioural studies have confirmed that memory does decline with age. Age-related deficits are particularly evident in episodic memory; however, the degree of impairment appears to be task-dependent. Compared to young adults, older adults generally perform reasonably well on simple item recognition tasks, but are markedly compromised on more complex tasks, such as those that require memory for context. Dual process theory suggests that this pattern of ageing deficits results from an age-related decline in recollection, whilst familiarity remains relatively intact. This thesis reports a series of event-related potential (ERP) studies conducted to examine the effect of ageing on the neural correlates of simple item recognition and more complex associative recognition. Behaviourally, as anticipated, the young outperformed the elderly, particularly in associative recognition. Electrophysiologically, the age-related reduction of the left parietal effect in item recognition appeared to support the dual process view that recollection becomes compromised as people grow older. Likewise, an early right frontal component, evident in both item and associative recognition, may reflect the preservation of familiarity in elderly adults. However, the ERP data also suggest that dual process theory may represent an oversimplification of episodic memory age decline. While the presence of a left parietal same/rearranged difference in young adults was interpreted as evidence of the adoption of a target-specific recollection strategy in associative recognition, the modulation's absence in older adults suggests that they are unable to similarly inhibit the retrieval of goal-irrelevant information. Moreover, the older participants also demonstrated widespread

left-sided negative activations that may represent two components: First, the fronto-central negativities elicited by both tasks may index the compensatory operations recruited by older adults to maximise their performance. Second, a central/posterior negativity in item recognition, which strongly resembled a modulation that had been previously observed in source memory ageing studies, was interpreted as reflecting the task-irrelevant retrieval of contextual information.

Chapter 1

Episodic Memory

The layman's view of memory is as a single mental operation that allows us to recall past events, to remember what we plan to do at a later date, and to learn new information. In contrast, from the cognitive psychologist's perspective, memory is a complex, non-unitary faculty comprising a number of distinct subcomponents, one of which is generally referred to as episodic memory. The term episodic memory, first proposed by Tulving (1972), describes a form of self-aware memory that may be unique to humans and is defined as "memory for personally experienced events, or remembering what happened where and when" (Tulving, 2002a, p270).

Before embarking on a detailed discussion of episodic memory, it is important to consider its relation with the other subcomponents of memory, for example short-term memory, semantic memory, procedural memory and priming. Accordingly, the purpose of this introductory chapter is to orientate the reader within the taxonomy of memory, and to describe the background against

which the research reported in this thesis was conducted. The chapter will commence with an examination of the ways in which memory has been fractionated, before concentrating on the subset of long-term memory operations that are commonly described as declarative memory. The focus will then turn to episodic memory, with a particular emphasis on recognition memory. As the experimental results in this thesis will be largely interpreted in line with dual process models of recognition memory, the final sections will describe some prominent dual process theories and consider several experimental methodologies that are commonly employed in an attempt to identify the contributions of the two component processes of recognition; familiarity and recollection.

The organization of memory

Short-term and long-term memory

The modern conception of memory as a family of associated subcomponents dates back to Hebb's (1949) proposed distinction between short-term memory (STM) and long-term memory (LTM). STM was considered to be based on temporary electrical activity in the brain; whereas LTM was thought to depend on the establishment of more permanent neurochemical changes. However, the area of research that has arguably been most influential in the development and substantiation of the taxonomy of memory has been the study of the mnemonic capabilities and deficits of amnesic patients, who have acquired selective memory loss as the result of organic brain damage. The classic example of an amnesic patient is H.M., who suffered bilateral medial temporal lobe (MTL) damage following surgery for intractable epilepsy (Scoville

& Milner, 1957). H.M. clearly demonstrated that MTL damage does not result in global memory impairment, by showing a gross reduction in LTM functioning whilst performing well on STM tasks, such as tests of digit span (for other similar cases, see Baddeley & Warrington, 1970; Cave & Squire, 1992).

Such single dissociations in isolation cannot, however, provide conclusive evidence of functional independence between two memory systems. For example, H.M.'s LTM deficit might simply have been due to the increased difficulty of retrieving information after long delays compared to short delays. Consequently, in seeking to provide clear evidence for distinct memory systems, researchers must show double dissociation of function, where typically, one variable affects task 1 but not task 2, and another variable affects task 2 but not task 1. The case of patient K.F., who demonstrated the opposite pattern of memory impairment to H.M., namely a severely impaired auditory STM, in conjunction with intact LTM performance, provided the necessary double dissociation to support the contention that STM and LTM are functionally separate forms of memory (Shallice & Warrington, 1970).

Further evidence in support of an STM/LTM distinction has come from studies of healthy humans (e.g. Brown, 1958; Peterson & Peterson, 1959) and animal research (e.g. Kesner & Novak, 1982; Alvarez-Royo et al., 1992). Furthermore, reports of functional double dissociations within STM in neurological patients, normal adults and animals have led to the general acceptance of a multi-component view of short-term (or working) memory (Baddeley & Hitch, 1974; Baddeley, 1986; 2002a; see also Gathercole, 1999).

Nevertheless, it is important to acknowledge that double dissociations are not incompatible with single systems models. The interpretation of double

dissociations as evidence for separate systems depends critically on the selective influence assumption, which states that each variable must selectively affect only one process, and that each process must contribute to only one task (Dunn & Kirsner, 1988). The process purity issue (see "Process purity", below) means that this assumption is rarely met. Consequently the STM/LTM distinction and the multi-component view of working memory should not be viewed as inviolable (Estes, 1999; Ranganath & Blumenfeld, 2005).

Long-term memory systems

The foregoing caveat notwithstanding, studies of lesion patients, healthy adults and animals suggest that LTM may also be best conceptualised as multi-component. For example, densely amnesic patients appear capable of certain types of learning, including the acquisition of motor skills, classical conditioning, habit learning and priming (e.g. Milner, 1968; Warrington & Weiskrantz, 1968; 1970). Two influential taxonomies therefore view LTM as being composed of a number of qualitatively separate systems; within each of which, encoding, storage and retrieval mechanisms are characterised by distinct rules of operation (Sherry & Schacter, 1987).

Tulving (1983; 1985a) originally proposed a ternary monohierarchical classification of LTM in which procedural memory (comprising skill and habit learning, classical conditioning and priming) contained a specialized semantic memory subsystem (comprising factual knowledge about the world), which, in turn, contained an episodic memory subsystem (comprising memory for personally-experienced events). Procedural memory was described as a behavioural action system, where learning occurred in the absence of

awareness and was measured by changes in behaviour. Semantic memory and episodic memory, by contrast, were described as cognitive representational systems.

The observation that perceptual priming (see "Implicit and explicit memory", below) is expressed through cognition rather than through action has proved problematic for Tulving's original (1983; 1985a) classification scheme. Accordingly, an additional perceptual representation system (PRS), comprising specialised modules for different sensory inputs (e.g. visual, auditory, etc.), has subsequently been proposed to separate perceptual priming from procedural memory (Tulving & Schacter, 1990). The PRS is viewed as operating at a pre-semantic level in a less flexible manner than the other cognitive representational systems. The procedural, PRS, semantic and episodic systems are considered to operate serially at encoding, in parallel during storage, and independently at retrieval (Tulving, 1995).

Squire and colleagues (Cohen & Squire, 1980; Squire & Zola-Morgan, 1991; Squire et al., 1993; Squire, 1994) use the umbrella term 'declarative memory' to describe all memory for facts and events. Declarative memory incorporates semantic and episodic memory, and is held to be dependent on the integrity of the MTL and diencephalon. Other forms of non-declarative learning (skills, habits, classical conditioning and priming) are assumed to be dependent on brain regions outwith the MTL and diencephalon. Encoding, storage and retrieval operations are conducted in parallel by the declarative and non-declarative systems, but the division between the two may not always be distinct (e.g. Clark et al., 2002).

Implicit and explicit memory

Both Tulving's and Squire's classifications make important distinctions between conscious and non-conscious forms of remembering. The procedural, PRS and non-declarative systems represent phenomenologically unaware (or implicit) learning, the declarative system represents phenomenologically aware (or explicit) memory, and Tulving (1983; 1985a) makes a further distinction between semantic and episodic awareness. Semantic memory is associated with noetic consciousness, an introspective awareness of the internal and external world; whereas episodic memory is associated with auto-noetic consciousness, which allows an individual to remember events from their past and to be aware of their own identity and existence in subjective time.

The distinction between implicit and explicit memory has provided the impetus for a distinct field of research that has notably informed the debate over the organization of LTM (for reviews, see Graf & Schacter, 1985). By definition, implicit memory describes situations where “previous experiences facilitate performance on a task that does not require conscious or intentional recollection of those experiences” (Schacter, 1987, p501). Conversely, explicit memory is revealed when “performance on a task requires conscious recollection of those experiences”. The implicit/explicit distinction has largely been studied through the observation of dissociations in the performance of both amnesic patients and normal adults on tasks involving intentional retrieval (e.g. free recall, cued-recall and recognition memory), and on tasks where no intentional learning is required (e.g. lexical decision; and see Schacter, 1987; 1995; Richardson-Klavehn & Bjork, 1988; Roediger & McDermott, 1993).

Although some authors (e.g. Roediger & McDermott, 1993) describe the psychological paradigms used to study unintentional and intentional memory as implicit and explicit tasks, this usage is problematic because most tasks can tap more than one type of process. For example, the performance of amnesic patients on a priming task can be concluded with reasonable confidence to reflect implicit remembering, as their explicit remembering is generally severely impaired. In contrast, involuntary intentional remembering may contribute to the performance of normal adults on the same priming task (Squire et al., 1987). Accordingly, other terminology, for example, indirect and direct tasks (Richardson-Klavehn & Bjork, 1988), is often considered more appropriate to refer to the paradigms designed to study implicit and explicit remembering, respectively.

Rigorous comparison of implicit and explicit memory require that the indirect and direct tasks employed fulfil the retrieval intentionality criterion (Schacter et al., 1989). The retrieval intentionality criterion requires that all overt experimental conditions are held constant, with the sole exception of the instructions given at the time of test. Adhering to this criterion ensures that test performance reflects only the type of retrieval (implicit or explicit) involved and is not confounded by other extraneous factors. For example, according to the retrieval intentionality criterion, contrasting some form of repetition priming (indirect) task with a recall or recognition (direct) task should be achieved through initial exposure to the same set of materials (e.g. a list of words) with identical instructions in both instances. At test, the same retrieval cues should be presented (e.g. word stems) and subjects instructed either to complete the stems with any word that comes to mind (word stem completion – indirect task),

or to try to complete the stems using words from the study phase (cued-recall – intentional retrieval). Implicit remembering (as measured by the level of previously-seen words being used to complete the stems in the indirect task) can then be directly compared with explicit remembering (as measured by the level of recall of previously-seen words in the direct task), and dissociations between the two forms of remembering assessed by contrasting different experimental conditions.

Experimental evidence for the existence of separate memory systems

As discussed above, in order for two forms of memory to be considered as independent systems, they must be shown to be functionally distinct (Sherry & Schacter, 1987; but for the methodological limitations of functional dissociations, see Dunn & Kirsner, 1988). Double dissociations between implicit and explicit remembering have been observed in healthy adults when different experimental variables are manipulated. For example, depth of processing at study has been shown to affect performance on direct, but not on indirect, tasks; whereas changes between study and test modalities have been shown to affect indirect, but not direct, tasks (Jacoby & Dallas, 1981). Nevertheless, although often cited as evidence for separate implicit and explicit memory systems, such dissociations may equally reflect the differential sensitivity of each task to the same memory operation (Jacoby & Kelley, 1991), or the fact that the tasks impact on a single memory system in opposite directions (Dunn & Kirsner, 1988).

The demonstration of statistical or stochastic independence between two types of memory, however, places tighter constraints on theory, and is therefore generally considered to constitute more robust evidence towards the existence of separate memory systems (Tulving, 1985a). Stochastic independence refers to the relationship between performance on two tests, aggregated across participants and across items. If performance across the tests is uncorrelated, then they are assumed to tap different memory systems. Nevertheless, critics of stochastic independence methodology have proposed different explanations for the lack of correlation between tests. For example, stochastic independence has been discounted as an artifact produced by the influence of the first test on the second test (Shimamura, 1985), or as an artifact of the way items (and participants) are selected (Hintzman & Hartry, 1990). In addition, as stochastic independence has been observed between indirect memory tasks, which according to systems theory should be stochastically dependent (e.g. Hayman & Tulving, 1989; Witherspoon & Moscovitch, 1989), Roediger and colleagues (1999), among others, have argued convincingly that stochastic dissociation does not exclusively require a memory systems interpretation.

Long-term memory processes

The demonstration that two indirect memory tasks may be stochastically independent highlights the weakness of the use of dissociation methodology to define separate memory systems. The variation in the observed functional relationships between different tasks is a clear demonstration that the assumption of selective influence has been violated (Dunn & Kirsner, 1988). Instead, the complex pattern, which includes parallel effects between implicit

and explicit tasks as well as dissociations between two implicit and two explicit tasks, suggests there may be considerable overlap between the memory operations contributing to direct and indirect tasks (Dunn & Kirsner, 1989; for reviews of direct/indirect comparisons, see Richardson-Klavehn & Bjork, 1988; Roediger & McDermott, 1993).

Accordingly, a second theoretical interpretation of the reported between-task dissociations rejects the systems account of LTM, arguing that memory is better conceptualised in terms of its underlying mental processes. Instead of reflecting the operation of distinct systems, performance differences on separate tasks are considered to reflect the degree of overlap between the operations performed at study and those performed at test. This principle has been referred to as 'transfer-appropriate processing' (Morris et al., 1977), 'encoding specificity' (Tulving & Thomson, 1973), or simply as a process account of LTM (Dunn & Kirsner, 1988; 1989; Roediger et al., 1989a; Roediger et al., 1989b; Roediger & McDermott, 1993).

Process accounts of LTM consider the critical distinction underpinning dissociations in performance on indirect and direct memory tasks to be between data-driven (bottom-up or perceptual) processing and conceptually-driven (top-down) processing. As indirect tasks are mostly (but not exclusively) data-driven, and direct tasks are mostly (but not exclusively) conceptually-driven, process theory can readily explain the differential effects of experimental manipulations on indirect and direct tests (Jacoby, 1983; Blaxton, 1989; Roediger et al., 1989a; Roediger & McDermott, 1993). Crucially, however, process theory can also account for dissociations between two indirect or two direct tasks, which

appear more problematic for systems theory, by assuming that one task is data-driven and one task is conceptually driven (Roediger & McDermott, 1993).

Nevertheless, process accounts of LTM cannot readily explain all direct/indirect task dissociations. Toth and Hunt (1990) reported an orthographic (perceptual) manipulation that affected performance on a perceptual implicit task and on a conceptual explicit task. Likewise, McDermott and Roediger (1996) reported conceptual manipulations that produced dissociations between conceptual indirect and direct tests. These studies illustrate an important shortcoming of both systems and process theories of LTM. Although both accounts initially appeared to provide elegantly parsimonious interpretations of memory task dissociations, it has subsequently proved necessary to postulate new system and process distinctions to account for such awkward findings. McDermott and Roediger (1996) suggested that the dissociation between implicit and explicit conceptual tests reflected the processing of different types of semantic information. Similarly, Hayward and Tulving (1989) attributed their finding of stochastic independence in completions of different fragments of the same previously-seen words to the hypersensitivity of perceptual operations within one implicit memory system.

However, Witherspoon and Moscovitch's (1989) demonstration that two perceptual implicit tasks (word fragment completion and perceptual identification) can be either stochastically dependent or independent according to the degree of contextual similarity between them, is even problematic for modified versions of systems and process accounts. Witherspoon and Moscovitch therefore proposed a new conceptualisation of LTM organization where separate memory tasks require the operation of different components,

some of which may be common between tasks. Critically, however, any two dissociable tasks must differ in at least one component (Hintzman, 1990).

Components of processing

This components of processing model (Witherspoon & Moscovitch, 1989; Moscovitch, 1994; 1995), which appears to contain elements of both systems and processes theories, describes four major interrelated components, each being responsible for different forms of memory. First, implicit memory is assumed to be mediated by a non-frontal, neo-cortical component comprising various perceptual and semantic modules. Second, a basal-ganglia component is thought to support procedural learning. Third, associative/cue-dependent, explicit/episodic remembering is considered to be dependent on a hippocampal/medial temporal modular component, which acts in a rapid, obligatory, and cognitively impenetrable fashion on information that is consciously apprehended. Fourth, a strategic control (or executive) frontal lobe component is assumed to be the site of more effortful, largely consciously accessible, 'working-with-memory' processes.

An important difference between process (and to a lesser extent systems) theories and the components of processing model, is that the former provide primarily functional accounts of the way in which memory is fractionated, whilst the latter represents a neuropsychological account of LTM organization. Functional accounts are principally based on behavioural evidence of the differential effects of experimental manipulations on separate memory tasks. In contrast, neuropsychological accounts rely primarily on data from lesion patients to provide a biologically-valid conceptualisation of the

division of memory with reference to specific brain structures (but for consideration of the biological basis of memory systems, see Cohen & Squire, 1980; Squire & Zola-Morgan, 1991; Squire et al., 1993; Squire, 1994).

The main advantage of the components of processing model is that it does not assume a direct one-to-one mapping between memory tasks and components/systems/processes, and can easily accommodate the complex pattern of observed behavioural dissociations. This lack of specification of the relationship between components and tasks, however, also constitutes the principle limitation of the components of processing approach; it restricts the testability of the model and exemplifies the process purity issue, which remains one of the fundamental challenges for memory researchers.

Process purity

The scale of the problem posed by the process purity issue was eloquently summarised by Schacter and colleagues (1989) "... just because a test does not require a subject to think back to the study episode does not prevent the subject from doing so anyway. Once we acknowledge this possibility, the basis for drawing an implicit vs. explicit distinction becomes hazy indeed." (pp52-53). Furthermore, just as indirect memory tests may be contaminated by some degree of involuntary consciousness, so direct tests may draw on incidental memory without the participant being aware that this is happening (Jacoby et al., 1993; Reingold & Toth, 1996). Consequently, an important aim of cognitive psychologists is to produce a reliable, objective measure of memory processes that is uncontaminated by the response strategies resulting from different testing procedures. Three attempts to achieve

this goal will be discussed in the "Separating recollection and familiarity" sections below.

Summary

The foregoing section on the organization of memory has made it clear that although there may be some debate over appropriate forms of classification, there appears to be widespread agreement that memory is not a unitary operation (Tulving, 1999). Theories of LTM fractionation range from primarily functional accounts (e.g. process theory) that focus on behavioural dissociations, to primarily neuropsychological accounts (e.g. components of processing theory) that relate the way memory is organised to specific brain regions. Neuropsychological accounts can consequently be viewed as having some biological validity (Tulving, 2002b).

The fundamental limitation of behavioural studies is that, because memory tasks rarely (if ever) map directly onto psychological operations, they can only provide a measure of the combined output of all the systems/ processes/components contributing to a particular task. Although the process purity issue is not entirely resolved in neuroanatomical and neuroimaging studies, these methodologies do allow a more precise quantification of the patterns of neural activation underlying particular tasks. Neuroanatomical and neuroimaging research thus provide supporting evidence for the view that different forms of memory have distinct neurocognitive substrates (Wheeler et al., 1997). The debate over the properties and functional organization of memory is therefore best informed through convergent evidence from behavioural, neuroanatomical and neuroimaging studies. The following sections

will draw on research from all three areas as further subdivisions in memory are explored.

Declarative memory

Although it is widely accepted that the distinction between implicit and explicit memory represents a real theoretical advance (Squire, 1992; Baddeley, 2002b), other proposed divisions within LTM remain more contentious. The remainder of this chapter will focus on the fractionation of explicit (or declarative) memory itself, beginning with an examination of the evidence for a distinction between semantic and episodic memory. It is agreed that the semantic/episodic dichotomy has proved valuable heuristically, but some investigators remain unconvinced that they represent separate forms of memory, whilst, for others the principle debate focuses on the functional and neuroanatomical nature of the semantic/episodic division.

Episodic and semantic memory

Semantic memory and episodic memory have many shared properties: both are large, complex, and highly-structured, but flexible, cognitive systems with an unlimited capacity for information. Such commonalities have led some authors to argue against the independence of semantic and episodic memory systems (e.g. McKoon et al., 1986; Glenberg, 1997; Craik, 2000; Rajah & McIntosh, 2005). Moreover, the most parsimonious explanation for the observation that although amnesic patients typically have preserved semantic memory for facts acquired prior to the onset of their condition, some also have preserved early episodic-type memories (Wilson & Baddeley, 1988), is that

semantic memory simply reflects the accumulation of many episodes, rather than being qualitatively different from episodic memory (Baddeley, 2002b).

Nevertheless, the proposed distinction between episodic and semantic memory continues to be highly influential in guiding research into the functional and neuroanatomical organization of LTM. Tulving and colleagues (e.g. Tulving & Schacter, 1990; Tulving & Markowitsch, 1998; Tulving, 2002b) view episodic memory as an evolutionary extension of semantic memory with certain unique capabilities. According to this 'episodic theory' of explicit memory (Tulving & Markowitsch, 1998), the integrity of the hippocampus is critical to episodic memory, but not to semantic memory, and episodic encoding can only occur 'through' semantic memory.

Alternatively, Squire and colleagues (e.g. Shimamura & Squire, 1987; Squire & Zola, 1996; 1998) claim that episodic and semantic memory are equally dependent on the integrity of the hippocampal/MTL formation, with episodic memory being additionally reliant on the frontal lobes. In direct contrast to the episodic theory, this 'declarative theory' of explicit memory states that episodic memory acts as a gateway to semantic memory, with new knowledge always being encoded as part of an event.

The declarative theory predicts that all amnesic patients with lesions of the hippocampal/MTL formation should be equally impaired in memory for events and memory for facts. In contrast, the episodic theory predicts that an additional category of amnesic patients, with a disproportionate impairment of event learning, should exist. Support for the episodic theory was provided by a study of developmental amnesic (DA) children who, having sustained focal bilateral hippocampal damage between birth and 9 years of age (Vargha-

Khadem et al., 1997), exhibited pronounced episodic memory impairment, but spared semantic capabilities. Moreover, case studies have demonstrated that adult amnesic patients with bilateral MTL lesions can acquire new semantic knowledge, despite suffering severe episodic memory deficits (Tulving et al., 1988; Bayley & Squire, 2002).

However, as discussed previously, such single dissociations do not necessarily demand that episodic and semantic memory must be viewed as functionally separate within the hippocampal/MTL formation. Proponents of declarative theory argue that the semantic knowledge of DA children may reflect residual episodic memory (Squire & Zola, 1998), because although the children perform poorly on tests of delayed recall, their recognition memory is often relatively preserved (Vargha-Khadem et al., 2001). Moreover, one DA patient showed improved recall performance when stimuli were repeatedly presented over a period of time, indicating that some episodic learning had taken place. Likewise, semantic learning in adult amnesic patients (which is typically slower than in normal controls) could either be interpreted as reflecting residual episodic operations (Squire & Zola, 1998), or as the activity of a separate inflexible, non-declarative, neo-cortical learning system (Bayley & Squire, 2002). Finally, the reverse dissociation, namely patients with early onset semantic dementia (SD) who show preserved episodic remembering, particularly for recent events from up to 5 years previously (Hodges & Graham, 2001), is extremely difficult to reconcile with the episodic theory assertion that episodic encoding is dependent on semantic memory.

These findings from SD patients also initially appear to contradict the declarative theory of explicit memory, which would predict that their typical

MTL/left hippocampal atrophy should produce equivalent degrees of semantic and episodic impairment. However, although normal episodic recognition has been demonstrated in SD patients, this only occurs for pictorial stimuli when perceptual integrity is maintained between study and test. One explanation of such findings, which is consistent with the declarative theory, is that perceptual information can feed directly into the episodic system (Hodges & Graham, 2001). Alternatively, the left asymmetry of the hippocampal damage (the right hippocampus typically remains comparatively intact in SD patients) may lead to a disproportionate impairment for the recognition of verbal stimuli.

An alternative account of hippocampal and MTL function emphasises the temporal properties of a memory trace. One influential theory of LTM consolidation (Graham & Hodges, 1997) proposes that whilst the hippocampus is essential for the encoding and retrieval of recent episodic memories, a more permanent, hippocampally-independent memory representation forms in the temporal neocortex over time. Furthermore, a recent study contrasting the rapid and slow acquisition of new semantic knowledge in a patient with focal hippocampal damage, indicated that rapid semantic learning (of word definitions) may also be hippocampus-dependent (Holdstock et al., 2002; for related findings, see Manns et al., 2003).

The foregoing temporal distinctions are also consistent with declarative theory, as they indicate that episodic and semantic memory are similarly dependent on the hippocampus and MTL. Declarative theory further states that the frontal lobes are critical for episodic memory, but not for semantic memory. This assumption is supported by findings from lesion patients with restricted prefrontal brain pathology, who show specific impairment on episodic memory

tasks (for reviews, see Wheeler et al., 1995). Moreover, (1997) source memory deficits have been shown to be independent of the degree of hippocampal/MTL atrophy in SD patients, but to correlate with neuropsychological measures of frontal functioning (Hodges & Graham, 2001).

Evidence from positron emission tomography (PET) studies, however, suggests that the frontal cortex is also activated during semantic retrieval (for a review, see Tulving et al., 1994). Specifically, an area of left inferior prefrontal cortex has been associated with verbal semantic retrieval, and a more anterior/ventral area appears activated when retrieval of meaning is required (Buckner, 1996). Drawing on this and other neuroimaging evidence, the hemispheric encoding/retrieval asymmetry (HERA) model (Tulving et al., 1994; Nyberg et al., 1996b) proposes that whilst the left prefrontal cortex is involved in both semantic retrieval and episodic encoding, the right prefrontal cortex is specifically involved only in episodic retrieval. Although subsequent evidence implicating the left prefrontal cortex in verbal episodic retrieval (Buckner, 1996; Buckner & Wheeler, 2001) has partially discredited the HERA model, the right prefrontal dissociation between episodic and semantic memory remains widely accepted (e.g. Buckner, 1996; Wiggs et al., 1999; but see Rajah & McIntosh, 2005, for evidence that the right prefrontal differences found when comparing episodic and semantic memory may represent degree of functioning, rather than sole engagement by a separate episodic system).

Neuroanatomical basis of episodic memory

Having established the involvement of the prefrontal cortex and hippocampal/MTL formation in episodic memory, the precise role of each region

in episodic encoding and retrieval will now be examined. A hierarchical relationship seems to exist between the prefrontal cortex (PFC) and hippocampal/MTL formation during episodic encoding and retrieval. Studies of amnesic patients indicate that MTL lesions produce specific episodic memory impairments, whereas frontal lesions produce more comprehensive cognitive deficits (Buckner et al., 2000). During episodic encoding, the frontal lobes appear to modulate the input of information into the hippocampus (Moscovitch, 1994), where it is bound and integrated into a coherent memory trace (e.g. Moscovitch, 1994; Schacter et al., 1998; Eichenbaum, 2000). At retrieval, in a process known as *ecphory* (Tulving, 1983), the consolidated memory trace is automatically reactivated through a hippocampally-mediated interaction with an external (or internally-generated) retrieval cue (Moscovitch, 1994).

The contribution of the hippocampal/MTL formation to episodic encoding and retrieval is rapid, obligatory and cognitively impenetrable, and allows memory for personal events to occur in the absence of conscious effort. This area appears to have a specific role in successful retrieval; strong correlations have been reported between PET-measured activation of the left MTL and accuracy on a task involving episodic retrieval of verbal information (Nyberg et al., 1996c). Whilst hippocampal/MTL operations are cognitively obscure, frontal lobe involvement in episodic retrieval is largely accessible to consciousness. Indeed, Wheeler and colleagues (1997) argue that *autonoetic* consciousness is specifically mediated by the prefrontal cortex (especially the right PFC). Frontal lobe patients exhibit general behavioural impairments on a range of episodic tests, including recall, source memory and, to a lesser extent, recognition (Wheeler et al., 1995; 1997); and neuroimaging studies, which allow a more

detailed elaboration of frontal functioning, indicate that the frontal lobe contribution to episodic memory is complex.

Posterior PFC regions appear to exhibit domain specificity, with left and right lateralization according to whether verbal or non-verbal materials, respectively, are being retrieved (Wagner et al., 1998; Buckner, 2003). Activation of these areas also occurs during non-mnemonic verbal tasks, indicating that they may not reflect memory-specific operations (Buckner & Wheeler, 2001). The recruitment of anterior PFC appears to be dependent on the demands of the retrieval task, or on the degree of cognitive effort, or controlled processing, required. For example, anterior PFC activation (often left-sided) has been associated with the retrieval of detailed source information (Nolde et al., 1998), or of weakly-encoded information (Miller, 2000; Wheeler & Buckner, 2003).

As discussed in the previous section, right PFC activation appears to distinguish episodic retrieval from semantic retrieval; however, the involvement of this region does not appear to be contingent upon retrieval success or effort. Instead, the recruitment of right PFC regions may reflect the engagement of a specific retrieval mode, i.e. a cognitive state that causes events to be processed as episodic retrieval cues rather than as mere environmental inputs (Nyberg et al., 1995; Düzel et al., 1999; Buckner & Wheeler, 2001; Velanova et al., 2003; and for an overview of frontally-mediated memory control processes, see Buckner, 2003). Right PFC activity generalises across verbal and non-verbal materials and shows an atypically long response in event-related functional magnetic resonance imaging (fMRI) studies, indicating a possible role in the ongoing monitoring of retrieval attempts (Buckner & Wheeler, 2001).

This extended duration also invites comparison with the late right frontal old/new effect often reported in event-related potential studies of episodic memory (see "ERPs, Recognition Memory and Ageing" chapter).

Summary

The evidence for a functional and neuroanatomical dissociation between semantic and episodic memory within the hippocampal/MTL formation remains highly speculative, however, the right PFC does appear to have a specific involvement in episodic remembering. This region has particularly been associated with autonoetic consciousness, the engagement of episodic retrieval mode and ongoing monitoring during retrieval attempts. Both right and left PFC seem sensitive to task demands, but recruitment of left PFC has been shown to be particularly contingent upon retrieval effort and the degree of controlled processing required. PFC activation occurs independently of retrieval success, which, instead, appears to be related to hippocampal/MTL functioning. In short therefore, prefrontal cortex plays a supervisory, monitoring role in episodic memory; it modulates the input of information to the automatic hippocampal/MTL encoding operations, and mediates hippocampal/MTL output during retrieval through control or 'working-with-memory' processes (c.f. Moscovitch, 1994).

A variety of tasks, including free-recall, cued-recall, source memory and recognition, have typically been used to study episodic memory in the laboratory. However, as the research reported in this thesis employs two recognition tasks (item and associative), the remainder of this chapter will focus

on recognition memory, beginning with a discussion of several key theoretical accounts.

Recognition memory

Recognition memory research has traditionally employed item recognition tasks, where participants are generally instructed to study sets of stimuli, and then to distinguish between old (previously-studied) and new (unseen) stimuli. Many classic models of recognition assumed that old/new decisions were based purely on a unidirectional assessment of memory strength (e.g. Green & Swets, 1966; Banks, 1970). Test items fell along a familiarity continuum, where old items were assumed to be more familiar on average than new items. Dual process models, however, consider that this familiarity judgement is insufficient, and that an additional recollection process is required to fully account for the data both from manipulations of simple item recognition tasks and from more complex recognition paradigms (e.g. those requiring retrieval of source, or associative, information). As the research conducted in this thesis primarily adopts a dual process perspective, the remainder of this chapter will focus heavily on dual process interpretations of recognition memory; but first, a brief overview of single process theories will be provided.

Single-process theories of recognition memory

Most single process models of recognition memory are founded on a version of signal detection theory, whereby variability in the memory strength of old and new items is assumed to result in partially overlapping Gaussian distributions along a memory strength continuum. A response criterion

differentiates between previously-studied and new test items, with items whose strength falls above the criterion being judged old, and those falling below the criterion being judged new. The hit rate is the proportion of the old item distribution exceeding the response criterion; the false alarm rate is the proportion of the new item distribution exceeding the response criterion (for an overview of signal detection theory, see MacMillan, 1993).

Global matching models are sophisticated variants of traditional single process signal detection models that were developed with the aim of combining aspects of separate "search" and "direct access" models of memory into one rapid decision process. The major strength of global matching models (e.g. SAM, Gillund & Shiffrin, 1984; MINERVA2, Hintzman, 1988; TODAM2, Murdock, 1997; REM, Shiffrin & Steyvers, 1997; BCDMEM, Dennis & Humphreys, 2001) is their ability to account for recognition judgements that are sensitive not only to the characteristics of a single test item, but also to the characteristics of other previously-studied items. The detailed mathematical specifications of global matching models are beyond the scope of this thesis (for an overview, see Clark & Gronlund, 1996), however, the basic premise of the MINERVA2 (Hintzman, 1988) model will be outlined as an illustration of the general principles underlying all such models.

MINERVA2 bases recognition decisions on the computation of the likelihood that a test probe was previously studied. This calculation follows an assessment of the degree of match between the test probe and all items currently held in memory. All items in memory are assumed to be represented by a vector of features (with every feature taking the value +1, 0, or -1). Each feature of a test probe (also represented by a vector) is then multiplied by the

value of the corresponding feature of each memory trace to produce a degree of match, or activation value. Finally, following several normalisation procedures to reduce the signal-to-noise ratio, the sum of the resultant activation values over all the memory traces is compared to an internally-set criterion on which the recognition judgement is based.

Traditional global matching models provide an extremely parsimonious interpretation of recognition memory, and, by representing a memory trace as a vector, they can account for a wide range of experimental data, including recognition tasks that involve contextual and associative information. The authors of these models, however, have often had to resort to the inclusion of specific modifications to account for certain problematic results, such as the mirror effect (the finding that more memorable stimuli produce more hits but fewer false alarms than less memorable stimuli, see Glanzer & Adams, 1985), or the shape of ROC slopes (see "Separating recollection and familiarity – the ROC procedure", below). Some models have been forced to add new parameters (SAM, Gillund & Shiffrin, 1984; TODAM2, Murdock, 1997); others have included specific task-dependent, decisional factors (BCDMEM, Dennis & Humphreys, 2001); and others have resorted to incorporating an additional recall mechanism (SAM, Ratcliff et al., 1995; REM, Malmberg et al., 2004). As a result, global matching models have become increasingly complicated, and in view of the admission that "There are no viable single-factor models of recognition..." (Dennis & Humphreys, 2001, p471), it is not surprising that many cognitive psychologists now appear to accept that dual process theories offer the most parsimonious account of their data.

Dual-process theories of recognition memory

Although global matching models may be unable to explain all recognition memory phenomena without resorting to various modifications, they nevertheless offer a testable, mathematically-based account of many experimental manipulations, and accordingly cannot be completely discounted. Single-process proponents criticise dual-process models of recognition for lacking specification and for offering extravagant accounts of data when one (usually multidimensional) process may be sufficient (e.g. Donaldson, 1996; Banks, 2000; Heathcote, 2003; Leboe & Whittlesea, 2002; Dunn, 2004; Rotello et al., 2004). The next section will therefore begin by considering some of the evidence supporting the involvement of two processes in recognition memory, before describing five influential dual process models.

Evidence for two recognition processes

One major limitation of single models of recognition memory is that they are too static to account for the retrieval dynamics of recognition memory. The response signal technique (e.g. Reed, 1973), which uses a variable lag between the onset of a test item and a signal requiring an immediate old/new response, is one method employed to study the time-course functions of recognition. This technique has demonstrated that simple old/new discriminations are typically made more rapidly (by approximately 100 ms) than complex discriminations requiring the recognition of specific details, such as differentiating between targets and lures where the plurality is changed from study to test (Hintzman & Curran, 1994; Hintzman & Caulton, 1997; Hintzman et al., 1998). Moreover, the observation that the time-course functions for false

alarms to lures that are highly similar to targets are non-monotonic (i.e. the false alarm rate first rises then falls) is particularly problematic for single-process models based solely on memory strength distributions. In contrast, these results are easily accommodated by assuming that two types of process are differentially applied across retrieval (Gronlund & Ratcliff, 1989).

Accordingly, dual process theories posit that recognition decisions can be based on familiarity and/or recollection. Familiarity-based decisions tend to be fast, which accounts for the rapidity of simple old/new decisions in the response signal experiments reported above. Familiarity is generally considered to be a relatively automatic process, and to reflect an acontextual form of memory that is associated with a feeling of oldness. In contrast, recollection-based decisions involve conscious awareness of qualitative information about a study episode, and thus provide information about the context in which an event occurred. Furthermore, as demonstrated by the temporal delay in response signal experiments for recognition decisions involving memory for detail, recollection is typically slower than familiarity (McElree et al., 1999; Rotello & Heit, 2000; and for a recent review of recollection and familiarity, see Yonelinas, 2002).

Dual process theorists cite behavioural experiments, such as those described above, as support for their models, but also draw on evidence from neurological patients, animal research, and, more recently, from functional neuroimaging studies. For example, Huppert and Piercy (1976; 1978) reported that although the performance of amnesic patients on recognition, recency, and frequency judgements could be accounted for by a trace strength memory process, healthy controls appeared to be able to utilise additional specific

information about a study episode. Likewise, Mayes and colleagues (1985; 1992) argued that amnesic patients' recognition deficits could be accounted for by a selective impairment of memory for contextual information where item memory appears to be relatively preserved. Moreover, Srinivas and Verfaellie (2000) demonstrated that although amnesic patients, like normal controls, were sensitive to an object orientation manipulation designed to affect familiarity, they were unable to explicitly recognise the study orientation.

Investigations using rats and non-human primates provide direct evidence that recollection and familiarity may be neuroanatomically dissociable. Whilst parahippocampal lesions appear to selectively disrupt the discrimination of familiar from novel items, hippocampal lesions appear to lead to a specific deficit in memory for associations between different aspects of a prior event. Such findings suggest that the parahippocampal region supports familiarity and the hippocampal formation supports recollective-type processes (Eichenbaum et al., 1994; Fortin et al., 2004). Aggleton and Brown (1999) extend the familiarity/recollection dissociation to include diencephalic structures: they propose that familiarity is mediated by the perirhinal cortex and dorsal medial nucleus of the thalamus, and that recollection is mediated by the hippocampus, fornix, mamillary bodies and anterior nucleus of the thalamus. Aggleton and Brown further consider the familiarity and recollection systems to be independent, and to interact with the prefrontal cortex. However, the prefrontal contribution is thought to be more critical to recollection than to familiarity (see also Quamme et al., 2004).

Finally, a recent fMRI study (Yonelinas et al., 2005), which employed confidence ratings during a recognition memory task to identify the brain

regions associated with recollection and familiarity in normal human adults, reported that both processes produced prefrontal, lateral parietal and medial parietal activations. Within each region, however, the precise areas associated with recollection and familiarity were distinct. Moreover, whilst recollection produced increased hippocampal activation, an inverse relationship was demonstrated with familiarity. This latter finding is particularly difficult to reconcile with the single process view that recollection merely represents one extreme of a memory strength continuum.

Dual process models of recognition memory

The Atkinson and Juola model – contingency

According to the Atkinson and Juola (1973; 1974) model, recognition judgements are based either on a rapidly-assessed familiarity index, or on an extended search procedure which is initiated only if the familiarity rating is ambiguous. The model assumes that long-term memory is partitioned into a lexical store and an event-knowledge (E/K) store, in a similar fashion to Tulving's (1983; 1985a) semantic/episodic distinction. When a test item is presented, its corresponding node in the lexical store is accessed directly and a familiarity rating (a function of the delay since the node was last activated and the number of times it was previously accessed) is calculated. A rapid recognition judgement is then based on a modified version of signal detection theory with two response criteria. If the familiarity rating exceeds a high criterion the test item will be judged old; if the rating falls below a low criterion the item will be judged new. An intermediate familiarity rating leads to the initiation of an extended search of the E/K store. This search process will produce an old

judgement if the test item is matched against a previously-seen study list; if no direct match is achieved, the item will be judged new.

The Atkinson and Juola model assumes that familiarity is the primary basis for recognition and that recollection is only used when familiarity information is ambiguous. A recent study, however, is inconsistent with this assumption. Quamme and colleagues (2002) tested source recognition using a paradigm where familiarity should have been sufficient for accurate list discrimination (a high memory strength list vs. a weak memory strength list), and demonstrated that their participants used recollection nevertheless. This finding poses problems for the Atkinson and Juola model, but is consistent with other dual process theories that assume that familiarity and recollection operate independently.

The Mandler model – independence

The Mandler model (Mandler, 1980; 1991) posits that familiarity is a fast activation process whereby items are judged either old or new according to a signal detection model with a single response criterion. As the assessment of an item's activation strength is thought to be based solely on the perceptual characteristics of that item, familiarity is considered to support performance on some priming tasks, for example, word stem completion (Mandler, 1991). In contrast, recollection is assumed to reflect a slower search process whereby elaborative information (e.g. information relating the event to its previous context or associations) is retrieved. As familiarity and recollection are assumed to be independent and to operate in parallel, the probability that an item will be

recognised is the sum of the probability that the item will be judged familiar and the probability that the item will be recollected if not judged familiar.

The Tulving model – synergistic ecphory

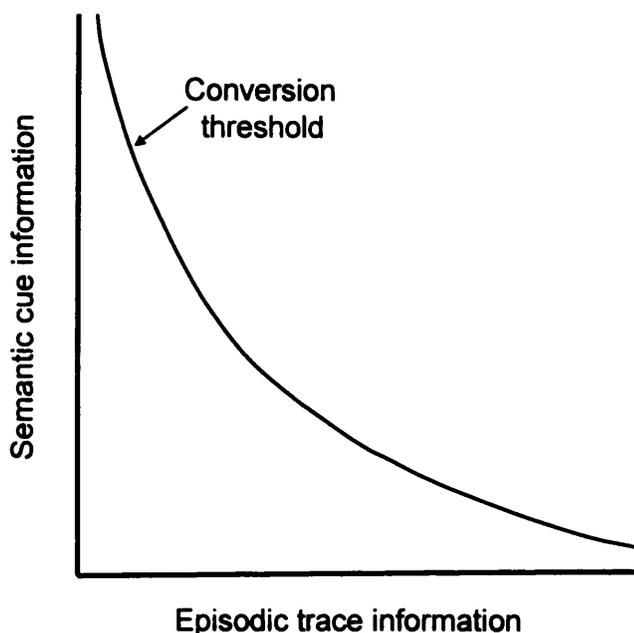


Figure 1. Schematic diagram of the synergistic ecphory model of retrieval. Adapted from Tulving (1985b).

The Tulving model (1982; 1985b) states that the nature and characteristics of any recollective experience are determined jointly by the episodic and semantic systems. During recognition both episodic trace information and semantic cue information contribute independently to the ecphoric information that determines whether retrieval takes place. Overt remembering will occur if the value of the ecphoric information lies above a situationally-determined conversion threshold (Figure 1). A trade-off relationship exists between semantic and episodic information: impoverished episodic traces can be compensated for by richer retrieval cues, and weak retrieval cues can be compensated for by more detailed episodic traces. The precise relation

between the two types of information determines the nature and content of the retrieval experience. High levels of episodic information will lead to the subjective feeling of recollection; whereas high levels of semantic information when episodic information is low will produce the subjective feeling of familiarity.

The Jacoby model – automatic vs. consciously-controlled processing

Jacoby and colleagues (e.g. Jacoby & Dallas, 1981; Jacoby, 1983; Jacoby & Kelley, 1991) also view familiarity and recollection as independent, parallel processes. Familiarity was originally considered to be a relatively automatic, unintentional assessment of an increase in the perceptual fluency of an item following a previous exposure. However, later versions of the Jacoby model added conceptual fluency (i.e. the enhanced processing of the meaning of an item) to the definition of familiarity. Conversely, recollection is described as an intentional, elaborative process that is mediated by consciousness. Recollection provides contextual details about the previous occurrence, is dependent on the extent and meaningfulness of prior processing, and is held to be more conservative and reliable than familiarity. In contrast to previous dual process theories, the Jacoby model (Jacoby, 1983) views familiarity as reflecting memory for a particular presentation of an item, rather than the activation of a general perceptual, or semantic, representation, and therefore considers both familiarity and recollection to be reliant on detailed, episodic-type memory for prior episodes.

The Yonelinas model – a signal-detection/threshold model

The Yonelinas model (e.g. Yonelinas, 1994; Yonelinas et al., 1996; Yonelinas, 1999; Yonelinas, 2001a) posits that familiarity and recollection differ in the type of information (quantitative vs. qualitative) they produce and the degree of confidence with which they are associated. Familiarity is assumed to be based on an equal-variance signal detection model (see Yonelinas et al., 1996, for a discussion of different signal detection models) and to reflect the assessment of quantitative memory strength information. In contrast, recollection reflects a threshold process whereby qualitative information about a previous episode is retrieved. Recollection and familiarity are assumed to be independent processes that are initiated in parallel, but with familiarity producing more rapid responses than recollection. Moreover, recollected items are associated with high levels of confidence, whereas familiarity-based responses are associated with a wide range of confidence ratings (Yonelinas, 2001b). One important caveat to the Yonelinas model is that although an item will only be recollected if the qualitative information associated with it exceeds a certain threshold, recollection is not necessarily an all-or-nothing process. Different experimental manipulations (e.g. specifying the aspects of an episode that should be studied) can determine which type of information about an event is likely to be recollected (Yonelinas & Jacoby, 1996a).

Summary

The foregoing description of five prominent dual process accounts of recognition memory reveals a high degree of consistency in the way that familiarity and recollection are conceptualised. The models agree that familiarity

is faster than recollection, and most assume that the processes are initiated in parallel and that they function independently at the time of retrieval. Familiarity is generally considered to reflect a continuous index of memory strength, whereas recollection is thought to reflect retrieval of specific information about a study episode. Moreover, most models are consistent with Jacoby's (1996) assertion that familiarity can be considered to be a relatively automatic process, whereas recollection reflects controlled, conscious, more effortful processing.

The models, however, disagree over the relationship between familiarity and implicit memory. Mandler and Jacoby argue that the same processes that underpin recognition can support some forms of perceptual priming, whereas Tulving views the memory systems that support recognition memory as being completely independent from priming. Moreover, the models differ in their assumptions about the extent to which familiarity can support the acquisition of new information. Whereas the Atkinson and Mandler models view familiarity as the activation of existing representations and thus incapable of learning new information, Tulving and Jacoby both predict that familiarity should be able to support novel learning. The Yonelinas model agrees with Tulving and Jacoby that familiarity can underpin the learning of new items (such as non-words), but is more conservative with regard to the learning of new associations, which it suggests can be supported by familiarity only under limited circumstances (Yonelinas et al., 1999; Yonelinas, 2001a; for a review, see Yonelinas, 2002).

Although the dual process models outlined above are those most commonly cited as representing important contributions to recognition memory research, other influential dual process theories also exist. Johnson and colleagues' (1993) source monitoring framework makes a distinction between

rapid 'heuristic' judgements based on qualitative information (i.e. the amount of perceptual information or the match to a schema or template), and slower analytical 'systematic' judgements based on more extended reasoning (e.g. retrieving additional information or deciding whether a memory is consistent with what is already known). However, since the source monitoring framework typically views source judgements as heuristic, familiarity and recollection do not readily map onto the 'heuristic-systematic' distinction. Brainerd and colleagues' (1999) conjoint recognition theory adheres more closely to the concepts of familiarity and recollection, and distinguishes between gist information (representations of an item's meaning and other relational information) and verbatim information (item-specific representations of surface features). The retrieval of gist information gives rise to the feeling of familiarity, whereas verbatim retrieval is experienced as recollection (see also Reder et al., 2000).

One fundamental criticism of dual process models is that they have not been specified at the computational level and rely mainly on behavioural data to test their assumptions. This reliance on behavioural testing leads to circular argumentation, as the paradigms designed to investigate dual process assumptions are themselves predicated on those assumptions. The Complementary Learning Systems (CLS) model (McClelland et al., 1995; O'Reilly & Norman, 2002; Norman, 2002; Norman & O'Reilly, 2003), whose conceptions are founded on the observed graded neurophysiological differences between the hippocampus and the neocortex, directly addresses this issue. The model assumes that the hippocampus and surrounding neocortex support complementary, interactive memory operations, with the

hippocampus being the locus of the rapid memorizing and recalling of specific events, whilst the neocortex is specialized in the slow acquisition of information about the statistical regularities of the environment (c.f. Eichenbaum et al., 1994; Aggleton & Brown, 1999). CLS theory has been successfully used to construct computational models of various behavioural properties of recognition, including list strength effects (where distractor items are strengthened at study with respect to target items, Norman, 2002) and interactions between lure-relatedness and test format (O'Reilly & Norman, 2002).

The importance of any memory model should be assessed by its contribution to the theoretical advancement of the field. Three of the dual process models outlined above have proved particularly noteworthy in this respect. The Tulving, Jacoby and Yonelinas models have all produced experimental paradigms that have been widely adopted in attempts to measure the separate contributions of familiarity and recollection to recognition memory. The following sections examine each of these procedures in turn.

Separating recollection and familiarity – the remember/know procedure

Tulving's (1982) synergistic ephory model of recognition memory asserts that the semantic cue and episodic trace information that contribute to retrieval are associated with different forms of awareness; noetic (knowing) and auto-noetic (remembering, or self-knowing), respectively. The remember/know paradigm (Tulving, 1985b) was originally developed to measure these different forms of awareness by asking participants to subjectively report whether they

remembered an item's occurrence on a study list, or whether they simply knew on some other basis that the item had been presented previously.

Although the remember/know procedure has been widely used to support dual process accounts of recognition (for a review, see Gardiner & Richardson-Klavehn, 2000), it is not clear how closely remembering and knowing correspond to recollection and familiarity. Using the response signal paradigm, Toth (1996) failed to fulfil the dual-process prediction that shorter response deadlines should be associated with more know responses and that longer deadlines should produce more remember responses. Processing theorists have therefore suggested that the distinction between remembering and knowing can be better described by conceptual/perceptual (Rajaram, 1993) or distinctiveness/processing fluency (Rajaram, 1996) dichotomies. Moreover, single process theorists argue that remember/know data can be readily accounted for using signal detection theory, by assuming that remembering and knowing represent strict and more lenient (respectively) response criteria along the same memory strength continuum (e.g. Donaldson, 1996; Dunn, 2004; Rotello et al., 2004). Finally, even for those authors who view remember responses as corresponding to some form of recollective memory, know responses have proved more difficult to define, and it has even been suggested that know responses may simply represent a residual category which includes guesses (Gardiner et al., 1998; for reviews, see Rajaram & Roediger, 1997; Gardiner, 2001).

An additional limitation in reconciling the remember/know paradigm to most dual process models, is that the latter generally assume that familiarity and recollection are independent and can co-occur, whereas remember/know

methodology treats the two processes as mutually exclusive. According to the independence account, the contribution of familiarity will be underestimated by the remember/know procedure as know responses can only be produced when an item is familiar, but not recollected (Yonelinas, 2002; and for a description of the independence remember/know method that aims to address this issue, see Yonelinas & Jacoby, 1995; and "General Discussion" chapter).

Separating recollection and familiarity – the process dissociation procedure

The reliance of the remember/know procedure on subjective reports of phenomenological experience introduces the possible confound that different interpretations of the same remember/know instructions may alter response patterns (Baddeley, 2002b). Although remember/know estimates of familiarity and recollection often appear to be fairly consistent with those obtained from other process estimation methods (for a review, see Yonelinas, 2001a), Gardiner (2001) suggests that subjectivity may be the reason that while some studies show convergence between remember/know data and confidence ratings, others show divergence.

The process dissociation procedure (PDP) provides an objective measure of recollection and familiarity by manipulating the degree of intentional control associated with retrieval (Jacoby, 1991). Consciously-controlled recollection is separated from unconsciously-influenced familiarity by contrasting performance on facilitation and interference paradigms. In facilitation tasks (the inclusion condition), both intentional and unintentional processes contribute towards accurate recognition. In interference tasks (the

exclusion condition), only intentional processes will support accuracy; unintentional processes will undermine performance.

In a typical PDP recognition experiment, two sets of study materials are presented (e.g. words are either shown visually or heard aurally). In the inclusion condition, participants are instructed to respond old if a test item appeared previously, regardless of modality. In the exclusion test, participants respond old only to those items delivered in a particular modality (e.g. visual), and respond new to the items from the other modality and to unseen items. Separate estimates of recollection and familiarity are obtained by contrasting performance on the inclusion and exclusion conditions (for details of the equations used to obtain these estimates, see Jacoby, 1991).

One of the critical assumptions of the PDP is that familiarity and recollection act independently. Although most dual process theories assume independence, there may be cases in which this assumption is violated (Yonelinas, 2002). Indeed, plausible arguments can be advanced in support of a redundancy (Joordens & Merikle, 1993) and an exclusivity (Jones, 1987) relationship between recollection and familiarity. If the independence requirement is not met, the estimate of familiarity is altered and may give rise to artifactual dissociations between familiarity and recollection (Curran & Hintzman, 1995; Russo et al., 1998).

The second critical assumption of the PDP is that the probabilities of the occurrence of recollection and familiarity are invariant across inclusion and exclusion conditions. Changing the test instructions between the conditions may violate this requirement; as recollection is explicitly required for exclusion task, but not for inclusion, it may be more likely to occur in the exclusion task.

The use of opposing list discriminations (i.e. identifying previously-seen words as old in the inclusion task, but as new in the exclusion task) addresses this problem by allowing the test format to be kept constant between conditions (e.g. Yonelinas & Jacoby, 1994; Yonelinas et al., 1995; Yonelinas & Jacoby, 1996b; Wainwright & Reingold, 1996). A further limitation of the PDP is its strict definition of recollection: defining recollection purely as the ability to determine which study list an item belongs to precludes measurement of non-criterial recollection (Yonelinas & Jacoby, 1996a).

Separating recollection and familiarity – the ROC procedure

The third process estimation procedure, which employs receiver operating characteristic (ROC) analysis (e.g. Yonelinas, 1994; 1999; Yonelinas et al., 1996; 1998), deals explicitly with the problems of response bias and variability in task instructions by using a single test procedure to examine the effect of shifting response criteria on hits and false alarms (e.g. Yonelinas, 1994). Based on classic signal detection theory, the ROC technique, which plots the sensitivity (hit rate) against the specificity (false alarm rate) for all possible response criteria (e.g. confidence levels), has been highly influential in theoretical advances in memory research in recent years.

Recognition memory tasks typically demonstrate skewed asymmetrical ROCs with a y-intercept exceeding zero, which appear to be inconsistent with many global matching memory models (Ratcliff et al., 1992). However, recognition ROCs can be accounted for by assuming an independent signal detection/threshold dual process model; where a signal-detection-based familiarity process predicts a curvilinear ROC that is symmetrical along the

diagonal and intercepts the y-axis at zero, and a threshold recollection process predicts a linear ROC with a y-intercept above zero (Yonelinas et al., 1996). Accordingly, the precise contributions of recollection and familiarity can be determined by fitting dual process equations to the observed ROC and solving them for each data point (for details of the ROC equations, see Yonelinas et al., 1998).

The precision of the ROC method is highly dependent on the degree of fit between the signal detection/high threshold dual process model equations and the observed data. For example, ROCs are sometimes more curvilinear than dual process theory would predict (e.g. Yonelinas, 1994). This divergence is often attributed to noise in the data, but might equally indicate that recollection should be viewed as a graded process, rather than as an all-or-none threshold process (Yonelinas, 2001a). Finally, single process theorists claim that two processes are not required to account for recognition ROCs and that the observed data can be equally well fit by an unequal-variance signal detection model that assumes that the variance of the old distribution is greater than the variance of the new distribution (e.g. Ratcliff et al., 1995; Glanzer et al., 1999).

Summary

The foregoing process-estimation procedures attempt to isolate the contributions of recollection and familiarity to recognition memory. However, these paradigms all suffer from the problem of circularity (p35), and are based on certain assumptions that may not necessarily be valid. It is therefore advisable to avoid reliance on any one method, and instead to look for

convergence across a variety of procedures. Accordingly, the research reported in this thesis uses event-related potentials to measure the putative neural correlates of recollection and familiarity as the two processes are manipulated using a task dissociation procedure. Elements of two of the above process estimation procedures (remember/know judgements and confidence ratings) are also incorporated. The experiments employ a direct comparison of item and associative recognition, therefore the final section of this chapter will consider the evidence that item and associative recognition differentially engage recollection and familiarity.

Item and associative recognition

Support for the view that item recognition (the discrimination between previously-seen and unseen items) and associative recognition (the discrimination between intact/same and rearranged associations) are dissociable comes from several sources. First, amnesic patients with hippocampal damage have shown deficits on associative recognition tests, but not on item recognition tests (Turriziani et al., 2004; but for evidence that the associative impairment may be restricted to between-domain, e.g. face-voice, associations, see Vargha-Khadem et al., 1997; Mayes et al., 2001). Second, neuroimaging studies of healthy adults have demonstrated selective increases in hippocampal activation during associative, compared to item, encoding, and differential left PFC activation during associative, compared to item, retrieval (Henke et al., 1999; Badgaiyan et al., 2002). Finally, behavioural studies have indicated that item information is accessible before associative information (Gronlund & Ratcliff, 1989); that item information is forgotten more rapidly than

associative information (Hockley, 1991; 1992); that associative decisions attract more remember, and fewer know, responses than item decisions (Hockley & Consoli, 1999); and that high frequency words enhance associative recognition, whereas low frequency words enhance item recognition (Clark, 1992).

Dual process theories generally predict that item recognition relies on a combination of familiarity and recollection, but that associative recognition, which requires contextual memory for the co-occurrence of previously-seen items, relies on primarily on recollection (for a review, see Yonelinas, 2002). The foregoing behavioural studies are all consistent with an increased role for recollection in associative recognition, and other research supports the dual process prediction that familiarity is unimportant for associative decision-making. First, promoting familiarity through priming has been shown to affect item recognition, but not associative recognition, except when speeded responses were used to eliminate recollection (Westerman, 2001). Second, the revelation effect, where items are more likely to be called old if they are preceded by a cognitive task involving similar stimuli, and which is considered to be mediated by familiarity (Hicks & Marsh, 1998; Westerman & Greene, 1998), only occurs in item recognition (Cameron & Hockley, 2000). Finally, associative recognition ROCs are linear, whereas item recognition ROCs appear more curvilinear (Yonelinas, 1997).

However, not all dual process theorists agree that familiarity does not contribute to associative learning. For example, the Jacoby model (e.g. Jacoby & Dallas, 1981), which proposes that both familiarity and recollection require detailed memory for previous episodes, implies that both processes should support associative learning. Furthermore, the Yonelinas model (e.g. Yonelinas,

1994; Yonelinas et al., 1996; 1999) states that familiarity can contribute to associative recognition when the information is 'unitized' during encoding; specifically, if a participant treats two aspects of a study event as a whole. Accordingly, familiarity has been implicated in decisions involving compound words (e.g. sea-horse) and non-related word pairs that were encoded as a coherent whole (e.g. where the study instructions required participants to generate a definition for a novel compound word such as bed-horse, Yonelinas, 2001a).

It is important to acknowledge that dissociations between item and associative recognition do not necessarily demand a dual process interpretation. Indeed, some global matching models (e.g. TODAM2, Murdock, 1982; 1997) were explicitly formulated to account for observed performance differences between item and associative recognition. These differences include the slower rate of forgetting in associative recognition (Hockley, 1991),(1992) and the differential attention effect (Hockley & Cristi, 1996), where instructions to focus on single items at encoding impair associative recognition, but instructions to focus on associative information at encoding appear to leave item recognition unchanged. Moreover, item and associative recognition are not always experimentally dissociable; manipulations of the mirror effect in item and associative recognition suggest that similar processes underlie both tasks (Hockley, 1994).

Data from other associative recognition studies, however, appear more problematic for single process models. Clark and colleagues (Clark et al., 1993; Clark & Hori, 1995) asked participants to study word pairs (e.g. AB, CD, and EF) and reported that performance was better in a forced-choice associative

recognition test when there was no overlap (NOLAP) between 3 test pairs (e.g. AB vs. CF vs. ED), than when one word was common to all three (e.g. AB vs. AD vs. AF) (OLAP). Single process models predict that performance will be better for the OLAP pairs because although the mean difference in familiarity is the same for both test conditions, the increased covariance in the OLAP condition reduces its standard deviation compared to that for the NOLAP condition. Since there are more recall cues in NOLAP pairs than in OLAP pairs, the superior performance in the NOLAP condition has been interpreted as strong evidence that a recollection process is involved in associative recognition.

While the high frequency word advantage in associative recognition is similar to that found in cued-recall (Clark, 1992), it cannot be inferred that the recollection processes involved in associative recognition and cued-recall are identical. A more likely interpretation is that although there may be similarities between associative recognition and cued-recall, both paradigms also involve other task-specific processes. This view is supported by evidence that associative recognition and cued-recall can be dissociated by certain experimental manipulations. For example, semantic similarity between paired words improves cued-recall accuracy (e.g. Hirshman, 1988), (Tulving & Thomson, 1973) but impairs associative recognition performance by producing a higher false alarm rate for related rearranged pairs (Greene & Tussing, 2001).

The lack of specification about the nature of the recollection process in recognition memory is a major shortcoming of dual process models as it limits their testability. Although in item recognition, recollection can be accounted for by a single high threshold process whereby a previously-seen item is

recollected if it exceeds a certain threshold (e.g. Yonelinas, 1994; 1997), associative recognition studies suggest that this model may not always be adequate (see also Yonelinas et al., 1996). An alternative conceptualisation of recollection is that it operates on a recall-to-reject basis with information retrieved from memory being used to reject test foils that are similar to studied items. Rotello and colleagues (Rotello & Heit, 1999; Rotello et al., 2000) employed response signal and ROC methodologies to demonstrate the operation of a recall-to-reject strategy in associative recognition. However, the ROC curves also indicated that a recall-to-accept strategy was operational, implying that in associative recognition recollection may involve a two-threshold process where one threshold determines whether old stimuli will be accepted as old and the second threshold determines whether new stimuli will be accepted as new (Snodgrass & Corwin, 1988; but see Macho, 2004, for evidence against a two-threshold signal detection model).

Summary

The complexity of memory has proved a major challenge to cognitive psychologists aiming to produce a neurologically valid model of its operation. Whilst some functional distinctions, such as the STM/LTM dichotomy, have become well established, others, such as the semantic/episodic division, remain more controversial. The indirect mapping between tasks and putative memory processes makes the interpretation of behavioural data in terms of underlying cognitive operations extremely complex, and although novel methodologies have been developed to address this problem, the debate between single and dual process theories of recognition continues.

The contribution of neuroanatomical and neuroimaging studies has become increasingly significant as the underlying technologies have improved. The development of event-related neuroimaging methodologies, such as event-related potentials (e.g. Coles & Rugg, 1995; Rugg & Coles, 1995) and event-related fMRI (e.g. Donaldson et al., 2001) has proved particularly valuable in allowing the neural correlates of memory processes to be monitored on a trial-by-trial basis. Nevertheless, neuroimaging studies suffer their own limitations (e.g. Sarter et al., 1996) and have failed to resolve the process purity issue. Consequently, the availability of convergent evidence from behavioural, neurological, animal and neuroimaging research is still of paramount importance in the pursuit of theoretical advancement. Chapter 4 provides a detailed consideration of the contribution of event-related potentials (ERPs) to recognition memory research, in addition to examining the impact of ageing on the neural correlates of episodic retrieval. But first, Chapter 2 describes the background against which such ERP ageing studies have been conducted.

Chapter 2

Episodic Memory and Ageing

As people age they invariably complain that their memory is not as good as it used to be. Such subjective reporting of age-related memory deficits is widely supported by objective experimental data, which has clearly demonstrated that the ability to learn and remember does decline as people grow older. It is also widely agreed that age-related memory deterioration is not universal; whereas explicit memory for recent events appears to become impaired with age, procedural, implicit, and semantic memory, as well as memory for events that occurred in childhood and early adulthood are relatively spared (for reviews, see Light, 1991; Craik et al., 1995; Balota et al., 2000; Zacks et al., 2000).

Over the last 20 years, research into memory and ageing has been continuing at an accelerating rate. It is therefore beyond the scope of this thesis to provide a comprehensive review of all aspects of the field. Instead, this chapter aims to provide a focused overview of the effect of normal, healthy

ageing on explicit or declarative memory, and in particular on episodic retrieval, with reference to the key theoretical concepts that have guided the research.

Before considering the patterns of age-related memory impairment that are generally observed, it is necessary to acknowledge that numerous factors, such as educational level and lifestyle, can produce significant variability in cognitive functioning among individuals in the same age range. One study, which assessed the relative contributions of age, social, and personality factors to memory performance in older people, found that education, intellectual activity and personality traits accounted for more variance in memory performance than chronological age (Arbuckle et al., 1986). Medical history has also been shown to play an important role in cognitive and mnemonic functioning (Nilsson et al., 1997; Jelcic et al., 1999), and the following section provides a brief overview of the potential impact of some of the common health problems experienced by older people on cognition in general, and on memory in particular.

Ageing, cognition and health

Ageing is frequently accompanied by deterioration in health: approximately 80% of adults over the age of 65 suffer from at least one chronic disease (Fozard et al., 1990). The relation between growing older and the prevalence of diseases affecting cognitive function is well established (e.g. Nolan & Blass, 1992), and health problems appear to be an important contributory factor to the increase in the variability of performance on tests of cognitive ability in old age. The deleterious effect on memory of disorders such as Alzheimer's disease and other forms of dementia is self-evident, but other

health problems may also be associated with mnemonic deficits in the elderly (for a concise overview, see Bäckman et al., 2000a).

Vascular factors, such as hypertension, have been linked to poor memory, learning and attention across the adult lifespan (Elias et al., 1995; Waldstein, 1995; 2003; Saxby et al., 2003). Moreover, incidences of untreated high blood pressure in midlife appear to contribute towards changes in brain structure in old age. These alterations include increases in pathological structures such as cerebral white matter hyperintensities (WMHs), which have been shown to be related to memory deficits (Söderlund et al., 2003; Van Petten et al., 2004; but for discrepant findings, see Schmidt et al., 1995).

Depression in older adults has also been widely associated with increased subjective memory complaints (Albert, 1981; Feehan et al., 1991; Williams et al., 1987), but objective studies of memory and depression have produced mixed results. Some researchers have reported depression-related memory deficits in the elderly (e.g. King et al., 1991; Rubin et al., 1991; Bäckman & Forsell, 1994; Van Boxtel et al., 2004), but others have failed to find any relationship (e.g. Derry & Kuiper, 1981; O'Hara et al., 1986; Rohling & Scogin, 1993). Such discrepancies may, in part, reflect differences in the depression measures employed, as motivation-related symptoms of depression appear to be more detrimental to older people's memory performance than mood-related symptoms (Bäckman et al., 1996). Moreover, although reliable associations between depression and episodic memory impairments across the adult lifespan were demonstrated by two extensive meta-analyses, the effect may be greater in young and middle-aged adults than in older adults (Burt et al., 1995; Kindermann & Brown, 1997).

Due to the complexity and expense of obtaining detailed objective health measures, and the lack of consensus over which indicators to use, many studies of cognitive ageing rely on subjective health reports. A relationship has been demonstrated between self-reported health and self-reported memory problems (Bazargan & Barbre, 1994), and declines in self-rated health status have been linked to a decrease in objective measures of memory performance (Field et al., 1988; Perlmutter & Nyquist, 1990; Hultsch et al., 1993). However, when using subjective health ratings in age-comparison studies, it is important to recognise that young and older people may rate their health from quite different perspectives (Hooker & Siegler, 1992).

Summary

Although the precise relations between common age-related health problems and memory have yet to be specified, it is likely that medical history will impact on performance, particularly when conditions are co-morbid (Waldstein, 2003). Older people's health problems will contribute to variation in cognitive ability, and thus may inflate the estimation of the magnitude of normal age-related changes in memory. Moreover, the increased use of medications to control some of these conditions in later life may also influence cognitive function; for example, benzodiazepines have been shown to have a deleterious effect on episodic memory in older adults (e.g. Kruse, 1990; and for information about the cognitive, sensory, and motor side effects associated with specific medications, see Batsakes et al., 2002).

The research reported in this thesis aims to investigate the effect of normal healthy ageing on episodic memory. To that end, efforts were made to

ensure that all participants were free from any major health problems that might impact on their performance. Measures taken include asking participants for a brief medical history and a self-reported rating of their current health status, and screening them for depression and dementia.

Memory changes in healthy older adults

Although the main focus of this chapter is the impact of ageing on episodic memory, short-term memory and semantic memory have also been implicated in episodic encoding and retrieval (Tulving, 1995; Zacks et al., 2000; for a review, see Park & Hedden, 2001). Moreover, as no tasks can be assumed to be process pure, it is also highly probable that implicit memory operations are involved in most episodic memory tests (see Rybash et al., 1998, for convincing evidence that implicit processes are involved in cued-recall in both young and older adults). The role of ageing in short-term, implicit and semantic memory will therefore be considered briefly, before ageing changes in episodic memory are examined in more detail.

Short-term memory and ageing

Short-term memory is commonly conceptualised as consisting of two types of operations. The first of these, primary memory, describes situations where information is simply held in mind. Individual studies of primary memory (often assessed using forward digit span tasks) generally suggest a small, but non-significant, advantage for young participants, but a meta-analysis has demonstrated that the age-related deficit in primary memory is reliable (Verhaeghen et al., 1993).

The second form of short term memory operation, working memory, describes more complex situations that involve the simultaneous storage and manipulation of information. Age-related decrements on working memory tasks (e.g. reading span) are typically larger and more robust than those found in primary memory tasks (Daneman & Carpenter, 1980; Salthouse & Babcock, 1991; Salthouse, 1993). Moreover, an intimate relationship between working memory and episodic memory has consistently been demonstrated. Cherry and Park (1993) showed that individual working memory differences accounted for much of the age-related variance in spatial memory for everyday objects, whilst Frieske and Park (1993) reported that working memory performance mediated ageing differences in the recognition of complex scenes (for a meta-analysis of studies investigating working memory, episodic memory and ageing, see Verhaeghen & Salthouse, 1997).

Implicit memory and ageing

As with primary memory, individual studies of implicit memory either tend to report the absence of age-related performance deficits, or small, statistically unreliable declines (for reviews, see LaVoie & Light, 1994; Light et al., 2000; Moscovitch & Winocur, 1995). Hence, some authors have concluded that "...the consensus is that implicit memory and learning are generally intact in older people" (Craik et al., 1995, p230). Nevertheless, non-significant trends in the direction of an age-related impairment are consistently demonstrated on some implicit tests; for example, older adults appear to perform more poorly on word stem completion tasks than young adults (Chiarello & Hoyer, 1988; Hultsch et al., 1991; Winocur et al., 1996; but for discrepant findings, see Light & Singh,

1987). Moreover, while individual implicit memory studies may lack the statistical power to detect the ageing effects, two meta-analyses have demonstrated a small, but reliable, age-related decrement for both item priming (where performance is facilitated by the repetition of previously-seen stimuli) and associative priming (where performance is facilitated by the repetition of novel connections between stimuli, LaVoie & Light, 1994; Light et al., 2000).

Semantic memory and ageing

Many forms of semantic memory appear to be relatively immune to the effects of ageing: vocabulary knowledge (Albert & Kaplan, 1980; Dahlgren, 1998; Park & Hedden, 2001), general knowledge (Nyberg et al., 1996a), and performance on word association tasks (Burke & Peters, 1986) typically appear to be unimpaired or superior in older adults (for reviews, see Light, 1991; Burke & Light, 1981). Moreover, a blocked fMRI comparison of young and healthy older adults failed to detect any significant age-related changes in the neural networks associated with semantic memory (Clarke et al., 2001).

Nevertheless, some ageing deficits in semantic memory have been documented. Compared to young adults, older adults have increased difficulty in retrieving words from their definitions (Bowles & Poon, 1985; Bowles, 1989), have more problems in name retrieval tasks (Cohen & Faulkner, 1986; Rendell et al., 2005), and report more 'tip-of-the-tongue' word retrieval failures (where despite managing to access the meaning of a word, they are unable to name it, Burke et al., 1991; 2000; Dahlgren, 1998). Moreover, an important distinction needs to be drawn between well-learned semantic information and new semantic information. Whereas the former is often preserved with age, the latter

generally appears impaired in older adults (unless the older adults have more expertise in the domain being tested, e.g. McIntyre & Craik, 1987).

Episodic memory and ageing

In contrast to implicit and semantic memory, where age-related deficits are generally small, the ageing effects reported for episodic memory tasks are often moderate to large. In recall paradigms, the elderly tend to produce more omissions (failures to recall) and intrusions (recall of never-presented items), and to repeat more previously-recalled items than young adults. In recognition paradigms, older adults are more likely to produce false alarms, particularly when non-target items resemble target items either perceptually or conceptually (Zacks et al., 2000). Recall typically appears to be more impaired in the elderly than recognition (Moscovitch & Winocur, 1995), and this difference is not simply due to the fact that recall is usually more difficult than recognition. When an easy recall task (immediate cued-recall) was compared to a difficult (delayed) recognition task, recall still showed a disproportionate ageing deficit (Craik & McDowd, 1987).

Although age-related episodic memory impairment is typically assessed through retrieval performance, it is evident that ageing also affects episodic encoding. It has been argued that older adults naturally tend to use inadequate encoding strategies (Craik & Byrd, 1982; Rabinowitz et al., 1982; Perfect & Dasgupta, 1997; Naveh-Benjamin, 2000), but the promotion of deep encoding techniques has produced inconsistent results. In some studies, older adults have shown an increased benefit from elaborative encoding instructions; in others, the young have appeared advantaged (for a review, see Zacks et al.,

2000). Such discrepancies are likely due to the fact that memory involves the interaction of encoding and retrieval operations (e.g. Tulving & Thomson, 1973; Craik, 1983), therefore differences between retrieval tasks are always a potential confound in studies of ageing effects on encoding, and vice versa.

Consequently, as the research reported in this thesis focuses on age-related changes in the ERP correlates of episodic retrieval, the experimental design ensured that encoding conditions were held constant between retrieval tasks and between participants. Deep encoding was promoted, with all participants being asked to generate sentences using study words and word pairs. Moreover, as it cannot be assumed that the strategies adopted by the young and older age groups were identical, a post-experimental questionnaire was also used to assess any individual differences in encoding techniques.

Source memory

As well as being disproportionately disadvantaged in recall compared to recognition, older adults appear to have a specific impairment with source memory (e.g. memory for the context in which an item was presented, Burke & Light, 1981; Johnson et al., 1993; Craik & Anderson, 1999; Zacks et al., 2000; Glisky, 2001). Experiments using fictitious facts presented by two different voices have demonstrated that whilst the elderly are reasonably good at remembering the facts themselves, they show marked impairments in recollecting the voice in which the facts were presented (McIntyre & Craik, 1987; Schacter et al., 1991). Likewise, in reality monitoring paradigms, older adults have more difficulty than young adults in discriminating between previously-read and previously-generated words (Rabinowitz, 1989), and in

remembering whether they watched, performed, or imagined certain actions (Cohen & Faulkner, 1989). Furthermore, a meta-analysis of studies contrasting memory for content (including the recognition or recall of words or pictures) with memory for context (including temporal or spatial contexts, different colours, modalities or presenters, and reality or source monitoring paradigms) has confirmed that the ageing effect is moderate for content, but large for context (Spencer & Raz, 1995).

There are occasions, however, when source memory age deficits are greatly reduced or even abolished. Older adults are less impaired on memory for intrinsic context than for extrinsic context (e.g. colour vs. voice, Spencer & Raz, 1995), and they can more readily discriminate between an external and an internal source (e.g. words spoken by someone else or by themselves) than between two external sources, or two internal, sources (Hashtroudi et al., 1989). Likewise, elderly adults' source memory has been improved to the same level as that of young adults by increasing the degree of distinctiveness between two external contexts (e.g. by using a male voice versus a female voice, rather than two male or two female voices, Ferguson et al., 1992).

Performance on source and context memory tasks is often inferior to performance on tasks that require memory for content. However, the demonstration that ageing effects for context and content can be dissociated experimentally, indicates that difference in task difficulty cannot adequately account for the differential impairment of memory for context in older adults: Directing participants to concentrate on either source or content at study does not generally affect the size of the ageing deficits in source retrieval, but does influence the size of ageing deficits in the retrieval of content (Schacter et al.,

1994; Spencer & Raz, 1995; but for discrepant findings, see Glisky, 2001).

Similarly, age-related impairments in memory for content, but not for context, have been shown to be sensitive to changes in retrieval effort (Spencer & Raz, 1995).

Most of the foregoing examples employ many-to-few mappings between items and sources, where a large number of stimuli are associated with a small number of sources or contexts. However, elderly people appear equally impaired on one-to-one mappings, for example where separate fictitious facts are all presented by different people (Schacter et al., 1994). Similarly, associative recognition, which involves individual associations between two unique stimuli, has consistently shown disproportionate ageing impairments when compared to simple item recognition (e.g. object/location and object/colour associations, Chalfonte & Johnson, 1996; word/nonword, word/word and word/font associations, Naveh-Benjamin, 2000; and word/word associations, Castel & Craik, 2003). Moreover, older adults have proved less able than young adults to profit from deliberately encoding the associations. This observation has led to the elaboration of the associative deficit hypothesis (Naveh-Benjamin, 2000), which posits that any age-related associative memory impairment may reflect a specific difficulty with the encoding and retrieval of the associations between units of information, rather than problems with the individual episodes themselves.

Recollection and familiarity

Where age-related comparisons have been conducted using associative recognition paradigms, a clear pattern has emerged. The elderly typically

produce fewer hits to same pairs (where the test pairing is identical to the study pairing) than young adults, and show a marked increase in the false alarm rate to rearranged pairs (where the members of separate study pairs have been interchanged). Whilst the associative deficit hypothesis focuses on the encoding and retrieval of new associations to explain these findings, dual process theories of recognition memory suggest that they reflect the older adults' increased reliance on familiarity as recollection becomes impaired.

Specific evidence that the elderly depend more on familiarity than the young in associative recognition comes from an experiment where the familiarity of study word pairs was manipulated by presenting them once (low familiarity) or four times (high familiarity, Light et al., 2002). Young participants showed an increased false alarm rate to rearranged pairs for the high familiarity condition only when familiarity-based responding was promoted through the use of a short test response deadline (for the underlying logic of the response signal technique, see "Episodic Memory" chapter). The older group, in contrast, showed this increased false alarm rate for the high familiarity encoding condition regardless of whether the test deadline was short, long, or self-paced (and for further evidence that conjunction errors such as false alarms to rearranged pairs reflect familiarity in the absence of recollection, see Jones & Jacoby, 2001).

Dual process theory, likewise, considers the disproportionate ageing deficit in source memory to reflect the fact that recollection is required for the accurate retrieval of context. Support for this interpretation comes from the 'false fame' paradigm (Dywan & Jacoby, 1990; Jennings & Jacoby, 1993) where participants are initially instructed to read a series of non-famous names,

then are given another list of names (some of which they saw in the first phase) and asked to decide whether the people are famous. Older adults are more likely than younger adults to identify previously-seen non-famous names as famous. Using the process dissociation procedure, Jennings and Jacoby (1993) confirmed that this ageing effect arose because, compared with young adults, older adults depended less on recollection and relied more on familiarity.

Process dissociation methodology has been used in a range of paradigms to demonstrate that whilst recollection becomes impaired with ageing, familiarity remains largely intact. These paradigms include both artificial laboratory experiments using verbal stimuli (Hay & Jacoby, 1996; Jacoby et al., 1996; Jennings & Jacoby, 1997; Jacoby, 1999; Benjamin & Craik, 2001) and more real-to-life situations, such as looking for objects in the rooms of a house (Caldwell & Masson, 2001; and for a review, see Light et al., 2000).

The more subjective remember/know procedure has produced similar findings with regard to recollection; older adults consistently produce fewer remember responses than young adults. However, estimates of familiarity, as measured by know responses, vary: age constancies (Mantyla, 1993; Java, 1996; Norman & Schacter, 1997; Perfect & Dasgupta, 1997); age-related increases (Parkin & Walter, 1992; Perfect et al., 1995, Experiments 1 and 2B; Jacoby et al., 1996); and age-related decreases (Perfect et al., 1995, Experiment 2A) have all been reported. A meta-analysis of remember/know recognition studies has also produced mixed results (Light et al., 2000): although the original mutually-exclusive remember/know procedure demonstrated a small age-related increase in know responses, when the data

was re-analysed using the independence remember/know procedure (Yonelinas & Jacoby, 1995), an age-related decline in familiarity was observed.

The foregoing inconsistencies in the estimates of familiarity may, however, be partly due to experimental confounds. For example, in remember/know experiments, as recollection increases, the number of items available for familiarity-based responses decreases. As the measure of familiarity becomes based on fewer and fewer responses, it becomes increasingly unreliable. Moreover, if performance approaches ceiling, recollection and familiarity may no longer contribute independently to retrieval, and thus estimates of their involvement will become biased (Yonelinas, 2002).

Summary

It is clear that elderly people's memory deficits are not universal: episodic and working memory appear most vulnerable to ageing; primary, semantic, and implicit memory less so. The magnitude of the age-related episodic memory impairment appears to be task-dependent, with recall, source memory and associative recognition paradigms producing larger ageing effects than item recognition paradigms. Dual process theory states that whilst recollective processes are compromised by ageing, familiarity should be relatively spared. Moreover, empirical findings consistently demonstrate that recollection is impaired in older adults, and although the experimental evidence on familiarity is less conclusive, the current consensus is that familiarity is largely unaffected by ageing (Light et al., 2000; Yonelinas, 2002).

Dual process theories provide one account of the effect of ageing on episodic memory, but several other frameworks also exist. The associative

deficit hypothesis (see above) has been elaborated to account for the specific difficulty older people experience in remembering associations. Other influential theories address cognitive ageing in general. The following section describes four of these more global accounts: namely, the speed of processing, reduced inhibition, reduced processing resources, and frontal lobe theories of cognitive ageing.

Theoretical perspectives on ageing and memory

Speed of processing

One of the best-documented observations in gerontological research is the increased time required by older adults to perform a wide range of cognitive tasks (e.g. Brinley, 1965; Salthouse, 1996; Verhaeghen & Salthouse, 1997). Accordingly, processing speed theorists postulate that a reduction in the speed at which many basic-level cognitive processes are executed is a major contributory factor to age-related memory impairment. Salthouse (1996) proposes two mechanisms through which general slowing may cause errors and disrupt performance. Firstly, some cognitive operations may be executed too slowly for successful completion in the time available. Secondly, the speed at which information from different sources becomes available may have slowed to the extent that earlier information is no longer active when later information arrives. Consequently, mental processes that depend on both types of information cannot be accurately executed.

Speed of processing theory can account for various memory deficits in older people. Perceptual speed has been shown to mediate age-related differences in accuracy on a continuous associative memory task, even under

self-paced conditions (Salthouse, 1994), and to underpin ageing changes in recollective experience as assessed by the remember/know procedure (Bunce & Macready, 2005). Reviews of both short- and long-term memory tasks demonstrate that up to 70% of the age-related variance in accuracy may be shared with variance in processing speed measures (Salthouse, 1996; Verhaeghen & Salthouse, 1997; see also Park & Hedden, 2001). Finally, age-related slowing becomes accelerated from the sixth decade onwards, and may be an important determinant in the increase in episodic memory decline in later life (Verhaeghen & Salthouse, 1997).

However, although speed of processing undoubtedly plays a major role in age-related episodic memory (and other cognitive) impairment, it seems unlikely to be the sole determinant. Age itself appears to be a direct mediator of episodic memory decline throughout adulthood, and working memory and general fluid intelligence measures, such as reasoning, may also be implicated (Verhaeghen & Salthouse, 1997). It seems apparent therefore, that multiple independent factors (both general and specific) are required to account for the complete pattern of spared and impaired cognitive performance in older adults. Furthermore, some of these factors appear to act in a linear fashion across adulthood, whilst others seem to accelerate in later life.

Reduced inhibitory control

An alternative to the processing speed account, the inhibition deficit hypothesis (Hasher & Zacks, 1988; Zacks & Hasher, 1994; Hasher et al., 1999), proposes that a decline in the attentional control of the contents of working memory mediates general cognitive impairment in the elderly. The

inhibition deficit hypothesis assumes that activation of the memory representation of previously-seen material is normally modulated by excitatory and inhibitory attentional control processes that operate in the pursuit of goals and expectations. The inhibitory processes, which suppress activation of extraneous goal irrelevant information, are thought to be disrupted by ageing, making older people slower, less able to focus on goal-relevant tasks, and poorer at recalling details.

Support for the inhibition deficit account of memory and ageing comes from directed-forgetting paradigms, where, following exposure to blocks of unrelated items, participants are instructed either to remember or to forget the studied stimuli. In subsequent recall tests, older adults typically produced a higher proportion of 'to-be-forgotten' intrusions than young adults (Zacks et al., 1996). Moreover, the 'fan effect', where increasing the number of associations learned with a single concept produces slower and more error-prone retrieval, has been demonstrated to be larger in older adults than in young adults (Gerard et al., 1991; Radvansky et al., 1996).

According to the inhibition deficit account, the increased 'fan effect' demonstrates that the elderly are less able to inhibit goal-irrelevant information and have more 'mental clutter'. It has been argued, however, that this age-related impairment of inhibition may be part of a more general inability to exert conscious control over cognitive processing. Jacoby and colleagues (Jacoby et al., 1996) trained young and older adults on a word fragment completion task, where words were paired with a fragment of a related word. As a result of the training, one possible completion became more dominant than a second possible completion (e.g. knee-bone would be used to complete the fragment

knee-b_n_ twice as often as knee-bend, and thus become dominant). The participants then studied a list of word pairs from the previous training session, before completing word fragments (e.g. knee-b_n_) with words from the study list. In keeping with the inhibition deficit hypothesis, older adults were less able than young adults to inhibit the habitual dominant completion when the weak completion had been studied. However, the inhibition deficit prediction that the ageing deficit should be eliminated when habit would produce the correct response (i.e. when the dominant completion was correct), was not upheld. Older adults were still less likely than young adults to recall the correct word, suggesting that instead of being unable to inhibit irrelevant information, the elderly were less able than young adults to use conscious processes, such as recollection.

Reduced processing resources

The forgoing result may be difficult to reconcile with the reduced inhibitory control hypothesis, but it is consistent with an alternative account of cognitive ageing, which suggests that the attentional resources required for conscious processing, such as recollection, are reduced in older people (Craik & Simon, 1980; Craik & Byrd, 1982; Craik, 1983). Accordingly, memory tasks that require a great deal of mental effort, or "self-initiated processing" (Craik & Byrd, 1982, p203), should be most susceptible to ageing.

Evidence supporting reduced processing resources theory comes primarily from dual task paradigms, where attention is divided between a primary task and a simultaneously-performed secondary task. When young adults encode under divided attention conditions, their performance at retrieval

is often reduced to the level of older adults (e.g. Rabinowitz et al., 1982; Craik, 1983; and for a review, see Craik & Anderson, 1999). Moreover, age-related deficits in secondary task performance during episodic retrieval, which are largest for free recall and smallest for item recognition, indicate that the primary memory task is more effortful for older people, particularly when the processing demands are high (Craik & McDowd, 1987; Anderson et al., 1998).

A general reduction in processing resources does not appear sufficient to fully account for the observed data, however. Although Anderson and colleagues (1998) initially concluded that a disproportionate disruption to the secondary task observed in older adults during recall and recognition tests supported the reduced processing account of cognitive ageing, a subsequent re-analysis of their secondary task RT data implicated two ageing mechanisms (Anderson, 1999). Whilst evidence of a more positive skew in the distributions of the RT cost (the additional RT required to perform the secondary task concurrently with the primary task, compared with the RT required to perform the secondary task alone) of older adults supported an age-related reduction in attentional resources, the age-related variance in the slowest RTs indicated that an additional slowing mechanism was also operational.

The three theoretical frameworks for cognitive ageing outlined thus far are not mutually exclusive. Cognitive slowing is generally agreed to play some role in the ageing process (Craik & Anderson, 1999), and, as indicated in the previous paragraph, almost certainly operates in conjunction with other ageing mechanisms, such as reduced attentional resources. Moreover, as control processes require substantial attentional resources, an age-related reduction in processing resources is likely to result in reduced inhibitory control. Such

commonalities highlight one important criticism of all three frameworks; namely that they currently lack specification. For instance, whilst it is assumed that cognitive slowing has a neural basis, the precise anatomical substrates are yet to be identified (see Salthouse, 1996). In contrast, the frontal lobe hypothesis of cognitive ageing (most clearly formulated by West, 1996; but see also Moscovitch & Winocur, 1995) is predicated on direct evidence from neurological and neuropsychological studies. This neuroanatomical theory states that the cognitive processes supported by the prefrontal cortex (PFC) deteriorate earlier and to a greater degree than the cognitive processes supported by other brain regions. Importantly, however, differences between the level at which the aforementioned functional theories are specified and the level at which the frontal lobe hypothesis is specified mean that they not should necessarily be regarded as direct competitors when attempting to account for cognitive ageing.

Frontal lobe hypothesis

Neuroanatomical research has consistently demonstrated that ageing is associated with decreases in brain volume and increases in cerebrospinal fluid (Stafford et al., 1988; and for a review, see Raz, 2000). However, the extent of age-related cortical volume reduction is region-specific, with the PFC being disproportionately affected (10% - 17% reduction in PFC volume vs. 1% - 8% reduction elsewhere, Coffey et al., 1992; West, 1996). Although actual neuronal loss appears to be less extensive than once thought (Esiri, 1994; Peters et al., 1994), other accelerated ageing changes that likely impact on cognitive functioning have been observed in the frontal lobes. These alterations include reductions in glucose metabolism and cerebral blood flow (Madden & Hoffman,

1997; Raz, 2000), declines in neuronal synaptic density and dendritic arborisation (Esiri, 1994), and increases in white matter hyperintensities (WMHs), which appear to reflect a multitude of pathological vascular and neural changes (Kawamura et al., 1993; Pantoni & Garcia, 1997). Decreases in neurotransmitter function (particularly dopamine) have also been found in the frontal cortex (De Keyser et al., 1990; Suhura et al., 1991) and striatum, which receives projections from the PFC (Adolfsson et al., 1979). Furthermore, striatal dopaminergic functioning has been found to be a mediator of age-related episodic memory impairment (Volkow et al., 1998; Bäckman et al., 2000b).

Clinical reports of patients with discrete frontal lesions have revealed that memory disruption is a key characteristic of prefrontal damage (Stuss & Benson, 1987). Importantly, the pattern of memory deficits observed in frontal patients is highly similar to that found in normal ageing (Moscovitch & Winocur, 1995). Like healthy older adults, frontal patients are more impaired on recall tasks than on recognition tasks (for a meta-analysis, see Wheeler et al., 1995), show deficits in temporal order judgements (Shimamura et al., 1990), and perform poorly on tests of memory for context (Shimamura & Squire, 1987; Butters et al., 1994). Furthermore, correlations have been reported in normal elderly adults between psychometric measures of frontal function, such as verbal fluency (Spreeen & Benton, 1977) and the Wisconsin Card Sorting Test (Grant & Berg, 1948), and source memory, recall, and the recollective component of recognition (Craik et al., 1990; Parkin & Walter, 1992; Parkin & Lawrence, 1994; Glisky et al., 1995; 2001; Fabiani & Friedman, 1997; Glisky, 2001; but for discrepant findings, see Spencer & Raz, 1994).

Although these findings provide persuasive support for the frontal lobe hypothesis, several important limitations must be recognised: First, the lack of uniformity of frontal lesions will introduce a high degree of variability into patient data, and even when highly circumscribed, it is likely that they will affect functioning elsewhere in the brain. Second, neuropsychological tests of frontal function can at best only provide indirect evidence about the neural substrates of cognitive ageing, and furthermore are unlikely to reflect frontally-mediated processes alone (Berman et al., 1995). Third, whereas cognitive functions are dynamic, neuroanatomical data is static. Over the last decade, however, advances in neuroimaging techniques have allowed direct investigations of the relationship between the brain and cognitive ageing. The following section reviews the evidence from functional haemodynamic neuroimaging studies for age-related changes in regions of the frontal cortex that are implicated in episodic retrieval.

Neuroimaging and the frontal lobe hypothesis

Older people generally appear to exhibit a more bilateral pattern of brain activation than young adults during episodic retrieval: PET studies consistently demonstrate that the right PFC regional cerebral blood flow (rCBF) observed in young adults appears to be reduced in older adults and to be accompanied by left PFC activation (Cabeza et al., 1997a; Bäckman et al., 1997; Madden et al., 1999; Grady et al., 2002; and for reviews, see Grady, 2000; Grady & Craik, 2000). While the age-related reduction in right prefrontal rCBF has been associated with a decline in performance on cued-recall (Bäckman et al., 1997), and temporal order (Cabeza et al., 2000), tasks, increased left prefrontal rCBF

has been observed in older adults whose recognition performance was similar to that of young adults (Cabeza et al., 2000). This latter finding suggests that left PFC activation may reflect a compensation mechanism (see "Dedifferentiation or compensation?", below).

The foregoing evidence, along with similar findings from episodic encoding tasks, has contributed to the elaboration of the 'hemispheric asymmetry reduction in older adults' (HAROLD) model of cognitive ageing (Cabeza, 2002). HAROLD proposes that cognitive ageing in general is characterised by a reduction in the lateralisation of PFC activation. Other studies are, however, problematic for this model. For example, Grady and colleagues (1995) reported similarly right-sided prefrontal rCBF for young and elderly participants on a face recognition task, despite an age-related performance deficit. Moreover, Anderson and colleagues (2000) demonstrated that while young adults exhibited bilateral frontal rCBF during a cued recall task, older adults, whose performance was impaired, showed a strictly left-lateralised PFC activation.

Dedifferentiation or compensation?

The frontal activation observed in older adults, whether characterised by a reduction in lateralisation or by a different pattern of age-related change, could reflect either dedifferentiation, where the neural organisation found in the brains of young adults breaks down, or compensation, where additional brain regions are recruited to offset reduced cognitive efficiency. The dedifferentiation account is supported by reports that different cognitive measures become increasingly inter-correlated in older adults, indicating that normal neural

organisation and specialisation is reduced in the ageing brain (for a review, see Cabeza, 2002). Such a decrease in neural organisation has been modelled computationally, with age-reductions in dopaminergic function being shown to increase the levels of 'neural noise' in the ageing brain (Li et al., 2001). Furthermore, a meta-analysis of blocked-design fMRI investigations of intentional word encoding (Konishi et al., 2001) demonstrated an initial transient right frontal activation in young adults. One possible interpretation of this finding is that the participants may have originally recruited multiple potentially useful brain regions, but then quickly selected those areas most appropriate for the task (i.e. left, rather than right, PFC during episodic encoding in young adults). The extension of this account to age-related bilateral frontal activation implies that older adults may be unable to resolve the initial competition among separate brain areas.

The alternative compensation account gains support from several sources: First, a bilateral frontal BOLD response observed during episodic encoding and recognition tasks (in a blocked-design fMRI study) was correlated with less education and poorer recognition accuracy in young adults, but with more education in an older group whose recognition performance was inferior to that of the young (Springer et al., 2005). This pattern suggests that a non-specific compensatory cognitive reserve may be engaged by highly-educated older adults and by less-educated young adults (who are exerting more effort in recognising the stimuli than their better educated peers). Second, an event-related fMRI study has shown increased frontal bilaterality in older adults compared with young adults when episodic memory performance was equated (Morcom et al. 2003; and for discussion of the issue of equating performance,

see "ERPs, Recognition and Ageing" chapter). Third, a PET study demonstrated that older adults who scored well on neuropsychological indices of memory function showed bilateral prefrontal activation during a source memory task, whereas those with low memory function scores produced only right-sided activation (Cabeza et al., 2002).

In sum, there are persuasive arguments for both the dedifferentiation and compensation hypotheses of cognitive ageing. Although some of the empirical evidence may favour one account over the other, for example Cabeza and colleagues' (2002) findings appear difficult to reconcile with dedifferentiation, the two mechanisms are not necessarily mutually exclusive. It therefore seems likely that both neural dedifferentiation and neural compensation take place as people age (Cabeza, 2002; Reuter-Lorenz, 2002).

The hippocampus, medial temporal lobes and ageing

The frontal lobe hypothesis may represent a dominant view in gerontological psychology, but it nevertheless fails to account for all of the observed age-related changes in cognition in general, and in episodic memory in particular (e.g. Greenwood, 2000; Band et al., 2002). Although neuroanatomical and neuropsychological studies provide clear support for the involvement of the frontal lobes in cognitive ageing, age-related structural and neurochemical changes are found in other brain regions, and ageing effects are apparent in cognitive functions that are independent of frontal integrity (Greenwood, 2000).

The critical role of the hippocampus and medial temporal lobe (MTL) in episodic memory makes this brain region an obvious candidate to mediate

certain age-related mnemonic deficits. Moreover, a comparison of the memory performance of elderly adults and amnesic patients led Moscovitch and Winocur (1992) to conclude that "though the loss is not as severe in the elderly as in amnesics...the common pattern observed in both supports our hypothesis that progressive deterioration of the hippocampal system with age accounts for some of the age-related deficits" (p340; but for an alternative view that the MTL is mainly implicated in pathological ageing, see Hedden & Gabrieli, 2004). The current section will therefore provide an overview of the neuroanatomical and neuropsychological evidence that implicates the hippocampal/MTL region in age-related episodic memory impairment.

Although, the hippocampus and MTL generally appear physically less vulnerable to ageing than the frontal lobes, age-related volume reductions have been observed in this region (for a review, see Van Petten et al., 2004). Importantly, correlations have been reported between hippocampal volume loss and memory impairment in older adults (Golomb et al., 1994; and for a review, see Raz, 2000), with longitudinal studies indicating hippocampal reduction to be a predictor of memory decline (De Leon et al., 1997; Golomb et al., 1996). The evidence linking hippocampal volume to memory performance is not, however, entirely consistent; other investigators have reported negative correlations between hippocampal, or MTL, volume and memory performance (Sullivan et al., 1995; Van Petten et al., 2004), and a recent meta-analysis concluded that "the evidence for a positive relationship between hippocampal size and episodic memory ability in older adults is surprisingly weak" (Van Petten, 2004, p1394).

Other age-related changes, besides volume loss, have also been demonstrated in the hippocampal/MTL region. These alterations include

neuronal loss in specific subregions, such as the subiculum (West et al., 1994), the CA1 field (Simic et al., 1997), and the entorhinal cortex (Heinsen et al., 1994). Moreover, the CA1 field in normal ageing populations appears to be sensitive to several types of intracellular pathology; for example, the neurofibrillary tangles that are a hallmark of Alzheimer's disease have been observed in the CA1 field in healthy older adults (Raz, 2000). Neurochemically, dopaminergic functional decline has been found in the hippocampi of healthy older adults (Adolfsson et al., 1979), and, alterations in hippocampal NMDA receptors have been specifically linked to age-related memory impairments (Gazzaley et al., 1996; see also Morrison & Hof, 2003).

Importantly, convergent findings from neuropsychological tests of healthy older adults further suggest that the hippocampus/MTL contribution to age-related episodic memory deficits is distinct from that of the frontal lobes. Glisky and colleagues (1995) grouped elderly participants according to their scores on tests of MTL and frontal function. Performance on a simple item recognition test was impaired in a low MTL function group, but normal in a low frontal function group. In contrast, the low MTL group performed well on a source memory task, whereas the low frontal group demonstrated a robust source memory deficit (but for discrepant findings regarding the relation between MTL function and item recognition, see Glisky et al., 2001).

The dual process interpretation of the association between low MTL function and item recognition impairment, and between low frontal lobe function and source memory deficits, is that the medial temporal lobes primarily mediate declines in familiarity, whereas the frontal lobes mediate impairments in recollection. The familiarity interpretation of the MTL contribution to mnemonic

ageing is supported by a report that older adults with low MTL function were less able than their high MTL peers to discriminate between lures exhibiting different degrees of similarity to target stimuli (Rubin et al., 1999). However, correlations between MTL scores and performance on tests of cued-recall (Winocur et al., 1996) and context memory (i.e. discriminating between previously-seen and previously-imagined objects, Henkel et al., 1998) suggest that impaired recollection in older adults may also be related to reduced MTL function.

Neuroimaging studies of the hippocampus and medial temporal lobes

Whilst neuropsychological testing provides indirect evidence of the relationship between the hippocampus/MTL system and cognitive ageing, haemodynamic neuroimaging allows investigators to directly observe ageing changes in hippocampal/MTL activity during the performance of episodic retrieval tasks. An event-related fMRI investigation of the retrieval of autobiographical episodes reported a more bilateral hippocampal BOLD response in older adults than in young adults, even though performance was similar (Maguire & Frith, 2003). In a remember/know recognition paradigm, older adults showed a reduced hippocampal BOLD signal to correctly-identified old words, together with an increase in parahippocampal activity (Cabeza et al., 2004). As the elderly participants also produced more know responses than the young participants (even though accuracy was age-invariant), the authors concluded that this activation pattern reflected the older adults' increased reliance on familiarity (but for evidence of age equivalence in hippocampal

rCBF despite older adult's poorer performance on a cued-recall task, see Schacter et al., 1996). Similarly, Springer and colleagues (2005) interpreted an association between an increased MTL BOLD response in older adults and poor recognition accuracy in a blocked fMRI design as reflecting a greater reliance on familiarity (for similar findings from a PET study of cued-recall, see Bäckman et al., 1997).

A network view of age-related memory impairment

The evidence summarised thus far implicates both the frontal lobes and the hippocampus/MTL system in age-related episodic memory impairment. In focusing on these separate brain areas, however, it has been tacitly assumed that the ageing of episodic memory is regional. The regional account considers cognitive ageing to be restricted to individual brain areas; accordingly, a decline in right PFC activation during episodic retrieval in older adults will simply reflect an ageing change that is specific to right PFC (Cabeza, 2002). According to the alternative network account, cognitive performance is mediated by a functional network of interconnected brain regions, with ageing affecting not only the function of separate regions, but also the integrity of the myelinated connections between them (Greenwood, 2000; and for evidence that cerebral white, rather than grey, matter may be reduced in ageing, see Tang et al., 1997).

Support for a network account of age-related episodic memory impairment is provided by reports of synergistic MTL and frontal activations during the encoding and retrieval of object identity and location only in young adults (Schiavetto et al., 2002). Elderly adults seemed incapable of engaging

these encoding and retrieval networks, and instead showed decreased domain-specific posterior activations, in conjunction with increased domain-general PFC activations. Furthermore, structural equation modelling has demonstrated age-related changes in functional connectivity both within PFC, and between PFC and other brain regions, during episodic encoding and retrieval tasks (Cabeza et al., 1997b). Similarly, whereas in young adults a relationship was found between improved recognition memory and connectivity between the hippocampal, ventral PFC and extrastriate regions; in older adults, improved performance was associated with increased functional connectivity between the hippocampus, dorsal PFC and parietal regions (Grady et al., 2003). These findings were interpreted as indicating that the elderly participants were using more organisational and executive-type functions during episodic retrieval, instead of the perceptually-based processing network employed by the young.

Summary

The deleterious effect of ageing on episodic memory has been well-documented, with older adults generally exhibiting a disproportionate impairment in source or context memory tasks, compared with simple item recognition tasks. The dual process account of age-related memory deficits suggests that the source memory impairment reflects the reduced recollective capability of older adults, and their increasing reliance on familiarity. The influential frontal lobe hypothesis provides a neuroanatomical framework of cognitive ageing, which predicts that those functions subserved by the frontal lobes should be the most susceptible to ageing. Nevertheless, although the importance of the frontal lobes to episodic memory, and particularly to the

retrieval of source or context, has been well documented (e.g. Wheeler et al., 1995; 1997), the integrity of the hippocampal/MTL system is also crucial for episodic remembering (Eichenbaum et al., 1994; Aggleton & Brown, 1999; Fortin et al., 2004).

Haemodynamic ageing studies of episodic retrieval suggest that PFC activation may be more bilateral in elderly adults compared to young adults, and, whilst the contribution of the hippocampus to recognition memory may decline with age, MTL activation appears to show an age-related increase. As Chapter 4 will demonstrate, however, the electrophysiological evidence with regard to episodic retrieval and ageing has, to date, proved somewhat difficult to interpret. But before these findings are discussed, the principles underlying electrophysiological recordings must be understood. The following chapter therefore aims to provide an overview of the origins, recording, analysis and limitations of ERP methodology.

Chapter 3

Event-Related Potentials

75 years ago Hans Berger (1929) first demonstrated that electrical activity from the human brain could be recorded from electrodes placed on the scalp. This pattern of changing voltage over time, known as the electroencephalogram (or EEG), reflects the operations of the working brain; its current mental states and ongoing mental processes. The frequency of normal EEG ranges to 40 Hz and beyond, and its amplitude varies between approximately -100 and +100 μV (Coles & Rugg, 1995). However, as individual cognitive operations involve very small (5-10 μV) amplitude changes (Kutas & Dale, 1997), the EEG must be processed in order to extract meaningful information about cognitive states (“the signal”) from background brain activity (“noise”). This process involves partitioning the EEG into individual temporal segments (epochs) that are time-locked to a specific event (e.g. the presentation of a stimulus). Averaging over many such epochs attenuates the background noise and reveals the event-related potential (ERP), a record of the

voltage fluctuations that constitute the brain's response to the event being studied.

ERPs are either exogenous, evoked by extrinsic events such as the appearance of a stimulus, or endogenous, invoked by intrinsic events such as the brain's reaction to the stimulus. Exogenous ERPs, which are sensitive to physical characteristics, occur within 250 ms of the eliciting event and exhibit a stable latency from trial to trial. In contrast, endogenous ERPs, which are sensitive to changes in information processing demands, generally exhibit a later, and more variable, onset latency. Endogenous ERPs are of primary interest to cognitive psychologists as they offer a non-invasive, temporally accurate measurement of higher-order mental functions. However, the distinction between the two classes of ERPs is not always clear, particularly between 100 and 300 ms post-stimulus (Hillyard & Kutas, 1983; Van Boxtel, 1998).

One major advantage that ERPs offer over haemodynamic imaging techniques is their excellent temporal resolution. ERPs can provide information to the order of a few milliseconds about the time course of cognitive operations, while the temporal resolution of haemodynamic methods (PET and fMRI) is limited by their measurement of cerebral blood flow changes occurring over several seconds. In addition, although haemodynamic techniques can only make inferences about brain activation states from regional blood flow data, ERPs allow neural activity to be measured directly. In contrast, whereas haemodynamic techniques provide precise localization (within a few millimetres) of the brain regions corresponding to cognitive functions, the spatial resolution of ERPs is currently limited to tens of millimetres (Slotnick, 2005).

Furthermore, certain (undefined) regions of the brain are electrophysiological “black holes” whose neural architecture precludes their activity from being recorded at the scalp. Accordingly, ERPs should not be the tool of choice for investigators primarily interested in the localization of cognitive operations in the brain.

There are, of course, important methodological issues to be considered in the recording, extraction and identification of the ERP components of interest. This chapter will examine these issues, the relationship between physiological and psychological processes, and, critically, the inferences that can be drawn about cognitive operations from ERP components. First, however, consideration will be given to the manner in which ERPs are directly propagated from intracranial sources to the surface of the scalp.

Neuronal Electrogenesis

Individual cells

The voltage differences measured by ERP scalp recordings are the product of chemical changes within active neurons in the brain. Specifically, when a neuron is processing and transmitting information, the flow of ions across the cell membrane generates internal and external electrical potentials. The extracellular potentials, which are measurable by pairs of electrodes at separate scalp locations, primarily consist of graded post-synaptic potentials and index the transfer of information between neurons (Allison et al., 1986; Wood, 1987). However, all-or-nothing action potentials, reflecting the transmission of information along an axon from the cell body to the synaptic

terminals, can also influence scalp recordings when they occur in peripheral structures and exhibit high synchronicity (Wood & Allison, 1981).

The recording of extracellular potentials at the scalp is governed by several important generalizations (Lorente de Nó, 1947a). First, net inward current flow at active regions of the neuron, known as “current sinks”, produce a negative potential in adjacent extracellular space. Current sinks are balanced by net outward current flow producing positive extracellular potentials in passive regions, known as “current sources”. Second, the propagation of the extracellular potentials is instantaneous, but the specific potential recorded at any given scalp electrode depends on that electrode's location with regard to both the generator of the potential and the reference electrode (Kutas & Dale, 1997). Accordingly, the observed polarity is merely a function of the spatial relationship between the recording electrode and the active tissue at any given moment in time, and does not convey any meaningful information about underlying cognitive processes (Wood & Allison, 1981; Allison et al., 1986). Third, although the amplitude of extracellular potentials quickly decreases with distance from their origin, Helmholtz's principle of superposition (Allison et al., 1986; Wood, 1987) dictates that when a number of neurons fire synchronously, the resultant potentials will summate and may be large enough to be detected at a considerable distance from their origin. The period over which transmembrane current flow occurs also influences whether potentials are recordable at the scalp; the shorter the period of current flow, the greater the degree of synchronization required (Wood & Allison, 1981).

Groups of cells

Synchronicity of firing is only one determinant of whether neuronal activity is recordable at the scalp: other factors include the structure of the nerve cells and their relationship with each other. Neurons in the central nervous system are often complex, with dendrites and axons of irregular size, shape, number and orientation from the cell body. All of these variables influence the distribution of the electrical potential field (Wood, 1987), but the spatial relationship between the individual cells in neuronal populations is the most significant factor in dictating the manner in which the field propagates.

In the configuration of cells known as an “open field” (Lorente de Nó, 1947b), the cell bodies and their dendrites and axons are aligned in parallel (Figure 2, below). Synchronous depolarisation of the neurons produces a current sink at the cell bodies that is balanced by current sources at the dendrites. The resultant potential fields, known as equivalent dipoles, share the same orientation and summate to produce a potential that is detectable at a distance. Approximately 70% of the pyramidal cells in the neocortex are arranged in highly-aligned open field configurations and these cells are considered to be the primary contributors to scalp-recorded ERPs (Kutas & Dale, 1997). Pyramidal cells with open field configurations are also prominent in the paleocortex, hippocampus and cerebellum (Wood & Allison, 1981; Wood, 1987). However, although in principle, activity in these structures can also be detected at the scalp, in practice, the contribution of the hippocampus to scalp-recorded ERPs is thought to be minimal.

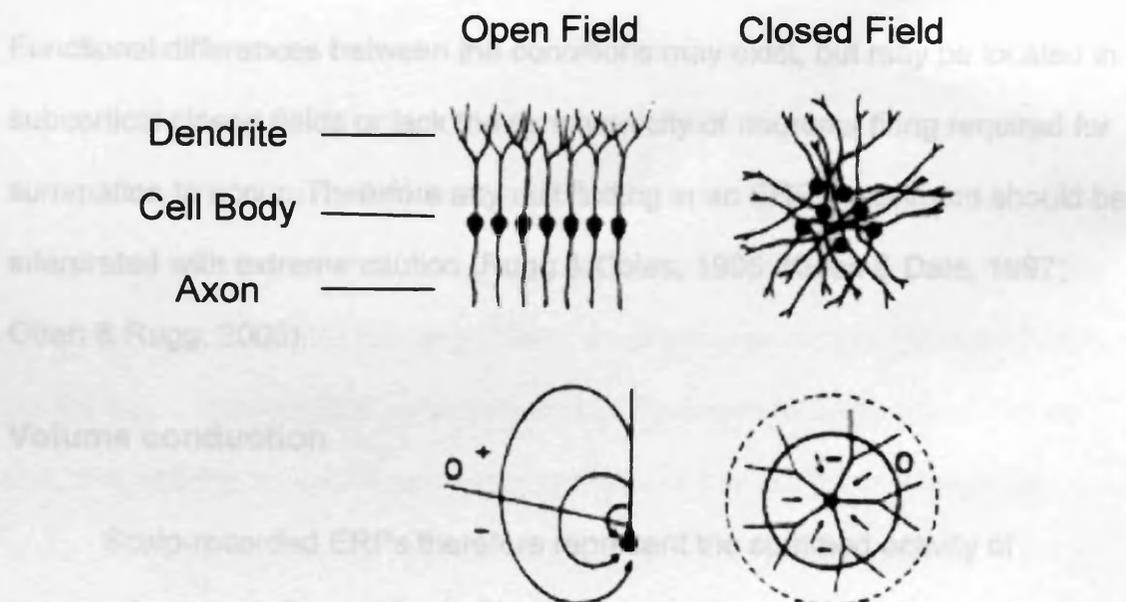


Figure 2. Predicted current flow and potential field produced by synchronous depolarization of the cell bodies of a row of neurons with parallel orientation (open field), and a group with cell bodies clustered in the centre and dendrites spreading radially (closed field). Adapted from Allison et al. (1986).

Where neurons are not aligned in parallel, the summation of extracellular potentials can produce radically different results. An extreme example is the “closed field” configuration (Lorente de Nó, 1947b) found in structures where the cell bodies are clustered at the centre with multipolar dendrites extending in all directions (Figure 2). Synchronous depolarisation of the cell bodies generates a negative potential inside the structure causing extracellular current to flow inward from the dendrites and resulting in a potential of zero outside the structure. Such closed field configurations, whose activity cannot be recorded externally, are commonplace in subcortical structures. This point highlights an important limitation in ERP recordings: failure to detect 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 subcortical closed fields or lack the synchronicity of neuronal firing required for summation to occur. Therefore any null finding in an ERP experiment should be interpreted with extreme caution (Rugg & Coles, 1995; Kutas & Dale, 1997; Otten & Rugg, 2005).

Volume conduction

Scalp-recorded ERPs therefore represent the summed activity of neurons in an undefined subset of brain regions where the requirements of synchronicity, timing and cell alignment are met. This neural activity is propagated to the scalp because the brain and its coverings (the meninges, skull and scalp) act as volume conductors. The brain, meninges and scalp are all efficient conductors, however, the skull is two orders of magnitude less conductive than brain tissue and causes attenuation and spreading of the potential over the surface of the scalp (Koles, 1998).

Changes in conductivity between the brain and its coverings, and differences in head geometry are two important issues when trying to determine the relationship between an intracranial generator and surface potential distribution. If the electrical properties and geometry of the volume conductor, and the location and orientation of a generator within that conductor are known, then the “forward problem” can be solved mathematically. The forward problem describes the modelling of the pattern of scalp potentials generated by a known intracranial source (Scherg, 1989; Picton et al., 1994), and its solution depends on the accuracy of the model chosen to represent the differing conductivity properties of the brain and its coverings. The simplest model, the 3-shell

spherical head model, comprises three concentric spherical surfaces representing the brain, skull and scalp. This model incorporates the changes in conductivity at the brain/skull and skull/scalp interfaces, but fails to account for variations in scalp and skull thickness, which are a major source of error in the predicted scalp potential (Scherg, 1989). An alternative model, the finite head model, which incorporates variations in skull thickness in conjunction with an eye hole and the important geometric features of real heads, improves the accuracy of scalp potential predictions by up to 10-20 percent (Nunez, 1990). Given an appropriate head model, therefore, the pattern of surface potentials generated by a known intracranial source can be predicted with reasonable accuracy.

Recording ERP Data

The foregoing description of the neural origins of the EEG has identified post-synaptic potentials in synchronously-firing pyramidal cells as the primary source of scalp potentials. Volume conduction throughout the brain and its coverings allows the instantaneous propagation of the summated post-synaptic potentials to the entire surface of the scalp. The following section will consider important issues in the recording of the scalp potentials; focusing primarily on considerations concerning the active and reference electrodes (but for a comprehensive review of current ERP recording guidelines, see Picton et al., 2000).

Active electrodes

An ERP waveform is simply a measurement of the voltage difference over time between two electrodes (one active, one reference) at separate

locations on the scalp. Simultaneous recording from a montage of electrodes covering multiple locations across the scalp is, however, necessary for the accurate quantification of distinct ERP components which may be maximal at different scalp sites. Multiple recording sites also permit components to be differentiated on the basis of their scalp distribution (topography), and artifacts such as eye movement to be more readily identified (Picton et al., 2000).

The location of the electrodes generally conforms to the standardised 10-20 system of electrode placement (Jasper, 1958; updated version, American Electroencephalographic Society, 1991; and see "General Methods" chapter for the electrode montage used in the research reported in this thesis). The 10-20 system employs cranial features (the nasion, inion, and periauricular points) to locate the electrodes on the scalp and assumes the skull to be symmetrical. However, although this assumption is rarely met in the normal human head, skull asymmetry does not appear to be a major factor in variability of electrode placement in relation to the underlying cortical structures (Binnie et al., 1982; Homan et al., 1987).

The 10-20 system accommodates up to 75 electrodes, one of which normally serves as a ground to minimize charge accumulation, leakage currents and to decrease artifacts. Although additional electrodes can be incorporated, these must be positioned midway between the standardised 10-20 positions. The system therefore only covers around two-thirds of the cortex (Binnie, 1987), limiting its ability to detect separate ERP components. Some authors argue that a minimum of 128 electrodes is necessary to accurately depict scalp topography (Srinivasan et al., 1998), and recently, high-density

electrodes arrays incorporating 128 or 256 recording sites have been developed to improve spatial resolution (e.g. Tucker, 1993).

Reference electrodes

Although precision concerning electrode placement is important, it cannot be assumed that the voltage measured at a particular location is produced by the brain area directly below that site. The principles of volume conduction and superposition mean that, at any instant, the potentials from all active neurons summate at every point on the scalp (Allison et al., 1986). Thus some of the recorded activity at any given scalp electrode will likely emanate from a distant generator. In addition, because the scalp potential is a relative measurement (the difference in voltage between the active electrode and a second reference electrode), activity at the reference site will contribute equally to the recording. ERP research typically uses a reference that is common to all active electrodes, assuming that, since activity from the reference site contributes equally to all the active electrodes, voltage differences between the active electrodes will remain informative (Dien, 1998).

Previous episodic memory studies have generally used the bony prominences (mastoids) behind each ear as reference sites. This linked mastoid reference effectively locates a virtual reference towards the midline thus avoiding biasing recording towards activity in one hemisphere (Miller et al., 1991). However, the EEG is often recorded using a left mastoid reference and algebraically reconstructed off-line to a linked mastoid reference to circumvent two potential problems associated with recording using a linked reference: First, the low-resistance current path between the linked electrodes may distort the

scalp potential (Katznelson, 1981). Second, if the reference electrodes have different impedances (electrical resistance), the virtual reference will move towards the electrode with the lowest impedance and produce hemispheric bias (Miller et al., 1991). Furthermore, although assumed to be less active than scalp sites, mastoid sites are not electrically inert (Lehtonen & Koivikko, 1971), and recording the right mastoid as a separate channel permits the monitoring of mastoid activity throughout data collection.

The reference position determines the morphology of the EEG waveform recorded at each active electrode. For instance, using a reconstructed linked mastoid reference attenuates the amplitudes at lateral electrodes in the vicinity of the reference electrodes (Dien, 1998). One alternative referencing system, the average reference, estimates the sum of all active equivalent dipoles, thus, provided that surface potentials are recorded evenly and comprehensively across the scalp, reference activity approximates to zero (Picton et al., 1994). The virtual average reference is located in the centre of the head, roughly equidistant from all sites. Although proponents argue that the average reference improves topographic contrasts by reducing artifact caused by reference site location (Dien, 1998), the research reported in this thesis uses the linked mastoid reference as it facilitates comparison with most previous episodic memory studies.

Analogue-digital (A/D) conversion

The voltage difference between each active electrode and the reference electrode is recorded as an analogue signal which must be converted into a digital form prior to computer processing. After amplification, the analogue

signal is filtered to suppress both very low frequencies, which might block A/D converters, and high frequencies, which might cause aliasing (Picton et al., 1994). Aliasing produces bogus low frequency components which are indistinguishable from the true signal. This problem only arises when a signal is under-sampled; aliasing is eliminated when the A/D sampling rate is set higher than the Nyquist frequency (i.e. twice the highest frequency present in the analogue signal).

Extracting the ERP signal from the noise

Filtering the analogue signal prior to digitization reduces contamination from the high frequency electrical activity that lies beyond the range of normal EEG (up to around 40 Hz, see Coles & Rugg, 1995). Nevertheless, the digitized signal still contains activity from ongoing background mental operations and artifacts (e.g. muscle tension, movement and eye blinks) in addition to the signal of interest, the event-related potential (ERP). To obtain any meaningful information about the cognitive processes under investigation, the ERP must be extracted from the background activity. The following section therefore examines the main techniques involved in the extraction of functional information from the EEG.

Ocular artifact reduction

Eye movement and blinking are two major sources of non-cerebral electrical contamination of EEG recordings. Ocular artifact (the electro-oculogram or EOG) results from differences in electric potential (in the order of millivolts) between the cornea and the retina of the human eye (Picton et al., 1994). As the EEG is always measured with respect to a baseline value to

which the EOG contributes, brain potentials are unaffected by an unchanging EOG. However, eye movement and blinking cause large transient disruption to the EEG signal, particularly at the front of the head.

One way to deal with EOG artifact is to minimize blinking and eye movement by instructing participants to fixate on one point throughout an experimental procedure, and to blink only when instructed. Trials containing EOG artifact are then rejected prior to averaging. The EOG rejection method has several disadvantages: First, a substantial amount of data may be lost, particularly when dealing with children, older adults or clinical populations. Second, the remaining artifact-free trials may be unrepresentative of the complete data set (Gratton, 1998). Third, residual EOG activity may contaminate the accepted trials. Finally, instructing participants to refrain from blinking effectively introduces a secondary task which may also interfere with brain activity (Verleger, 1991). The load imposed by the secondary task will vary from one participant to the next: a problem which becomes particularly acute when dealing with different populations and may confound main task or group effects (Wasman et al., 1970).

The foregoing considerations have led to the development of several EOG correction procedures, based in either the time or frequency domain. The majority of these procedures assume a linear relationship between EOG and EEG; they use regression techniques to compare EEG with EOG and to compute correction weightings for each individual scalp electrode. Corrections can be applied to the EEG for both blinking and eye movement artifacts, but as opening and closing the eyelids appears to influence the way the EOG propagates to the scalp, the same weighting factors should not be used to

correct all ocular artifacts (Corby & Kopell, 1972; Matsuo et al., 1975; and for a review, see Talsma & Woldorff, 2005). The majority of the research reported in this thesis employs a standard time domain regression technique to correct blinks (see Rugg et al., 1997), and epochs containing eye movement artifact are rejected.

Averaging

In addition to the signal of interest (the ERP), EOG-corrected EEG still contains background electrical noise. As the raw ERP is generally smaller than the noise, it cannot readily be distinguished in the EEG. The most commonly-used technique for enhancing the signal-to-noise ratio is averaging, which effectively summates the electrical activity occurring over a specific time interval (epoch) following a repetitive event. Four assumptions underlie averaging (Glaser & Ruchkin, 1976; Spencer, 2005): First, that the signal and noise sum linearly to produce the recorded waveform; second, that the signal waveform is the same for each repetitive event; third, that the noise is sufficiently irregular from event to event to be considered as statistically independent samples of a random process; fourth, that the noise is stationary (i.e. the means and variance of each sample are similar). If these assumptions are met, then the square root rule of averaging, which states that reduction of noise is directly proportional to the root mean square of the noise and inversely proportional to the square root of the number of samples, will apply (Perry, 1966).

In the real recording situation, however, noise is rarely completely stationary. For example, muscle activity will differentially contribute to the EEG throughout the recording, and although such contamination can be minimised

by rejecting epochs containing excessive artifact prior to averaging, it is unlikely, nevertheless, that the problem will ever be entirely eliminated. In addition, the signal is unlikely to be constant; periods of fatigue, boredom and attention lapses may produce ERP voltage fluctuations as the recording session progresses (Ruchkin, 1988), and the signal may even be absent from some trials (e.g. correct guesses in a memory experiment).

Another important consideration is that trial-to-trial variations in the latency of endogenous ERPs can distort the averaged waveform (Kerkhof & Uhlenbroek, 1981). Typically this "latency jitter" reduces the amplitude of an averaged signal and causes it to spread out in time, but, in extreme cases, a single smeared peak could result from averaging jittered individual waveforms with a bimodal distribution. Latency jitter can be corrected using techniques such as Woody filtering (Woody, 1967), which estimates ERP latency on individual trials by computing their cross-correlation with a template approximating the shape of the signal (often the uncompensated average waveform). However, as Woody filtering is capable of producing a credible signal from noise-only data, its output cannot be assumed to be entirely reliable (Ruchkin, 1988). An alternative solution to latency jitter, which eliminates the possibility of generating a bogus ERP from noise, is to adopt the median rather than the average as the measure of central tendency. The median method of signal extraction does not rely on the assumptions of signal invariance and stationary noise, and is valid even when the number of available trials is small (Yabe, 1998; Yabe et al., 1993).

In practice, however, provided the data exhibits a Gaussian distribution, as the number of trials contributing to the average signal increases,

contamination by latency jitter decreases. Thus because the average is a computationally simpler measure of central tendency, it remains the typical method of signal extraction. To guard against the distortion caused by a poor signal-to-noise ratio or latency jitter, participants are normally excluded if they fall below a pre-determined minimum number of trials contributing to the critical experimental conditions. The research reported in this thesis uses the averaging method and adopts a 16-trial minimum inclusion criterion for each condition of interest.

Component selection

Following extraction of the ERP signal using the procedures outlined above, the components of interest must be identified before inferences about underlying cognitive operations can be made. Traditionally, the positive and negative deflections (Figure 3, A, below) correlating with some experimental variable have been assumed to be the physiological indices of cognitive functions. In theory, the latency of a peak (its temporal relation to the event of interest) should provide information about the timing of the underlying cognitive operation, and its amplitude (with relation to a pre-stimulus baseline) should indicate the degree of activation of the process (Kutas & Dale, 1997). In reality, the principles of volume conduction and superposition mean that a single deflection recorded at any given scalp location, at any given time, contains contributions from the many cognitive operations occurring in parallel in different brain regions in pursuit of a particular task. This problem of “component overlap” (Coles & Rugg, 1995, p8) must be addressed before any meaningful inferences about cognitive processes can be drawn from ERPs.

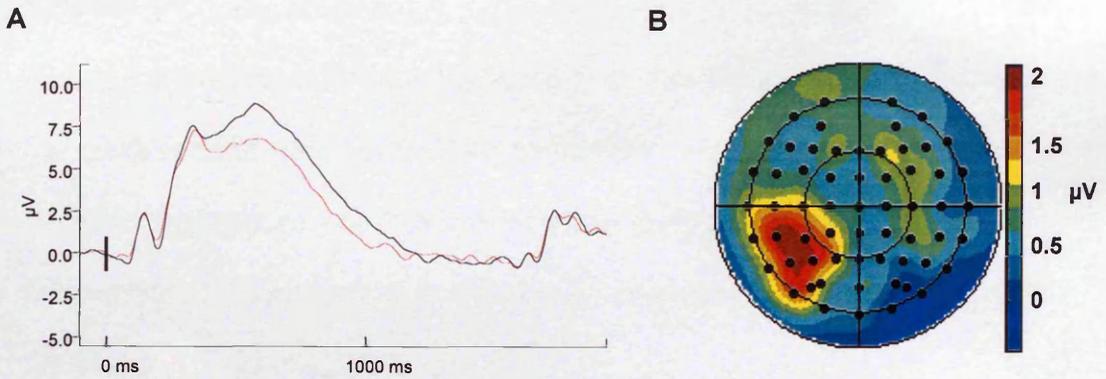


Figure 3. Two examples of ERPs. Panel A represents the grand average ERP waveforms from two different conditions: one shown in black, the other shown in red. 0 ms marks the stimulus onset, the duration of the epoch is approximately 2000 ms, and positivity is plotted upwards. The waveforms diverge from around 400 ms post-stimulus onset. B depicts a topographic map of the difference voltage between two conditions (as shown on the scale bar to the right of the figure). The map represents a birds-eye view of the head, with anterior sites towards the top of the page. The dots represent the electrode positions, the difference voltages in the intervening areas are estimated using a spline interpolation technique (Perrin et al., 1987; 1989). Data from Gray and Donaldson (unpublished).

One solution to the component overlap issue is to define the component of interest as the difference in activity between two separate experimental conditions. This functional approach towards component identification considers a component to be “some essential physiological, psychological or hypothetical construct whose properties are under study” (Donchin et al., 1977, p10). Definition of a component according to the functional approach is therefore based solely on its relationship with experimental variables. Subtraction of the ERPs elicited by two conditions isolates the component that reflects the cognitive process underlying the experimental manipulation.

The subtraction method of component identification is predicated on two assumptions: First, that the latency of the equivalent component in separate conditions is identical; a difference in latency in the same component would

produce separate peaks in the subtraction waveforms, suggesting that the underlying functions differed qualitatively (Coles & Rugg, 1995). Second, that the experimental conditions under comparison vary with respect to one cognitive process alone. This second assumption, which underpins all subtraction methodology, is known as the pure insertion principle (Donders, 1868).

The pure insertion principle presupposes that cognitive functions are additive and act independently of each other (Sternberg, 1969; 2001). Phenomenologically, however, the brain fails to conform to additive principles (Friston et al., 1996; Price & Friston, 1997). By definition, the two conditions being subtracted will have several shared components, the expression of which will be affected when new components are added. The difference between two conditions will therefore comprise the interaction between the added and shared components, in addition to the added components themselves. Nevertheless, although the principle of pure insertion may not be strictly adhered to in electrophysiology, this problem is not unique to ERP data. For instance, behavioural comparisons (e.g. RT or accuracy) between two conditions are also predicated on pure insertion.

Principal component analysis (or PCA) is one practical alternative to subtraction in the identification of components of interest, which does not assume pure insertion (Van Boxtel, 1998; Dien & Frishkoff, 2005). PCA exploits patterns of covariance between experimental conditions (reflecting differences in cognitive processes), and patterns of covariance between electrodes (reflecting differences in the source dipoles). However, the procedure has attracted criticism for its inability to extract temporally-overlapping components.

Applying PCA to a simulated dataset, Wood and McCarthy (1984)

demonstrated how variance that should have been attributed to one component was attributed to a second, supposedly orthogonal, temporally-overlapping component.

The ability to accurately identify ERP components is also limited by volume conduction effects (see “Volume conduction”, above) that cause spatial blurring, attenuation and other distortions of scalp-recorded potentials. Current source density mapping can be used to minimize these effects and to improve the temporal and spatial resolution of component characteristics (Perrin et al., 1989; Law et al., 1993; Srinivasan, 2005). Current source density mapping has the additional advantage of being independent of reference location, but the contribution from deep generators is minimised (Pernier et al., 1988).

The research reported in this thesis uses the subtraction method to extract ERP components of interest from scalp potential data, accepting the principle of pure insertion as a reasonable working hypothesis, even though cognitive operations may not necessarily be wholly independent. Each component is quantified by averaging the amplitude of the corresponding deflection over its duration. This area measure is less sensitive to noise than simply assessing the maximum deflection of a component (Handy, 2005), however, it is a conservative technique that may underestimate differences between conditions (Van Boxtel, 1998).

Source localization

In stressing the relation between experimental variables and the morphology, timing and distribution of scalp potentials, the functional approach

to ERP component identification virtually disregards the fact that the waveforms originate from sources in the brain. In contrast, the physiological approach (Nunez, 1981) considers an ERP component as a reflection of the activity of a neural generator (or set of neural generators) in the brain. According to the physiological viewpoint therefore, identification of an ERP component requires the localization of its anatomical source.

As discussed above, the “forward problem”, describing the distribution of the scalp potential produced by a known intracranial dipole, has a single unique mathematical solution. The “inverse problem”, describing the location of the intracranial generators from an observed scalp distribution pattern (Figure 3, B, above), is more intractable. As the potential field detected on the surface of any volume conductor is compatible with an infinite number of underlying generators, the inverse problem lacks a unique mathematical solution and is therefore insoluble (Kutas & Dale, 1997; Nunez, 1990; Scherg, 1989; Snyder, 1991).

In view of the limited spatial resolution of ERPs (see above), source localization techniques are not used in this thesis, and therefore detailed consideration of different approaches towards the solution of the inverse problem lies beyond the scope of this chapter (but for a recent review, see Slotnick, 2005). Nevertheless, the following brief summary should prove informative. A unique solution to the inverse problem can be made possible by adopting a number of constraints: For example, most source localization techniques assume the neural sources of scalp potentials to be situated in cortical grey matter, and use anatomical and functional information from MRI scans, and haemodynamic and lesion studies to further restrict the

hypothesized generator locations (Ahlfors & Simpson, 2004). ERP source localization accuracy is, however, dependent on three important factors. Firstly, imprecisions in the head model employed (see “Volume conduction”, above) can be a major source of error (Koles, 1998); local variations in skull thickness and conductivity have been shown to produce discrepancies of up to 10 mm (Ollikainen et al., 1999). Secondly, low signal-to-noise ratios make precise localization less likely, especially when the sources reside relatively deep in the brain (Wang & Gotman, 2001). Finally, the size of the generator can also create errors; large generators may be placed deeper in the brain than they are in reality (Coles & Rugg, 1995).

Making inferences from ERPs

The functional and physiological approaches described above represent two extreme views of component identification. In reality, the position adopted by most researchers tends to lie midway between the two, whereby a component is represented by the measurement of a deflection at a particular electrode (or group of electrodes) within a particular latency period. The fundamental assumption of the compromise approach, which considers a particular peak recorded at a given scalp location to be directly related to a specific cognitive operation (Kutas & Dale, 1997), will be examined in the following section.

The relation between neurophysiology and psychology

The supposition that cognitive operations and neural activity are isomorphic underpins cognitive neuropsychology. Consequently, differences in scalp-recorded brain activity are held to reflect differences in underlying

cognitive operations. It is further inferred (at least implicitly) that a one-to-one relation exists between cognitive function and neurophysiological structure (Rugg & Coles, 1995). Although one-to-one mapping has been widely accepted as the most parsimonious interpretation of the relation between cognition and physical activity, this account is open to debate. Mesulam (1990) argues that simple serial information processing (on which strict one-to-one mapping is inherently predicated) cannot sustain complex behaviour, such as memory. Citing neuropsychological studies demonstrating that patients with lesions in disparate brain regions can display similar cognitive deficits, Mesulam asserts that parallel distributed information processing through large-scale interconnected neural networks underpins higher order mental activity. This antilocalizationalist stance considers a single complex behaviour to be represented in multiple complex structures, and a single complex structure to subserve multiple behaviours.

However, for other authors (e.g. Squire, 1987) the important debate is not localizationism versus antilocalizationism per se, but rather “the size of the functional unit within which information is equivalently and statistically distributed” (p319). This view considers the neuronal substrates of cognitive functions to be ultimately localizable, whether at the level of individual neurons, groups of neurons, or neuronal networks. Currently it is impossible to define the level at which one-to-one mappings between specific structures and functions exist, nevertheless when used in conjunction with “bottom-up” approaches which conclude function from structure (such as lesion and intracranial stimulation studies), ERP data can be used to make strong inferences about brain-behaviour relationships (Sarter et al., 1996).

Making inferences from quantitative differences

In Figure 3, A (above), the divergent ERP waveforms produced by two experimental conditions suggest that different cognitive processes underlie each condition. Application of a series of t-tests to individual data points indicates the precise latency at which the waveforms diverge. However, this latency merely represents the latest time at which the cognitive operations associated with the two conditions begin to differ. Earlier differences may have existed in brain regions that do not contribute to scalp-recorded EEG (Rugg & Coles, 1995; Otten & Rugg, 2005; and see “Groups of cells”, above).

Differences between the amplitudes of a particular peak can be used to infer that a particular process is evoked more in one condition than in another. The reliability of such amplitude differences is typically supported by inferential statistics such as repeated-measures ANOVA, the method used throughout the experimental chapters of this thesis (for a recent review, see Dien & Santuzzi, 2005). Although evidence that changes in peak amplitude denote the differential engagement of cognitive operations is widespread (e.g. Hillyard & Kutas, 1983; Duncan-Johnson & Donchin, 1982), it is important to recognise that there are circumstances where amplitude differences do not necessarily reflect distinct cognitive operations. For example, in recognition paradigms, hits can either result from accurate recognition or from lucky guesswork. Assuming that accurate recognition is associated with mnemonic processing, but that guesswork is not, a reduced amplitude to hits in one condition could simply reflect an increased contribution of guessing in that condition.

Making inferences from qualitative differences

Qualitative differences in ERP data describe changes in the scalp distribution of components from one condition (or latency region) to the next. Although the inverse problem (see “Source localization”, above) precludes any firm conclusions being drawn about the actual locations of neural generators, demonstrating a qualitative difference between two conditions generally indicates that distinct sources and, by inference, distinct cognitive operations are engaged by each condition. Importantly, however, there are occasions where such topographic disparity may not reflect the activation of separate cognitive processes. For example, hemispheric differences in early ERP components found when participants selectively attend to their left or right visual fields represent the lateralization of equivalent cognitive operations, rather than functionally distinct processes (Schuller & Rossion, 2001).

As with quantitative differences, inferential statistics are used to assess the robustness of qualitative differences. However, the multiplicative nature of ERP data means it must be normalised before being analysed using the ANOVA model, which assumes data to be additive (McCarthy & Wood, 1985). If scalp-recorded brain activity were additive, a twofold increase in the strength of a neural generator would add a constant voltage to each electrode. In reality, because brain activity is multiplicative, a twofold change in source strength produces a corresponding twofold increase in voltage at each electrode. Normalisation effectively eliminates amplitude differences that reflect changes in source strength between conditions, thus reducing the likelihood of Type 1 errors.

There is some debate about whether such normalisation procedures are advantageous, or indeed necessary. Haig et al. (1997) argue that McCarthy and Wood (1985) fail to consider differences in variance between conditions, therefore their normalisation procedures can obscure (maximum/minimum method), or produce misleading (vector method), distributional differences (see also Urbach & Kutas, 2002). Ruchkin et al. (1999), however, advocate that normalisation should be routinely undertaken prior to topographic analyses, but that significant results should only be interpreted as confirming the presence of distributional differences between conditions. The precise nature of these differences should then be inferred from the pattern observed in the unscaled data. Accepting that normalisation may produce conservative results, the topographic analyses reported in this thesis employ the maximum/minimum method recommended by McCarthy and Wood (1985).

Temporal differences

As stated earlier, the main advantage of event-related potentials over haemodynamic imaging methods is their ability to provide accurate information about the time course of particular cognitive operations. Variation in the latency of an individual ERP peak between separate conditions therefore implies the existence of a temporal difference in the underlying cognitive processes. For example, the latency of the P300 component, which is elicited following the categorization of a stimulus (Donchin et al., 1986), was increased by a manipulation aimed at reducing the discriminability of a target stimulus (McCarthy & Donchin, 1981). Alternatively, the latency of separate peaks within a single condition can be used to infer the order in which functional processing

occurs. Importantly, however, two successive peaks do not necessarily represent successive functional processes. Neural generators whose configuration and orientation means they are undetectable at the scalp may be involved in intervening operations which do not appear in the ERP waveform (Johnson, 1995; and for comprehensive reviews of the inferences that can be drawn from ERP datasets, see Rugg & Coles, 1995; Kutas & Dale, 1997; Otten & Rugg, 2005).

Summary

Because the information obtained from ERPs is constrained by the physics of neural electrogenesis and issues surrounding the recording and extraction of ERP data, it is useful to use convergent evidence from other fields (e.g. intracranial recordings and haemodynamic imaging) in support of the conclusions drawn from ERP research. Although the precise nature of the relationship between cognitive operations and ERP components lacks clear definition, this problem is not unique to electrophysiology. It therefore seems justifiable to assume the existence of some degree of direct mapping between structure and function in order to produce meaningful inferences about cognitive operations. Having described the utility of ERPs as a tool in the study of cognitive operations generally, Chapter 4 will now consider the contribution of ERP methodology to the elucidation of the neural substrates of episodic memory in both young and older adults.

Chapter 4

ERPs, Recognition Memory and Ageing

The last two decades have seen a proliferation of research using event-related potential (ERP) methodology to study different aspects of the cognitive processing that underlies episodic memory (Rugg, 1995). First, the neural correlates of episodic encoding have been investigated using recall and recognition paradigms that allow comparison between the waveforms evoked by the first presentation of subsequently-remembered items and those evoked by the first presentation of subsequently-forgotten items. Second, the ERP components associated with retrieval attempts have been identified by comparing the waveforms elicited by new items following the manipulation of either encoding or retrieval tasks. Finally, studies of successful episodic retrieval most often employ recognition paradigms to contrast the ERPs evoked by correctly-identified previously-seen or 'old' items with those evoked by correctly-identified unseen or 'new' items (henceforth the terminology old and new will refer to accurate responses only, unless otherwise specified).

As the current research examines the impact of ageing on the ERP correlates of successful episodic retrieval; specifically, those elicited by item and associative recognition, this chapter does not aim to provide a comprehensive overview of all previous ERP memory-related research. For example electrophysiological studies of implicit memory fall outwith the scope of this thesis (but for reviews, see Rugg, 1995; Rugg & Allan, 2000). The main focus of the chapter will be on the ERP correlates of retrieval success, particularly those associated with recognition memory. In successful recognition, old waveforms generally become more positive-going than new waveforms from around 200 milliseconds (ms) post-stimulus onset. These differences, which can persist until the end of a 1500-2000 ms recording epoch, have been subdivided into a family of 'old/new' effects on the basis of their temporal and topographic signatures, and their differential responses to experimental manipulation. Four of the old/new effects typically associated with recognition memory tasks will be described in detail, and the findings of ageing research using recognition, source memory and exclusion paradigms examined. First, however, the ERPs elicited by episodic encoding and attempted retrieval will be briefly reviewed (see also Rugg, 1995; Allan et al., 1998; Wagner et al., 1999; Friedman & Johnson, 2000; Rugg & Allan, 2000; Rugg & Wilding, 2000; Donaldson et al., 2002, for excellent reviews of ERP investigations of episodic memory).

Episodic encoding and the Dm effect

Electrophysiological studies of episodic encoding have tended to focus on 'difference in subsequent memory' (Dm) effects. These modulations

constitute the observed difference between the waveforms evoked by studied items that were subsequently remembered and those evoked by studied items that were subsequently forgotten (Sanquist et al., 1980; Paller et al., 1987; 1988). Dm effects typically appear as a long-lasting positivity of subsequently-remembered waveforms onsetting at approximately 300 ms post-stimulus (but see Otten & Rugg, 2001; Mangels et al., 2001, for evidence of negative-going Dm effects).

The functional significance of Dm modulations remain uncertain, but because their timing and scalp distribution vary (a transient posterior modulation is often followed by a longer lasting, more anterior effect), it is unlikely that they represent a single set of encoding operations (Wagner et al., 1999; Mangels et al., 2001; Otten & Rugg, 2001). Increased anterior subsequent memory effects have often been associated with elaborative or deep encoding (Sanquist et al., 1980; Paller et al., 1987; Weyerts et al., 1997; Mangels et al., 2001), whereas posterior effects have been associated with rote learning (Fabiani et al., 1986; 1990; Fabiani & Donchin, 1995). Moreover, the Dm effect has been shown to be larger for subsequently recalled items than for subsequently recognised items (Paller et al., 1988), and in remember/know paradigms, the modulation is typically increased for subsequently-remembered items compared with subsequently-known items (Friedman & Trott, 2000; Mangels et al., 2001; but see Smith, 1993, for equivalent Dm effects for Remember and Know judgements).

A significant number of studies, however, fail to demonstrate robust Dm effects, particularly under shallow encoding conditions (Johnson, 1995; Wagner et al., 1999). This failure may in part be due to contamination of the trials that

were subsequently associated with veridical memory by those that were associated with guesses. Some support for this view comes from a study indicating that accurate verbal memory was supported by confident, but not non-confident, judgements, and that the study waveforms associated with subsequent non-confident hits were similar to those elicited by subsequent misses (Otten & Rugg, 2001).

ERPs and retrieval attempts

The manner in which a person interrogates their memory is dependent on the requirements of the retrieval task being undertaken. The neural correlates of such retrieval attempts are typically studied by contrasting the ERPs evoked by correctly-identified new test items from tasks with different retrieval requirements. This practice aims to eliminate any potential contamination by processes that are contingent upon retrieval success (for a fuller explanation of the underlying logic, see Wilding, 1999; Donaldson et al., 2002). Two classes of processes are generally considered to contribute to retrieval attempts. First, retrieval orientation, which describes the specific form of processing that is engaged in response to a particular retrieval cue, can be examined by contrasting different episodic memory tasks. Second, retrieval effort, which describes the recruitment of resources in pursuit of retrieval, can be assessed by comparing conditions that vary in difficulty, as measured by accuracy or by reaction times (Rugg & Wilding, 2000).

Precise investigation of either class of process ideally entails one process being manipulated independently of the other (Rugg & Wilding, 2000). Studies of retrieval orientation, where task difficulty has been held constant,

have revealed long-lasting (up to 1500 ms) ERP orientation effects that onset at about 300 ms post-stimulus (Wilding, 1999; Robb & Rugg, 2002; Dzulkifli & Wilding, 2005). These differences are typically evident over central and frontal sites, but their precise distribution varies according to the specific tasks being compared. Other studies have suggested that increased retrieval effort is associated with a left frontal modulation: new waveforms were more positive over left frontal sites between 400 and 1200 ms when participants were required to retrieve specific details about studied pictures than when they were required to remember general information (Ranganath & Paller, 1999; Ranganath & Paller, 2000; and see Rugg et al., 2000, for evidence that this effect is not contingent on pictorial stimuli). However, these paradigms failed to adhere to the independence requirement; their retrieval effort manipulations were confounded by the changes in retrieval orientation. In one study where an orthogonal manipulation of retrieval effort and orientation was conducted, ERP effort effects were confined to the initial 300 ms post-stimulus and appeared to be maximal over the midline (Robb & Rugg, 2002).

Finally, retrieval orientation effects in older adults have been shown to onset later and offset earlier than those observed in young adults (Morcom & Rugg, 2004). These findings, which appeared independent of task difficulty, suggest that episodic memory impairment in older adults may not simply reflect changes in the operations involved in successful retrieval. The reduced efficiency with which the elderly process retrieval cues may be another contributory factor to the memory decline observed as people grow older.

ERPs and retrieval success

Most ERP studies of retrieval success have examined the neural correlates of recognition-related processes. Consequently, the remainder of this chapter will concentrate on those ERP effects that are typically elicited during recognition tasks, namely the left parietal old/new effect, the early mid-frontal old/new effect, the late right frontal old/new effect and the late negative slow wave. However, a number of researchers have published investigations of the ERP correlates of cued-recall and associative recall. One cued-recall old/new effect, observed when participants were asked to recall studied items (e.g. LOVELY) with the aid of a three-letter word stem (e.g. LOV__), took the form of a positivity of the waveforms produced by correctly-recalled words compared to those produced by new completions. This slow wave modulation onset at about 300 ms and had an anterior, bilateral distribution (Allan et al., 1996). The effect was topographically distinct from recognition memory old/new effects, suggesting that the cognitive processes involved in cued-recall differ from those involved in recognition (Allan & Rugg, 1997; see also Johnson et al., 1998b).

Associative recall paradigms have typically required participants to study word pairs, and then to make old/new judgements on single words followed by an attempt to recall the study pair of those words judged old. Here, ERP comparisons are made between the waveforms generated by recognised words for which the study pair is successfully recalled, those elicited by correctly-identified new words, and, where trial numbers are sufficient, those elicited by recognised words for which the study pair is not recalled. In such comparisons, recalled words have produced larger left parietal old/new effects than those elicited by words that were merely recognised, but not recalled (Rugg et al.,

1996b). Two other modulations have also been identified in associative recall paradigms: Tendolkar and colleagues (1997) and Donaldson and Rugg (1999) reported an early mid-frontal effect, and Donaldson and Rugg additionally described a late right frontal effect. Both of these components appear to closely resemble the old/new effects typically found in recognition memory experiments. The morphology, functional significance and neural generators of four of these old/new effects will now be considered in detail.

Left parietal old/new effect

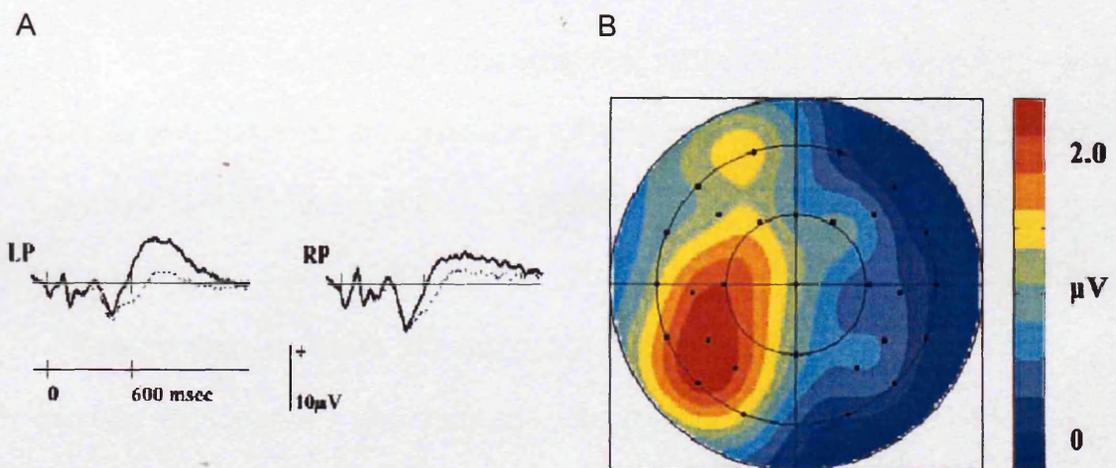


Figure 4. The left parietal effect. Panel A represents grand average ERP waveforms from two conditions at left and right parietal electrodes. Recollected waveforms are depicted by the solid line; new waveforms by the dashed line. Adapted from Rugg et al. (1998b). B depicts a topographic map of the difference voltage between two conditions (as shown on the scale bar to the right of the figure) from the 700-900 ms latency period. The map represents a birds-eye view with the front of the head towards the top of the page. The dots indicate the electrode positions. Adapted from Tsivilis et al. (2001).

The left parietal effect (Figure 4) onsets at about 400-500 ms post-stimulus, lasts for around 400 ms, and is maximal over the left parietal scalp.

The modulation has been observed in item recognition, source memory, cued-recall and associative recognition paradigms (for reviews see, Rugg, 1995; Friedman & Johnson, 2000; Mecklinger, 2000; Rugg & Allan, 2000; Donaldson et al., 2002). Although most often associated with verbal stimuli, the left parietal effect has also been observed for pictorial stimuli (e.g. Schloerscheidt & Rugg, 1997; 2004; Ranganath & Paller, 2000; Tsivilis et al., 2001; Duarte et al., 2004). However, different posterior distribution patterns have been reported when other types of material have been used (e.g. abstract patterns, Van Petten & Senkfor, 1996; abstract objects and spatial locations, Mecklinger, 2000; faces, Yovel & Paller, 2004).

The demonstration that the amplitude of the left parietal effect correlates with hit rate and decision confidence (Johnson et al., 1985; 1998a), and the absence of the modulation from the ERPs evoked by false alarms and misses (Sanquist et al., 1980; Rugg & Doyle, 1992), provide compelling evidence that it reflects veridical episodic retrieval processes. Proponents of dual process theories of recognition generally consider the left parietal effect to index recollection, and cite the following results in support of this view: First, ERP remember/know studies often produce larger left parietal effects for remember responses than for know responses (e.g. Smith, 1993; Düzel et al., 1997; Trott et al., 1997; Mark & Rugg, 1998; Duarte et al., 2004). Second, the modulation appears to be sensitive to various encoding manipulations (e.g. depth of processing, Paller & Kutas, 1992; Rugg et al., 1998a; divided attention, Curran, 2004). Finally, in source memory experiments, larger left parietal effects tend to be associated with correct source judgements than with incorrect source judgements (Wilding et al., 1995; 1996; Trott et al., 1997; Mark & Rugg, 1998;

Senkfor & Van Petten, 1998; but for equivalent left parietal magnitudes in correct and incorrect source judgements, see Cycowicz et al., 2001).

An alternative single process account of the left parietal effect proposes that it simply indexes trace memory strength and is not contingent on retrieval success. Finnigan and colleagues (2002) reported an increased left parietal amplitude for words presented three times at study compared with those presented once, regardless of whether or not they had been correctly recognised. However, the demonstration of left parietal differences between high and low confidence hits, but not between high and low confidence correct rejections (Curran, 2004), is inconsistent with this trace memory strength interpretation, and instead reinforces the view that the left parietal effect reflects successful retrieval.

Finally, recent studies have indicated although the left parietal effect appears contingent upon recollection, under certain circumstances the accurate identification of the context in which a stimuli was learned does not appear to produce a left parietal effect. Such strategic recollection has been observed in exclusion studies, where participants have to distinguish between two types of previously-studied stimuli (targets vs. non-targets). When targets and non-targets have been learned in elaborate encoding conditions, have been temporally segregated, or where accuracy to targets is high, correctly-identified non-targets do not produce a left parietal effect (Herron & Rugg, 2003a; 2003b; Herron & Wilding, 2005).

Neural substrates of the left parietal effect

The limited spatial resolution of ERPs makes it difficult to accurately deduce the neural origins of old/new effects from their scalp locations. Whilst intracranial recordings and studies of patients with neurological lesions provide convergent evidence that allows some inferences to be made, the conclusions that can be drawn from patient data exhibit a certain asymmetry. If an ERP component is insensitive to a lesion, it can be assumed that the affected brain region does not contribute to the component. In contrast, if the ERP component appears to be sensitive to the lesion, it can only be concluded that activation of this region is required for the component to appear, not that the neural generator has been located.

This caveat notwithstanding, the available evidence suggests that the medial temporal lobe (MTL) and hippocampus may be necessary for the appearance of the left parietal effect. First, patients with unilateral MTL lesions show reduced or absent scalp-recorded left parietal effects (Smith & Halgren, 1989; Rugg et al., 1991; Mecklinger et al., 1998; and for a review, see Johnson, 1995). Second, the involvement of the hippocampus is attested by the absence of the left parietal modulation in a patient with focused bilateral hippocampal damage (Düzel et al., 2001). Third, intracranial recordings from epileptic patients indicate that left parietal-type activation in MTL structures predicts performance on episodic memory tasks (Elger et al., 1997; see also Guillem et al., 1999). Finally, a recent review of event-related fMRI studies of episodic retrieval suggests that the neural generators of the left parietal effect may reside in the left inferior parietal lobe. Various experimental manipulations have

been shown to have a similar impact on both the left parietal effect and BOLD activation in this brain region (Wagner et al., 2005).

Early mid-frontal old/new effect

In contrast to the generally agreed view of the left parietal effect as an index of recollection, the functional significance of an early mid-frontal old/new effect (also known as the FN400, see e.g. Curran, 1999; 2000; Curran & Cleary, 2003) remains open to debate. This brief positivity (Figure 5, below) is generally evident between 300 and 500 ms post-stimulus, and is bilaterally distributed over frontal sites (although some investigators report a left-sided asymmetry, see Friedman & Johnson, 2000). In accordance with behavioural studies indicating that familiarity occurs more rapidly than recollection, one influential interpretation proposes that the early mid-frontal frontal effect is the ERP correlate of familiarity. For example, Rugg and colleagues (Rugg et al., 1998a) reported that whereas the left parietal effect was reduced when a shallow (orthographic) encoding condition was compared to a deep (semantic) encoding condition, the mid-frontal effect was insensitive to this levels of processing manipulation. Other findings consistent with a familiarity account include the demonstration that the mid-frontal effect disappears as study/test lags increase (Rugg & Nagy, 1989); the equivalence of modulations elicited by remember and know responses (Smith, 1993; Curran, 2004); and the presence of the mid-frontal component for studied words and plurality-reversed lures (Curran, 2000), for studied words and semantically-associated lures (Nessler et al., 2001; Nessler & Mecklinger, 2003), and for studied pictures and reversed-orientation lures (Curran & Cleary, 2003).

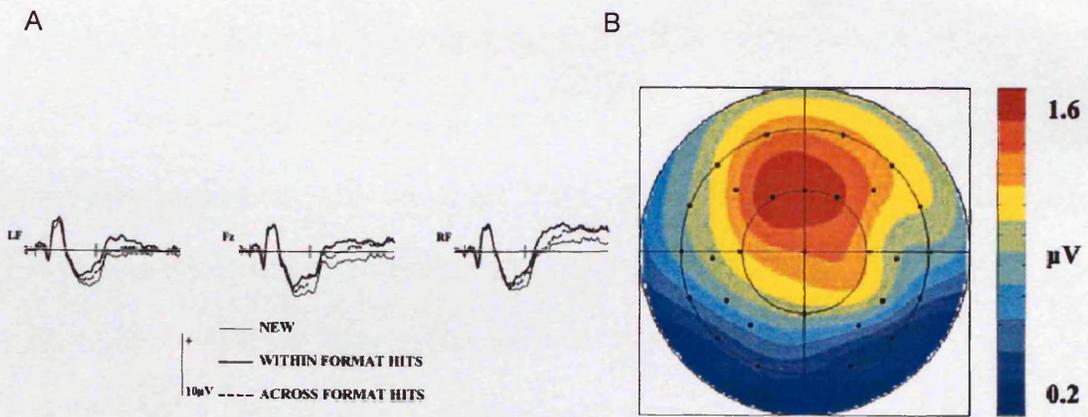


Figure 5. The early mid-frontal effect. Panel A represents grand average ERP waveforms from three conditions at frontal electrodes. Adapted from Rugg et al. (1998b). B depicts a topographic map of the difference voltage between two conditions from the 300-500 ms latency period. Adapted from Tsivilis et al. (2001). For further description of the topographic map, see Figure 4.

Other findings are more difficult to reconcile with the familiarity account, however. Whilst Rugg and colleagues' original levels of processing experiment (1998a) has often been cited as evidence that the mid-frontal effect reflects familiarity, the modulation disappeared from the shallow condition when the encoding tasks were blocked rather than interleaved (Rugg et al., 2000). This finding suggests that the mid-frontal effect might be related to trial structure (see also "ERPs and associative recognition", below). The mid-frontal effect was also absent when participants were familiar with a previously-studied face, but failed to recollect its associated occupation (Yovel & Paller, 2004). Finally, having observed an early mid-frontal effect for remember, but not know, responses to previously-seen pictures, Duarte and colleagues (2004) concluded that the modulation may be related to recollection. These authors further suggested that familiarity was indexed by an earlier (150-300 ms) fronto-

polar effect that was elicited by know responses (for reports of similar early fronto-polar effects, see Tsivilis et al., 2001; Düzel et al., 2004).

Another theory proposes that the early mid-frontal effect indexes novelty detection processes (Tsivilis et al., 2001; Schloerscheidt & Rugg, 2004). Tsivilis and colleagues asked participants to study pairings of everyday objects against background scenes, then to discriminate between old and new objects, regardless of background. The mid-frontal effect was similar for same pairings (old objects against their studied background) and rearranged pairings (old objects against a different studied background), but significantly, was absent for old/new pairings (old objects against a new background). As the relative contributions of recollection and familiarity were demonstrated to be similar for rearranged and old/new pairings, Tsivilis and colleagues (2001) suggested that the component was unlikely to reflect familiarity, but instead represented the modulation of a negative-going index of novelty.

Neural substrates of the early mid-frontal effect

Intracranial studies have shown that early mid-frontal-type activation is directly recordable from various frontal lobe structures. For example, dorsolateral PFC produces an old/new effect that disappears as study/test lag increases (Guillem et al., 1996). MTL structures also appear to be necessary for the modulation, as it appeared absent in patients with lesions restricted to this region (Mecklinger et al., 1998). The hippocampus does not seem to be implicated, however; the mid-frontal effect was intact in a patient with focal bilateral hippocampal damage (Düzel et al., 2001). This pattern of findings is consistent with the Eichenbaum (Eichenbaum et al., 1994; Fortin et al., 2004)

and Aggelton and Brown (1999) models of episodic memory (see "Episodic Memory" chapter), and provides convergent support for the familiarity interpretation of the early mid-frontal component.

Right frontal old/new effect

Whilst the left parietal effect and the early mid-frontal effect appear to reflect processes involved in the retrieval of information from episodic memory, the timing of the later right frontal effect has led to its interpretation as an index of post-retrieval operations. The right frontal component (Figure 6, below) typically onsets at about the same time as the left parietal effect, but appears maximal over the right frontal scalp, and often persists until the end of a two second recording epoch.

The right frontal modulation was first reported in source memory studies (Wilding & Rugg, 1996; 1997a) where it appeared larger for correct source judgements than for incorrect source judgements. Originally considered to index the retrieval of source or contextual information, this interpretation was questioned when several studies failed to show right frontal effects for correct source judgements. For example, in an exclusion study where words were presented in a male or a female voice, the right frontal effect was present for target hits, but not for correctly-identified non-targets (Wilding & Rugg, 1997b; see also Cycowicz et al., 2001; Cycowicz & Friedman, 2003). Moreover, the modulation has been found in the absence of overt source judgements; for example in remember/know paradigms (e.g. Düzel et al., 1997; Rugg et al., 1998b; Trott et al., 1999), and in item recognition tasks that involve a greater degree of complexity than normally found in item recognition (but see

Schloerscheidt & Rugg, 1997, for evidence of a right frontal effect in apparently low-complexity pictorial item recognition task).

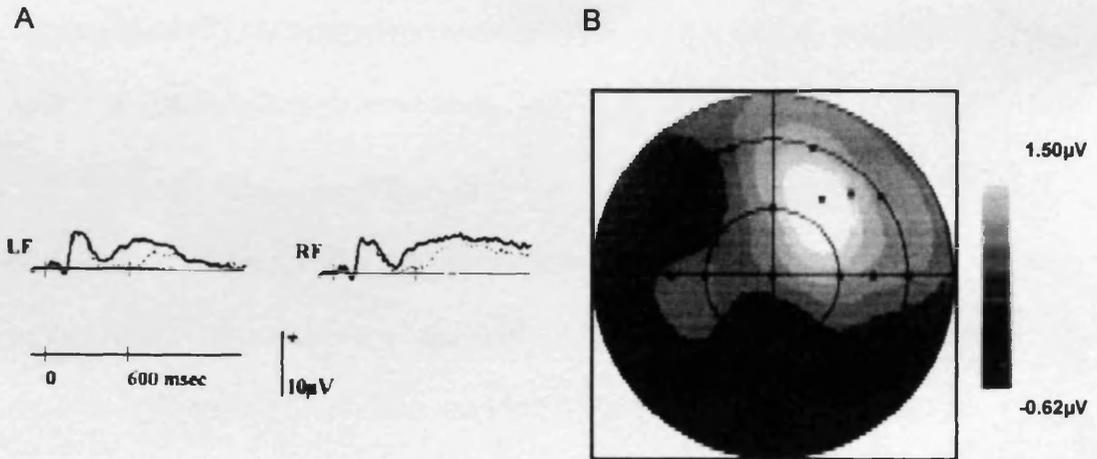


Figure 6. The right frontal effect. Panel A represents grand average ERP waveforms from two conditions at left and right frontal electrodes. Recollected waveforms are depicted by the solid line; new waveforms are depicted by the dashed line. Adapted from Rugg et al. (1998b). B depicts a topographic map of the difference voltage between two conditions from the 800-1400 ms latency period. Adapted from Rugg et al. (2000). For further description of the topographic map, see Figure 4.

The revised account of the right frontal effect as a reflection of the strategic processing of the products of recollection was, however, also discredited following demonstrations that the modulation is not always contingent upon retrieval success. In false memory studies, the right frontal effect often appears equivalent for true and false recognition (Mecklinger, 2000; Curran et al., 2001; but for divergent findings, see Rubin et al., 1999, Experiment 1), and the component was elicited by forgotten words in a directed forgetting task (Ullsperger et al., 2000). The foregoing findings suggest that the right frontal effect may be related to evaluation or monitoring processes. This interpretation is consistent with a levels-of-processing manipulation that showed the right frontal modulation to be greater following a shallow encoding task than following a deep encoding task (Rugg et al., 2000). The post-retrieval

evaluation/monitoring account gains further support from a false memory study that found the right frontal effect only in good performers, where the RT data suggested that good performers were more careful in their decision-making than poor performers (Curran et al., 2001).

The functional significance of the right frontal effect may be obscured by the practice of measuring the modulation over extended time periods, which would mask the presence of any temporally shorter subcomponents that may be differentially contingent upon task demands (Friedman & Johnson, 2000; Mecklinger, 2000). Distributional differences attest to the non-unitary interpretation of the right frontal effect. For example, although Düzel and colleagues (1997) found right frontal effects of equivalent magnitude for remember and know responses, the know modulation appeared to have a more widespread distribution than the remember modulation (Düzel et al., 1997). Moreover, late frontal effects do not always exhibit a right-sided asymmetry; bilateral distributions have been reported for auditory stimuli (Senkfor & Van Petten, 1998) and for pictorial stimuli (Ranganath & Paller, 1999; 2000; Van Petten et al., 2000). Currently therefore, although the right frontal effect is generally considered to be an index of post-retrieval evaluative or monitoring processes, these operations appear to be differentially engaged according to the demands of individual tasks.

Neural substrates of the right frontal effect

Several sources of convergent evidence strongly suggest that the generators of the right frontal old/new effect are located within prefrontal cortex (PFC). First, neuroimaging studies of healthy individuals reveal prominent

activations of right PFC during recognition and source memory tasks (e.g. Rugg et al., 1996a; Henson et al., 1999; 2000; Cabeza et al., 2000; and for reviews of the specific contribution of right PFC to episodic memory, see Nyberg et al., 1996b; Wheeler et al., 1997). Second, studies of frontal lesion patients have demonstrated specific source memory deficits (Janowsky et al., 1989; Schacter et al., 1984), and, in support of the post-retrieval evaluation account of the right frontal effect, patients with restricted right frontal lesions appear to have a selective impairment in retrieval monitoring (Stuss et al., 1994). Third, fMRI studies suggest that right frontal monitoring processes are differentially engaged in healthy adults when retrieval yields ambiguous information; more activation is produced by know, than by remember, responses, and by low confidence, compared to high confidence, responses (Henson et al., 1999; 2000). Finally, however, a region within right dorsolateral PFC, which has been specifically related to retrieval success, provides convergent evidence for the non-unitary nature of the right frontal effect (Henson et al., 2000).

Late posterior negative slow wave

A fourth ERP old/new effect consistently reported in recognition studies takes the form of a late posterior negative-going slow wave (the LPN, Figure 7, below) that is typically bilaterally distributed and maximal over parieto-occipital scalp (for an overview, see Johansson & Mecklinger, 2003). The modulation, which lasts for several hundred milliseconds, is often observed at around the time participants respond behaviourally, but its functional significance remains unclear. Following the finding of a negative correlation between RT latency and LPN amplitude in an exclusion study (Wilding & Rugg, 1997b), it was initially

argued that the effect reflected response-related processes, rather than mnemonic operations. However, this interpretation is inconsistent with a number of other studies that have reported similar RTs both in conditions that produce the LPN, and those that do not (Wilding & Rugg, 1996; 1997a; Rugg et al., 1998b; Cycowicz et al., 2001; Johansson et al., 2002).

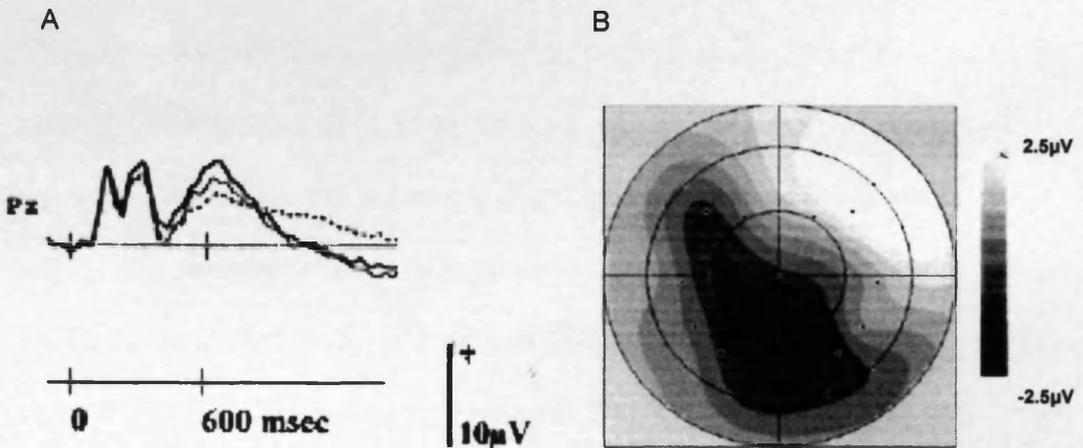


Figure 7. The late posterior negative slow wave. Panel A represents the grand average ERP waveforms from three conditions at a posterior midline electrode. Target hits are represented by the thick solid line, non-target hits by the thin solid line and correct rejections by the dashed line. Adapted from Wilding & Rugg (1997b). B depicts a topographic map of the difference voltage between two conditions from the 1100-1900 ms latency period. Adapted from Li et al. (2004). For further description of the topographic map, see Figure 4.

An alternative theory proposes that the LPN is an index of post-retrieval search processes that are initiated when a task demands the reconstruction of perceptual detail (Cycowicz et al., 2001; Cycowicz & Friedman, 2003).

Cycowicz and colleagues (2001) used the process dissociation procedure to investigate the ERP correlates of line drawings presented in one of two colours. Here, the LPN was elicited by all old items, regardless of source accuracy, in the source memory (exclusion) task, but was absent from the item recognition (inclusion) task. Additional support for the perceptual attributes account comes

from a reality monitoring task, where the LPN appeared greater for previously-perceived pictures than for previously-imagined pictures (Johansson et al., 2002; Leynes & Bink, 2002).

The perceptual attributes interpretation is, however, difficult to reconcile with other experimental findings: First, in item recognition and source memory tasks, LPN amplitudes were demonstrated to be invariant between one test condition where the colour of pictorial stimuli matched that at study, and a second condition where the test and study colours differed (Friedman et al., 2005). The perceptual attributes account would predict a larger LPN in the non-matching condition. Second, LPN's have also been observed when using non-pictorial and aural stimuli (e.g. Wilding & Rugg, 1996; Senkfor & Van Petten, 1998; Curran, 1999).

A third theory posits that, similarly to the late right frontal effect, the precise functions indexed by the LPN may be dependent on task demands (Johansson & Mecklinger, 2003). Accordingly, whereas the LPN is typically produced by tasks requiring the retrieval of contextual information (Cycowicz et al., 2001), and in these instances may be related to the retrieval of the attribute conjunctions (including perceptual details) that characterize the former study episode, when the modulation appears in item recognition it may reflect completely different operations. For example, whilst in source memory tasks a stimulus-locked LPN has been associated with high accuracy (e.g. Johansson et al., 2002), in item recognition a response-locked modulation typically appears in conjunction with high false alarms rates and long RTs (Johansson & Mecklinger, 2003). Such findings, together with the demonstration that response-locked LPNs were greater for false recognition than for true

recognition, have led to the proposal that the item recognition LPN specifically reflects the evaluation processes that are elicited by high levels of response conflict (Nessler & Mecklinger, 2003; see also Herron & Wilding, 2005).

Nevertheless, any conclusions about the functional significance of LPN remain highly speculative, and little is known about its neural correlates. A few tentative suggestions have linked the LPN observed in source memory studies to activation in posterior parietal cortex (Johansson & Mecklinger, 2003) or occipito-temporal cortex (Cycowicz et al., 2001; Cycowicz & Friedman, 2003). In contrast, Nessler and Mecklinger (2003) propose that the evaluation processes underlying the item recognition LPN may be mediated by anterior cingulate cortex.

Summary

Of the four old/new effects commonly elicited by episodic retrieval, a general consensus has been reached over the functional significance of only one; the left parietal index of recollection. Although the early mid-frontal effect is typically associated with familiarity, this interpretation remains open to debate. The current, rather vague, definition of the late right frontal effect, as an index of post-retrieval evaluative processes that are dependent on task demands, most likely owes its lack of specificity to the non-unitary nature of the modulation. Neuroimaging studies indicate that dorsolateral, ventrolateral and anterior PFC are each associated with different sets of cognitive processes (Fletcher & Henson, 2001), and if this ternary subdivision is accurate, the limited spatial resolution of ERP methodology may severely constrain more detailed elaboration of the functional significance of the right frontal effect. Finally, the

late posterior negative slow wave (LPN) has only recently been associated with mnemonic processes and therefore its functional significance remains speculative. However, the modulation generally appears to be associated with tasks that either require retrieval of contextual information or that generate high levels of response conflict.

The preceding section has chiefly focused on research using item recognition and source memory paradigms to elucidate the ERP old/new effects associated with episodic retrieval success. However, the majority of the experiments reported in this thesis employ an associative recognition, as well as an item recognition, task. The following section will therefore discuss the handful of previous studies that have specifically examined the ERP correlates of associative recognition.

ERPs and associative recognition

Dual process theory asserts that associative recognition tasks place an increased reliance on recollection compared to item recognition tasks. Not surprisingly therefore, ERP studies of associative recognition have generally reported early parietal and late right frontal old/new effects. For example, comparison of same (intact) pairs and new (two unstudied words) pairs produced a parietal old/new effect that onset later (at around 600 ms) than that normally reported in item recognition (Weyerts et al., 1997). This modulation also had an extended duration (approximately 600 ms) compared to its item recognition counterpart, and was bilaterally distributed. Despite these temporal and topographic differences, the sensitivity of this associative recognition component to a levels-of-processing manipulation (it was increased under a

deep encoding condition) suggested that it was related to the classic left parietal effect.

An important limitation of the foregoing paradigm is that accurate discrimination between same and new pairs does not necessarily promote recollection. Where rearranged pairs are employed (in addition to new pairs), the left parietal effect is typically reduced for rearranged pairs compared to same pairs, regardless of whether an old or a new response, or a one- or two-stage judgement, is required for the rearranged condition (Donaldson & Rugg, 1998; Van Petten et al., 2002). However, recent research suggests that the left parietal effect elicited by associative recognition may not always reflect veridical memory (Cheng & Rugg, 2004). When rearranged pairs were highly similar to same pairs, the left parietal effect was equivalent for same pairs and for false alarms to rearranged pairs, but was absent for correctly-rejected rearranged pairs. In this instance, therefore, the recollected information appeared to lack the specificity required to execute the task, and was counterproductive to performance.

Similarly to the left parietal effect, the late right frontal effect seems to be sensitive to the degree of preservation of the studied association. Accordingly, the right frontal component is typically severely reduced for correctly-identified rearranged pairs compared to same pairs (Donaldson & Rugg, 1998; Cheng & Rugg, 2004). However, highly similar false alarms were shown to elicit equivalent right frontal modulations to same pairs (Cheng & Rugg, 2004). According to the post-retrieval evaluation account of the right frontal effect, this finding indicates that comparable levels of monitoring were being undertaken

for both hits and false alarms, but that these were insufficient to allow rejection of the falsely-recollected rearranged pairs.

Two other ERP old/new effects have also been reported in associative recognition studies. An early (600-900 ms) bilateral frontal positivity has been observed for same, but not for rearranged, pairs (Donaldson & Rugg, 1998; 1999, Experiment 1). Although the functional significance of this modulation is not apparent, it may represent the delayed-onsetting, associative recognition equivalent of the putative mid-frontal correlate of familiarity. Alternatively, the bilateral frontal positivity may represent operations specific to contextual retrieval: it disappeared when an explicit same/rearranged discrimination was no longer required (Donaldson & Rugg, 1998, Experiment 2). A third account relates the component to trial structure: it was present in an associative recall task that was randomly intermixed with an associative recognition task, but not in a blocked version of the recall task (Donaldson & Rugg, 1999).

In addition, a late posterior negative slow wave has been observed for rearranged pairs from approximately 900 ms onwards. Again the functional significance of this modulation is unclear, but it may be related to the late posterior negative slow wave (LPN) observed in item and source recognition studies. Accordingly, the appearance of this posterior negativity when recognition performance was poorer for rearranged than for same pairs (Donaldson & Rugg, 1998, Experiment 1) suggests that it might reflect increased response conflict. However, the absence of the effect for correctly-identified similar rearranged pairs when poor performance indicated high levels of response conflict (Cheng & Rugg, 2004), appears to contradict this account. Alternatively, the posterior negativity may reflect processes involved in the

conscious discrimination between same and rearranged pairs (cf. the retrieval of attribute conjunctions account of the LPN, Johansson & Mecklinger, 2003). This interpretation is supported by the component's disappearance when the requirement to make an explicit same/rearranged judgement was removed (Donaldson & Rugg, 1998, Experiment 2).

Summary

Associative recognition has been shown to elicit four old/new effects. The left parietal index of recollection tends to onset later and last longer than its item recognition counterpart, and generally appears greater for correctly-identified same pairs than for correctly-identified rearranged pairs. Likewise, the right frontal effect appears sensitive to the degree of preservation of the studied association. An early mid-frontal positivity for same pairs might be related to the putative ERP correlate of familiarity. Finally, a late posterior slow wave elicited by rearranged pairs could index processes involved in the explicit discrimination between same and rearranged pairs.

Ageing effects on the ERP correlates of recognition

In contrast to the recent proliferation of electrophysiological investigations of episodic retrieval processes in young adults, ERP research into the effect of normal ageing on these operations has been relatively limited to date. The current section provides a comprehensive review of ERP age-comparison studies of recognition and source memory. In particular, age-related changes in left parietal and right frontal effects will be examined. However, age comparisons of encoding are beyond the scope of this thesis and

will not be discussed (but for comprehensive reviews, see Friedman, 2000; 2003).

Continuous recognition studies

Early ERP ageing studies of explicit memory typically employed continuous recognition paradigms in which participants were presented with a series of stimuli, some of which were repeated at different delays (lags), and had to distinguish between previously-seen and new items (Friedman et al., 1993; Rugg et al., 1997; Swick & Knight, 1997). Behaviourally, elderly adults perform less well on continuous recognition tasks than young adults, particularly at longer delays. Electrophysiologically, a positive-going old/new effect with a centro-parietal maximum, present for all lag conditions in young adults, was generally reduced in the older participants at short lags, and absent at long lags (Rugg et al., 1997; Swick & Knight, 1997; but for discrepant findings, see Friedman et al., 1993). Moreover, the modulation's duration was reduced and its onset delayed by approximately 100-200 ms in the older groups. Similar delayed onsets in elderly participants' waveforms were evident in most of the ageing research reported in this chapter, but likely reflect general cognitive slowing (Salthouse, 1996), rather than mnemonic processes. Therefore, in the interests of clarity, these delays are not individually described.

The foregoing studies used visually-presented verbal stimuli, but other continuous recognition experiments indicate that these age-related ERP differences are generalizable to auditory stimuli (Minamoto et al., 2001), and to pictorial stimuli (Nielsen-Bohlman & Knight, 1995). Importantly, in this final study, the waveforms elicited by new line drawings showed age-equivalence,

indicating that the observed ageing differences in ERP old/new effects reflected changes in retrieval processes (but for findings of age-related differences in new waveforms, see Friedman et al., 1993).

The centro-parietal modulation elicited by continuous recognition tasks typically exhibits a similar time course to the left parietal effect, but its distribution tends to be more bilateral. This topographic discrepancy may be an artifact of experimental design differences between continuous recognition and study/test paradigms, and it is often tacitly assumed that the two components are related (e.g. Friedman, 2000). However, as short lag conditions generally involve very brief delays and a limited number of intervening items between first and second presentations, it is unlikely that the centro-parietal modulation exclusively indexes long-term memory processes, even in the long lag condition.

Continuous recognition studies do not therefore necessarily provide direct evidence of age-related changes in episodic memory. However, Morcom and Rugg (2004) recently used a study/test paradigm to examine the episodic recognition of words in two age groups following the encoding of either pictorial or verbal stimuli. Here, a left parietal effect observed in young adults, was absent from older adults, regardless of whether or not performance was age-equated, and whether pictures or words had been studied previously.

The absence of the left parietal effect in the foregoing experiment suggests, consistent with dual process theory, that the elderly were relying less on recollection than the young. This reduction may either be due to an ageing deficit in recollective processes or to an under-deployment of recollection when familiarity-based responding will suffice. The following sections therefore

describe a series of ERP age comparisons that address this issue by using retrieval tasks that promote recollection-based remembering.

Source memory studies

ERP source memory ageing studies typically present stimuli under two study conditions (e.g. different lists, voices or encoding tasks), and instruct participants to make one-, two- or three-stage source judgements at test. For example, Trott and colleagues (Trott et al., 1997; and for a detailed description of the same study, see Trott et al., 1999) showed young and elderly adults two lists of sentences with instructions to memorise the nouns from each sentence and the list to which they belonged. At test, participants had to distinguish between old and new nouns, before making remember/know, then source, decisions for those words judged old. Despite the older adults showing a specific source memory deficit, correct source judgments elicited statistically similar left parietal effects in both age groups (and remember judgements produced the same electrophysiological pattern, even though no between-group behavioural differences were observed). In contrast, a right frontal effect, present in the young, was found to be severely reduced in older adults. A similar pattern of findings was also reported in a replication of the foregoing study that included a manipulation to improve the older adults' near chance performance on the source task (Wegesin et al., 2002).

However, two other source memory experiments, one employing source or remember/know judgements on words presented by a male or female voice (Mark & Rugg, 1998), the second asking participants to recollect which of two encoding tasks they had performed on pictorial stimuli (Li et al., 2004), found no

age-related right frontal differences (this result was also replicated in the aforementioned item recognition paradigm, Morcom & Rugg, 2004). Moreover, Li and colleagues (but not Mark and Rugg) observed an age-related reduction in the left parietal effect, although, notably, on this occasion, amplitudes over right posterior sites were equivalent.

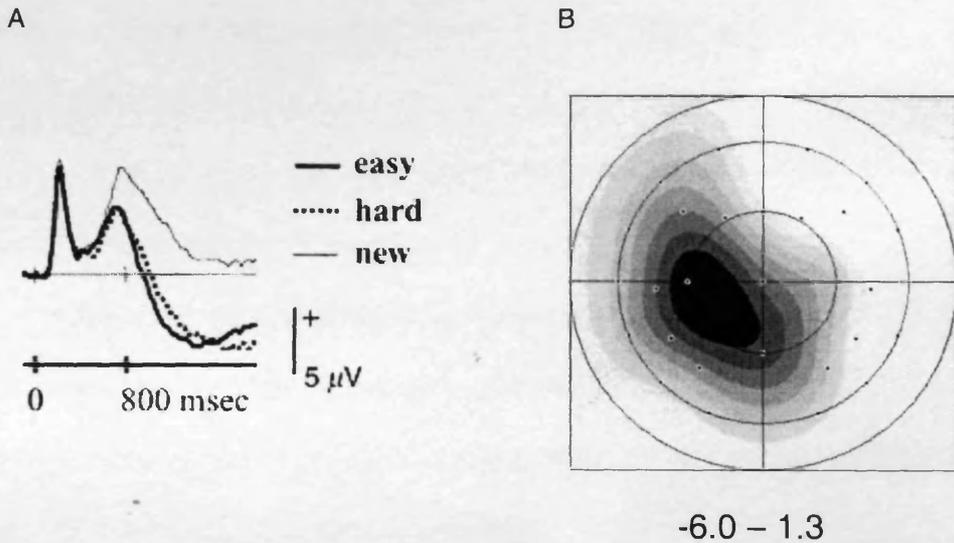


Figure 8. The central negativity in older adults. Panel A represents grand average ERP waveforms from three conditions in a source memory experiment at a left central electrode. B depicts a topographic map of the difference voltage between two conditions during the 1100-1900 ms latency period. The maximum and minimum voltage values are indicated beneath the map. Both panels adapted from Li et al. (2004). For further description of the topographic map, see Figure 4.

Three of the foregoing studies (Trott et al., 1997; Wegesin et al., 2002; Li et al., 2004) also demonstrated a negative-going old/new effect in older adults. The onset of this modulation varied from between 500 and 750 ms post-stimulus, but it appeared maximal at around 1100 ms with a central/posterior focus (Figure 8), and was apparent even when the groups' performance was matched (Li et al., 2004).

One possible interpretation of this central negativity is that it is homologous with the late posterior negative slow wave (LPN) observed in young adults, with the more posterior focus in the young merely reflecting the attenuation of the central negativity by the right frontal effect (Wegesin et al., 2002). However, Li and colleagues (2004) demonstrated that central age-related differences persist when the right frontal effect is equivalent across age groups. There have been two proposals as to the functional significance of this central negativity: First, the modulation has been linked to the engagement of different (possibly compensatory) processes that are likely related to the search for, or retrieval of, source information (Wegesin et al., 2002). Second, it has been suggested that the modulation reflects elderly people's increasing reliance on the reconstruction of perceptual information to make source judgements (Li et al., 2004; and c.f. Cycowicz & Friedman, 2003).

Exclusion studies

A series of ERP exclusion studies, where young and older participants distinguished between target (studied) words, new (unstudied) words and non-target lures (new words repeated at test), demonstrated that although target accuracy was equivalent in both age groups, the elderly made more false alarms to non-targets (Dywan et al., 1998; 2001; 2002). In young adults, greater positivities were observed for targets compared to non-targets (maximally at Pz), but the older participants' modulations were greater for non-targets than for targets (and were maximal at Fz, Dywan et al., 1998). These findings suggest that, consistent with the inhibition deficit hypothesis of cognitive ageing (see "Episodic Memory and Ageing" chapter), whilst young adults were able to

engage in strategic recollection and inhibit the recall of non-relevant information (see also Herron & Rugg, 2003a; 2003b; Herron & Wilding, 2005, and "Left parietal old/new effect", above), the elderly were not.

The possibility that the age-related performance deficit may have contributed to the ERP differences was excluded using a manipulation in which repeated test words were targets, and studied words were non-targets (Dywan et al., 2001). Here, with automatic and controlled processes working in concert (previously, the increased temporal recency of the non-targets had required automatic and controlled processing to work in opposition), the older adults' performance was comparable to that of the young adults for both targets and non-targets. Electrophysiologically, young adults produced greater positive-going old/new differences to targets than to non-targets, and older adults also demonstrated more positive-going ERPs to targets than to non-targets at Fz and Cz, but not at Pz. These findings confirm that young adults appear to be able to selectively inhibit non-target information, and further suggest that older adults are more reactive to recently-presented information, regardless of target status.

One important caveat to the foregoing conclusions is that the limited number of trials in some experimental conditions raised issues about the reliability of the data. However, a replication of Dywan and colleagues' (1998) Experiment 1, where the trial number was doubled and the number of electrodes increased from 3 to 27 (Dywan et al., 2002), confirmed that left parietal activation discriminated between target and non-target information only in young adults. The elderly adults failed to produce any left parietal effects, but did demonstrate a non-robust, early (400 ms onset) right-sided frontal positivity

to targets. (This latter finding may reflect lack of power in the experiment; only 13 participants contributed to the waveforms in each age group.)

Early mid-frontal component and ageing

Surprisingly few studies to date have reported any impact of ageing on early-onset ERP effects. Wegesin and colleagues (2002) reported that frontal modulations, evident between 300-600 ms post-stimulus in current source density data (see "Event-Related Potentials" chapter), had a similar magnitude, but different distributions, in young and older adults. In the young group, the bilaterally-distributed, prefrontal component closely resembled the early mid-frontal putative correlate of familiarity, whilst the older group's component was more right-sided. Likewise, Morcom and Rugg (2004) reported early (300-500 ms) frontal/central effects in both young and older adults that were more right-sided in the elderly. Such age-related distributional differences are difficult to interpret. Although in some instances they may demonstrate the engagement of different cognitive operations in young and older adults, minor topographic differences may simply reflect ageing changes in brain morphology that have altered the alignment of the neural generators of the ERP effects (for discussion of this issue, see Rugg & Morcom, 2004).

Age and performance

The main motivating factor for conducting ERP investigations into episodic memory and ageing is that older adults' performance tends to be impaired, particularly when tasks promote recollection rather than familiarity. This performance inequality is potentially problematic for the between-group electrophysiological comparisons. First, if older adults find a task more difficult

than young adults, they may exert more effort on it, and thus age effects on the neural correlates of successful retrieval may be confounded by differences in retrieval effort. Second, as performance decreases, the proportion of trials associated with a guess response or a very weak memory trace is likely to increase. As the number of "guess" or "weak memory" trials contributing to the grand average waveform rises, the neural correlates of successful retrieval will become increasingly diluted. Thus smaller ERP effects in older adults may simply be the result of this dilution, rather than ageing differences in the underlying retrieval operations per se. Third, weak memory may be processed differently from strong memory, such that post-retrieval evaluation may increase when memory is poor (Henson et al., 2000). Finally, when older adults perform less well than young adults, they may only remember a subset of "easy-to-retrieve" items. Ageing effects in the neural correlates of successful retrieval may therefore reflect differences in the characteristics of easy-to-retrieve and hard-to-retrieve information (see Rugg & Morcom, 2004, for a comprehensive overview of potential difficulties in conducting ERP comparisons across different age groups).

Summary

The foregoing studies have clearly demonstrated age-related changes in the ERP correlates of recognition and source memory; nevertheless, inconsistencies in their findings make the overall pattern difficult to interpret. Differences in parietal activation between young and older adults in item recognition and exclusion studies support the dual process view that recollection is impaired with age. However, age-related declines in the left

parietal index of recollection have not been found universally; several source memory paradigms have reported equivalent left parietal effects in young and older adults. Moreover, although a neural correlate of familiarity has not been identified in the elderly, two studies have reported early frontal old/new effects of equivalent magnitude, but which exhibit slight distributional differences, in young and older adults.

The right frontal index of post-retrieval evaluation processes appears sensitive to ageing only under certain circumstances. The lack of a clear logic governing the sensitivity of the right frontal effect to ageing most likely reflects its non-unitary nature, and a more precise definition of the modulation's functional significance is required before any conclusions can be reached. Moreover, a recent frequency analysis of Trott and colleagues' (1997; 1999) data suggests that the absence of the old/new effect in older adults does not necessarily reflect a lack of right frontal activation per se. The EEG alpha band indicated that a left posterior/right frontal neural network, which predicted young adults' source retrieval performance, was intact in the elderly (Luber et al., 2004). The network activity did not predict the older group's source accuracy, but this lack of correlation may reflect the fact that their performance was close to chance.

The foregoing frequency analysis, however, failed to demonstrate any compensatory activation in the older adults; a result that appears inconsistent with the view that the left central negativity observed in older adults in a number of ERP source memory studies (including that of Trott and colleagues) may index compensatory retrieval processes. Nevertheless, the relative paucity of ERP ageing comparisons of episodic retrieval necessarily means that any

functional accounts of ageing changes in the ERP correlates of episodic retrieval must remain speculative. The research reported in this thesis aims to address this deficiency through the use of an alternative item and associative recognition paradigm to further investigate the effect of ageing on the ERP correlates of episodic retrieval and on their underlying cognitive operations.

Chapter 5

General Methods

The previous chapters have presented reviews of the theoretical, methodological and experimental backgrounds against which the current research has been conducted. The focus now turns to the five experiments that will form the remainder of the thesis. Accordingly, the present chapter comprises an overview of the participants, stimulus materials, and experimental procedure, and of the ERP recording, processing and analyses. However, each individual experimental chapter will contain a separate methods section describing any procedures specific to that particular study.

Participants

Young participants were recruited from the student population at Stirling University; older participants were community-living volunteers. The following selection criteria were employed: right-handed, native English speakers, with normal (or corrected-to-normal) vision. The young group were aged between 16

and 30 years; the older group between 65 and 80 years. Participants were offered payment at a rate of £5.00 per hour; however, some of the young group opted for part payment in course credits. Prior informed consent was obtained from all participants.

Neuropsychological tests

Participants visited the laboratory on two occasions. Two to five days prior to the main experimental session, each volunteer undertook a battery of neuropsychological tests and was trained on the experimental procedure. The neuropsychological testing comprised the Matrix Reasoning and Vocabulary subscales of the Wechsler Abbreviated Scale of Intelligence (WASI, Wechsler, 1999), and the Logical Memory I and II, Verbal Paired Associates I and II and Letter Number Sequencing subscales of the Wechsler Memory Scale – Revised (WMS-R, Wechsler, 1987).

In view of the evidence of a weak, but specific, relationship between health factors and memory performance in older adults (Nilsson et al., 1997; Jelicic et al., 1999), participants were also required to rate their health on a 5-point scale; where 1 = 'poor', 2 = 'could be better', 3 = 'fair', 4 = 'good' and 5 = 'excellent'. A rating of 3 or above was necessary for inclusion. The Beck Depression Inventory (BDI, Beck et al., 1961) was used to screen for depression, and the older adults undertook the Mini Mental State Examination (MMS, Folstein et al., 1975) to ensure they had no pathological memory impairment (e.g. dementia). Moreover, any participant with a history of neurological or psychiatric illness, epilepsy, head injury, stroke, or 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 experimental instruction session consisted of a short training block followed by one full length experimental block for the young groups, and two full length blocks for the older groups. The elderly were given an extended training session because pilot studies had indicated that they required more practice than young adults before becoming comfortable with the task demands (see also Craik & Anderson, 1999).

Stimulus materials

Words were selected at random from a pool of 1185 medium frequency nouns and verbs (mean – 17.1 ± 5.8 per million, Kücera & Francis, 1967) from the MRC Psycholinguistic Database (Coltheart, 1981). The complete word pool is presented in Appendix A. The words were paired at random and then checked visually to ascertain that all the resultant pairings were semantically and associatively unrelated. In Experiments 1 – 3, 768 words were used to form pairs which were randomly assigned to two study lists, each containing 192 pairs. The study lists were matched for frequency and their presentation was counterbalanced across participants.

Test lists (in Experiments 1 – 4) contained equal proportions of 4 types of stimuli (Table 1, below); single words from the study list (old); single words from the unseen study list (new); intact study pairs (same); and pairs whose second word had been exchanged with the second word from another study pair (rearranged). The position of the words within a pair was held constant between study and test. The test lists were counterbalanced so that each study

pair served equally often as an old single word, a same word pair, and a rearranged word pair. In Experiments 1 – 3, 8 study/test blocks were presented randomly. Additional words were used for the initial practice session, which generally comprised a short training block containing 6 study pairs, followed by one or two full length blocks with 24 study pairs.

Table 1. Experimental design for a single study/test block in Experiments 1 – 3, showing the different classes of stimuli and associated responses.

Phase	Task	Stimulus Type	Example	Response
STUDY LIST	Paired Associate Learning	24 novel word pairs	TENNIS HUNT MISTER CHORUS NEON FIST POSTURE YARN	Generate a sentence
	Item Recognition	8 old words 8 new words	TENNIS PAVEMENT	OLD NEW
TEST LIST	Associative Recognition	8 same pairs 8 rearranged pairs	POSTURE YARN MISTER LIGHT	OLD NEW

The main experimental design was closely based on a behavioural paradigm first used by Hockley (1994). The programme was compiled using E-Prime software (Psychology Software Tools, Inc., www.pstnet.com). Stimuli were presented on a computer monitor using bold 18 point Courier New font. Upper case white letters were seen against a black background. The pairs were displayed with one word above the other, slightly above and below central vision. Single words were displayed in central vision. At the viewing distance of 97 cm, the stimuli subtended a maximum horizontal visual angle of approximately 3.7°, and a maximum vertical visual angle of approximately 1.4°.

Responses were made on a PST Serial Response box (Psychology Software Tools, Inc.).

Experimental tasks and procedures

The following description of the study and test trial structures applies to Experiments 2 – 4 only. The study phases were self-paced. Every trial began with an initial fixation cross (+) displayed in the centre of the screen for 1000 ms. The cross served to maintain the participant's gaze on the centre of the screen, and to warn them that the next trial was about to begin. A 750 ms blank screen then preceded the presentation of the study stimulus (1500 ms). The study pair was followed by another blank screen. Participants were instructed to generate a sentence using both words in each study pair, and to press a button on a Serial Response Box (www.pstnet.com) to terminate that trial. The hand used to respond was counterbalanced across participants. The encoding task was chosen to encourage elaboration in older adults, who, left to their own devices, tend to use less elaborative encoding strategies than young adults (e.g. Craik & Byrd, 1982).

The test phases immediately followed each study phase. Every test trial began with a fixation cross (1000 ms), then a blank screen (750 ms). The test stimulus appeared for 1500 ms, followed by a 2500 ms blank screen. Participants had to make an old/new decision within this 4 second interval. A question mark in central vision then signalled participants to make a self-paced confidence judgment about their old/new response. Here, the following 5-point scale was used: 1 = 'guess/mistake'; 2 = 'unsure'; 3 = 'think so'; 4 = 'pretty

certain'; and 5 = 'certain'. The confidence judgment was followed by a 1500 ms blank screen before the next trial began.

Participants were required to make old/new decisions for both single words and word pairs, but were advised that the recognition tasks were different. In item recognition, participants had to indicate whether the words had appeared in the study phase or not (i.e. if the words were old or new); in associative recognition, they had to differentiate between same and rearranged pairs. The instructions stressed that the old/new responses should be made as quickly and as accurately as possible. The hand-response mapping was counterbalanced across participants, who were also told to relax, to minimise body and head movement, and to fixate their gaze on the centre of the screen to reduce the number of trials containing EOG artifact.

Finally, following the removal of the electrode cap, participants were asked to complete a post-experimental questionnaire designed to assess their subjective experience of the study and test tasks. A copy of this questionnaire and tables of results for each experiment can be found in Appendix C.

Behavioural data

The following behavioural data were reported for each task; the proportions of hits and correct rejections, discriminability and bias [Pr ($phit-pFA$) and Br ($pFA/1-Pr$), respectively; Snodgrass & Corwin, 1988], test RTs for hits and correct rejections, and study RT. In Experiments 2 – 5 the confidence data were split into high and low confidence responses, where ratings of 5 were classed high confidence and all other ratings were classed low confidence. As dual process theory assumes recollection to be typically associated with high

confidence responses, this division was undertaken in an attempt to compare the contribution of recollection to each task in both participant groups (e.g. Yonelinas, 1994; 1997; 2002; Yonelinas et al., 1996; but see Yonelinas, 2001a and "Experiment 2" for a caveat to this interpretation).

In the age comparisons (Experiments 2 – 4), mixed ANOVAs were employed for the hits and correct rejections data [task (item vs. associative) by response category (hits vs. correct rejections) by age (young vs. older)]; the high confidence responses [task (item vs. associative) by response category (high confident hits vs. high confident correct rejections) by age (young vs. older)]; the discriminability and bias indices [task (item vs. associative) by age (young vs. older)]; and the test RT data [task (item vs. associative) by response category (RT hits vs. RT correct rejections) by age (young vs. older)]. All main effects, but only significant interactions involving the factor of age, were reported. The interactions were investigated using subsidiary ANOVAs and/or paired or independent t-tests. The study RT data were analysed using an independent t-test.

In Experiment 1, in the absence of any age comparison, the hits and correct rejections, and test RT, data were analysed using repeated-measures ANOVAs of the same design as previously, but without the factor of age. The discriminability and bias scores were assessed using paired t-tests. The behavioural analyses in Experiment 5 were similar to those in Experiment 1, but here the factor of lag (long vs. short) replaced that of task.

ERP recording and data processing

EEG was recorded during both study and test phases using silver/silver-chloride electrodes embedded in an elasticated cap (Neuromedical Supplies “QuickCap”, <http://www.neuro.com>). Recordings were made from 61 standard sites with reference to the international 10-20 system (Jasper, 1958): Fz, FCz, Cz, CPz, Pz, POz, Oz, FP1, FP2, AF7, AF8, AF3, AF4, F7, F8, F5, F6, F3, F4, F1, F2, FT7, FT8, FC5, FC6, FC3, FC4, FC1, FC2, T7, T8, C5, C6, C3, C4, C1, C2, TP7, TP8, CP5, CP6, CP3, CP4, CP1, CP2, P7, P8, P5, P6, P3, P4, P1, P2, PO7, PO8, PO5, PO6, PO3, PO4, O1, O2 (Figure 9, below). Vertical and horizontal EOG were recorded bipolarly from electrodes placed above and below the left eye, and on the outer canthi. All channels were referenced to the left mastoid, but an additional EEG channel was recorded from the right mastoid, and the waveforms algebraically reconstructed off-line to represent recordings with respect to a linked mastoid reference. The electrode impedances were kept below 5k Ω . EEG and EOG were filtered with a bandpass of 0.01-40 Hz, and digitized (16 bit) at a rate of 8 ms per point. The recording epoch was 2048 ms, beginning 104 ms prior to stimulus onset.

ERP waveforms were baseline corrected and digitally smoothed using a 5 point binomial filter with a low-pass frequency of 19.4 Hz. With the exception of Experiment 1, blink artifacts were minimised by estimating and correcting their contribution to the ERP waveforms via a standard temporal regression technique (Rugg et al., 1997). Trials were rejected if they contained A/D saturation or horizontal EOG movements greater than 100.04 μ V, if the EEG channels' base-to-peak amplitude exceeded 100.04 μ V, or if drift from baseline exceeded \pm 48.4 μ V. A minimum of 16 artifact-free trials was required from each

participant in each critical response category to ensure an acceptable signal-to-noise ratio.

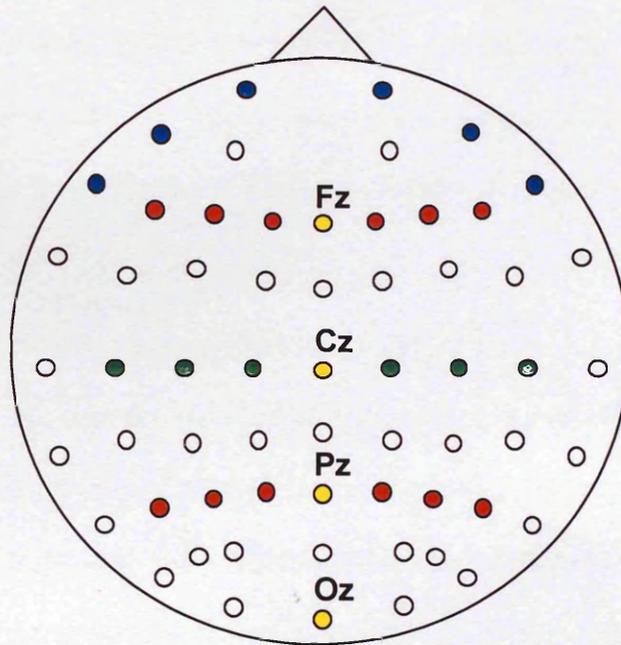


Figure 9. Schematic map of 61 EEG electrode sites. Electrodes used in the Main ANOVA are shown in red. Electrodes used in the Midline ANOVA are yellow, and those in the Central ANOVA are green. The additional Prefrontal electrodes employed in initial 100 ms bins ANOVAs are depicted in blue.

ERP analyses

Rationale

The aim of the research conducted in this thesis was twofold: First, to compare the ERP correlates of successful item and associative recognition in young adults; second, to examine the effect of ageing on these indices. Accordingly, for item recognition, the critical ERP comparison was between correctly-identified old words and correctly-identified new words (hereafter referred to as OLD and NEW, respectively). In associative recognition, the critical comparison was between correctly-identified same pairs and correctly-

identified rearranged pairs (hereafter referred to as SAME and REARRANGED, respectively). Although other ERP studies of associative recognition have included new pairs (comprising two unstudied words), here new pairs were not used because they can be distinguished from same pairs on the basis of familiarity alone, and the aim of the associative task was to promote recollection.

Furthermore, if a new pairs condition had been included, a three-choice decision would have been required in associative recognition, compared to the two-choice decision in item recognition. As a fundamental goal of the experimental design was to maintain constancy between the test conditions, it seemed more appropriate to present participants with a two-choice decision, between 'targets' (OLD/SAME) and 'non-targets' (NEW/REARRANGED) for each recognition task. The between-task and ageing comparisons were performed using the difference voltages for each task (OLD minus NEW for item recognition; SAME minus REARRANGED for associative recognition).

Magnitude analyses

The ERP amplitude data for each task was initially analysed separately using consecutive 100 ms bins to ascertain the presence and time course of reliable voltage differences in both age groups. Repeated-measures ANOVA employed the factors of response category 'RC' (OLD/SAME vs. NEW/REARRANGED), hemisphere 'H' (left vs. right), location 'L' (prefrontal vs. anterior vs. central vs. posterior), and site 'S' (inferior vs. mid vs. superior – for the precise electrode sites, see Figure 9). In addition, paired t-tests were conducted on the 256 data points in the difference waveforms at every

electrode site to establish the onset latency of ERP effects in each task. The criterion for determining the presence of robust modulations was fifteen consecutive significant results at a single electrode.

The preceding analyses, together with visual inspection, 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 condition of interest (OLD, NEW, SAME and REARRANGED) were then calculated for each latency period and subjected to analysis by repeated-measures ANOVA. Initially, two ANOVAs were planned to assess the reliability of frontal and parietal ERP effects separately for each task: the Main ANOVA employed factors of response category 'RC' (OLD/SAME vs. NEW/REARRANGED), hemisphere 'H' (left vs. right), location 'L' (anterior vs. posterior), and site 'S' (inferior vs. mid vs. superior); the Midline ANOVA employed factors of response category (OLD/SAME vs. NEW/REARRANGED) and location (Fz vs. Cz vs. Pz vs. Oz). However, because of the presence of positive-going activations over central sites in associative recognition, an additional ANOVA of the central location was also conducted [response category (OLD/SAME vs. NEW/REARRANGED) by hemisphere (left vs. right) by site (inferior vs. mid vs. superior)]. Only main effects and interactions involving the factor of response category are reported.

Between-task analyses were conducted on the difference waveforms. Similar to the within-task analyses, three ANOVAs (Main, Midline and Central) were performed, but here the factor of response category was replaced by task 'T' (item vs. associative), and the reported results were restricted to those involving the factor of task. Finally, to examine ageing effects on the ERP

components elicited by each task, between-group Main, Midline and Central ANOVAs were conducted separately on the item and associative recognition difference waveforms. Here, the factor of response category was replaced by age 'A' (young vs. older), and only those results involving the factor of age were reported.

Significant interactions were investigated using appropriate subsidiary ANOVAs and/or post hoc t-tests. Four-way interactions (e.g. response category by hemisphere by location by site) were investigated using three-way ANOVAs (e.g. response category by hemisphere by site) of separate locations. Three-way interactions (e.g. response category by hemisphere by location) were explored using two-way ANOVAs [e.g. response category by hemisphere (collapsed across site)]. Two-way interactions (e.g. response category by hemisphere) were followed up using paired or independent t-tests [e.g. of separate hemispheres (collapsed across site)]. Here, a conservative Bonferroni correction was applied to account for multiple comparisons, and only the corrected p-values are given. All interactions were investigated, but the subsidiary analyses are only reported where they inform the experimental findings. Finally, where the initial magnitude ANOVAs, or subsidiary ANOVAs, failed to reveal reliable main effects and/or interactions of interest, targeted analyses were conducted using the sites where ERP effects have typically been observed previously.

Topographic analyses

Topographic comparisons were only performed when the relevant within-task amplitude analyses revealed robust ERP effects. Topographic ANOVAs

were conducted on the item and associative recognition difference amplitudes for each latency period following normalisation (across all 61 EEG electrodes) using the maximum/minimum method (McCarthy & Wood, 1985). Within-task comparisons [Main – epoch 'E' (latency period 1 vs. latency period 2) by hemisphere (left vs. right) by location (anterior vs. posterior) by site (inferior vs. mid vs. superior); Midline – epoch (latency period 1 vs. latency period 2) by location (Fz vs. Cz vs. Pz vs. Oz); Central – epoch (latency period 1 vs. latency period 2) by hemisphere (left vs. right) by site (inferior vs. mid vs. superior)] were conducted to confirm distributional differences in the ERP correlates of item and associative recognition over time. Between-task and between-group topographic comparisons were performed using ANOVAs of the same design as the equivalent magnitude comparisons. Only interactions involving the factors of epoch, task or age, respectively, are reported.

The foregoing magnitude and topographic ANOVAs employed the Greenhouse-Geisser correction for non-sphericity of data (Greenhouse & Geisser, 1959), and the corrected *df* values and associated F ratios are reported where appropriate. Greenhouse-Geisser correction is necessary because the ANOVA model assumes that a dataset is spherical, and the probability of a Type-1 error increases if this assumption is violated. Sphericity requires the variances within all levels of any repeated-measures factor to be equal, and the covariance between the levels to be homogeneous. However, 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.

Accordingly, when an ANOVA involves a number of disparate electrode sites it is unlikely that the sphericity assumption will be met.

Summary

The foregoing description of the materials, procedure and analyses applies to some extent to most of the research reported in the forthcoming experimental chapters. Nevertheless, in most cases some departure will occur; in Experiment 1, for example, a remember/know response was required instead of a confidence rating, and in Experiment 5, the experimental design was radically altered. However, any such differences will be described in full in the relevant "Methods" or "Results" sections.

Chapter 6

Experiment 1

Introduction

In real life, our memory for prior events almost invariably requires us to remember an episode in the context in which it happened. Consequently, studies of recognition memory that investigate the way people recognise associations between items (associative recognition), rather than merely remembering the items themselves (item recognition), are of great interest. Given the correspondence between associative recognition and real-life remembering, it is surprising that the majority of neuroimaging studies of recognition memory have focused on item recognition, and that relatively few direct comparisons with associative recognition have been undertaken. This first experimental chapter therefore presents a direct comparison of item and associative recognition that uses event-related potential (ERP) methodology to provide evidence for dissociation of their neural correlates.

Behavioural studies indicating that item and associative recognition depend on different memory retrieval processes have provided convincing support for dual-process theories of recognition memory (Atkinson & Juola, 1974; Mandler, 1980; Jacoby & Dallas, 1981; Tulving, 1982; Yonelinas, 1999). From the dual-process perspective, item recognition can be based on either recollection or familiarity. In contrast, associative recognition should rely more heavily on recollection because it demands memory for context.

Previously, separate ERP studies have provided some evidence for dissociation of the neural correlates of item and associative recognition. Item recognition usually elicits the left parietal correlate of recollection (e.g. Rugg & Doyle, 1992; Smith, 1993) and the putative mid-frontal correlate of familiarity (e.g. Rugg et al., 1998a; Curran, 2000), whereas associative recognition generally produces the left parietal correlate of recollection and the right frontal index of post-retrieval monitoring processes (Weyerts et al., 1997; Donaldson and Rugg, 1998, 1999; Van Petten et al., 2002; Cheng & Rugg, 2004). However, comparison of the ERP correlates of item and associative recognition has always been confounded by the fact that different studies, and therefore different experimental designs and separate participant groups, have been used to investigate each type of recognition memory. The present experiment aims to eliminate these confounds by using a single paradigm for both item and associative recognition, thus allowing direct comparison of their ERP components independent of any effects of study task or separate participant groups.

Another goal of the current research is to provide an alternative means of investigating the mid-frontal old/new effect, the functional significance of

which is still in dispute. Although initially thought to index familiarity (Rugg et al., 1998a), the demonstration that the mid-frontal effect disappeared when shallow and deep encoding tasks were blocked, rather than interleaved, prompted the suggestion that it may be linked to trial structure (Rugg et al., 2000; see also Donaldson & Rugg, 1999). An alternative interpretation of the modulation as an index of recollective processes followed its appearance for remember, but not for know, trials in a remember/know paradigm (Duarte et al., 2004). Finally, the mid-frontal component has also been interpreted as a negative-going index of novelty (Tsvilis et al., 2001; see also Schloerscheidt & Rugg, 2004). The novelty account followed the demonstration that when participants were asked to recognise studied objects, regardless of the background against which they were presented, a mid-frontal effect was observed for old object/background (same) pairings and for old objects against a different studied background (rearranged), but not for old objects against a novel background (old/new).

In the current experiment, young participants studied a series of unrelated word pairs, before being instructed to discriminate either between old and new single words (item recognition), or between same and rearranged pairs (associative recognition). The retrieval tasks were randomly intermixed, and once the ERP recording was complete, a secondary remember/know judgment was required for each word, or word pair, judged old. In line with previous behavioural and ERP studies, and in accordance with the dual process proposal that both familiarity and recollection contribute to item recognition, but that associative recognition relies more heavily on recollection, we made two ERP predictions: First, that item recognition should elicit mid-

frontal and left parietal effects; and second, that associative recognition should produce left parietal and late right frontal effects.

Methods

Participants

31 participants (12 male, mean age 20.1 years; range 17-32) took part in the experiment. The data from seven participants was excluded because of technical difficulties; one further participant was excluded because of poor associative recognition performance. 23 participants (10 male, mean age 19.5 years, range 17-28) remained.

Stimulus materials, procedure and ERP recording

The “General Methods” chapter describes the stimulus materials, basic experimental procedure, and the ERP recording and analysis used in most of the experiments in this thesis. However, as Experiment 1 differs from that description in several respects, the current procedure is outlined below.

The study phases were self-paced. Every trial began with an initial exclamation mark (!) displayed in the centre of the screen for 1000 ms. Blink correction was not applied to the ERP data from this experiment, instead the epochs during which the participants blinked were rejected prior to averaging. Therefore, in order to maximise the number of blink-free epochs, participants were instructed to blink only when the exclamation mark was on the screen. A 2000 ms fixation mark (+) then preceded the presentation of the study pair. The study pair remained on the screen for an indefinite period. Participants were required to generate a sentence that contained both words in each study pair,

then to press a response key that triggered the presentation of the following pair. This response was followed by a 1000 ms fixation mark before the next trial began. The response hand was counterbalanced across participants.

Each study phase was immediately followed by a test phase. As participants were again required to restrict their blinking, every test trial began with an exclamation mark (1000 ms). A 2000 ms fixation mark followed this signal to blink. The test stimulus then appeared for 1500 ms, followed by a 2500 ms fixation mark. Participants were instructed to make an old/new decision within this four second interval (for the precise instructions, see “General Methods” chapter). The hand-response mapping was counterbalanced across participants.

Once the main experiment had been completed and the EEG cap removed, participants were presented with all those test stimuli to which they had responded "old" and were asked to indicate whether they remembered the word or word pair from the study phase, just knew they had seen it before, or whether their response had been a guess [see Appendix B for the precise remember/know/guess (RKG) instructions]. The reasoning behind the inclusion of the RKG phase was twofold: Firstly, the proportion of remember and know responses would provide a behavioural estimate of recollection and familiarity. Secondly, it was hoped that separation of remember and know response trials would allow an ERP comparison between a high recollection condition (remember trials) and a familiarity condition (know trials). Unfortunately, as very few participants produced enough know trials, this analysis could not be performed.

Results

Behavioural

The performance data are summarised in Table 2 (below). The hits and correct rejections ANOVA (for details of the behavioural ANOVA designs for this and the other experimental chapters, see “General Methods” chapter) produced a main effect of response category [$F(1,22) = 6.63, p < 0.05$], and a task by response category interaction [$F(1,22) = 48.94, p < 0.001$]. In short, the correct rejection rate was higher than the hit rate in item recognition [$t(22) = 7.49, p < 0.001$], but the two rates were equivalent in associative recognition [$t(22) = 1.26, n.s.$]. Participants showed a more conservative bias (Br) in item recognition than in associative recognition [$t(22) = 6.14, p < 0.001$], but there was no difference in task difficulty as indexed by discriminability (Pr) [$t(22) = 0.54, n.s.$].

Table 2. Mean performance data (\pm S.D.) for Experiment 1.

	Item Recognition	Associative Recognition
Accuracy		
Hits	0.75 ± 0.10	0.86 ± 0.10
Hits/Remember	0.45 ± 0.20	0.77 ± 0.25
Hits/Know	0.38 ± 0.16	0.17 ± 0.22
Correct Rejections	0.92 ± 0.06	0.82 ± 0.14
Pr	0.67 ± 0.13	0.68 ± 0.17
Br	0.24 ± 0.19	0.54 ± 0.24
RT(ms)		
Hits	1185 ± 260	1408 ± 285
Correct Rejections	1187 ± 263	1696 ± 379
Study RT(ms)	3640 ± 1472	

An ANOVA of the RKG responses [task (item vs. associative) by response (Hit/Remember vs. Hit/Know)] produced a task by response category

interaction [$F(1,22) = 26.19, p < 0.001$]. Subsidiary t-tests revealed that there were more remember responses in associative recognition [$t(22) = 5.67, p < 0.001$], but more know responses in item recognition [$t(22) = 4.19, p < 0.001$].

The test RT ANOVA produced main effects of task [$F(1,22) = 257.05, p < 0.001$] and response category [$F(1,22) = 46.53, p < 0.001$], and a task by response category interaction [$F(1,22) = 68.29, p < 0.001$]. Item recognition judgments were produced more rapidly than associative recognition judgments, and subsidiary t-tests demonstrated that hits were faster than correct rejections in associative recognition [$t(22) = 9.14, p < 0.001$], but not in item recognition [$t(22) = 0.11, n.s.$].

Summary of behavioural data

Performance (as indexed by Pr) on both item and associative recognition tasks was similar, a pattern which is consistent with previous findings (Hockley, 1994). In the current study, however, participants adopted a more conservative bias in item recognition. The remember/know results suggest that, as predicted, the contribution of recollection was larger in associative recognition, but familiarity was increased in item recognition. In associative recognition, hit responses were produced more rapidly than correct rejection responses, whereas there was no latency difference between the two classes of responses in item recognition. Finally, the slower response time for associative recognition most likely simply reflects the increased demands of reading two words instead of one (Hockley, 1994).

Event-related potentials

Initial examination of the grand average waveforms for both item and associative recognition revealed a timing error in the data. Close inspection showed there was a delay (mean = 155 ± 4 ms) between the trigger being sent to the recording computer and the test stimulus appearing on the screen. As this delay was consistent across retrieval tasks and response categories, the error could be eliminated by simply re-epoching the data for each participant. The results presented below are from the delay-corrected data.

Item recognition

Figure 10 (p161) shows the grand average OLD and NEW waveforms for item recognition from 30 EEG electrode sites. The mean number of trials (\pm S.D.) contributing to the ERPs was 40 (8) OLD and 48 (9) NEW. The waveforms diverge from approximately 250 ms post-stimulus onset, with the ERPs for OLD words becoming more positive than those for NEW words. This positive modulation is most evident over frontal sites, where it exhibits a bilateral distribution. From about 400 ms, an old/new positivity also becomes apparent over temporo-parietal sites. The effect appears to exhibit a left-sided distribution and starts to decline at around 700 ms. From 1100 ms onwards, the most prominent old/new difference is a right-sided positivity over frontal sites.

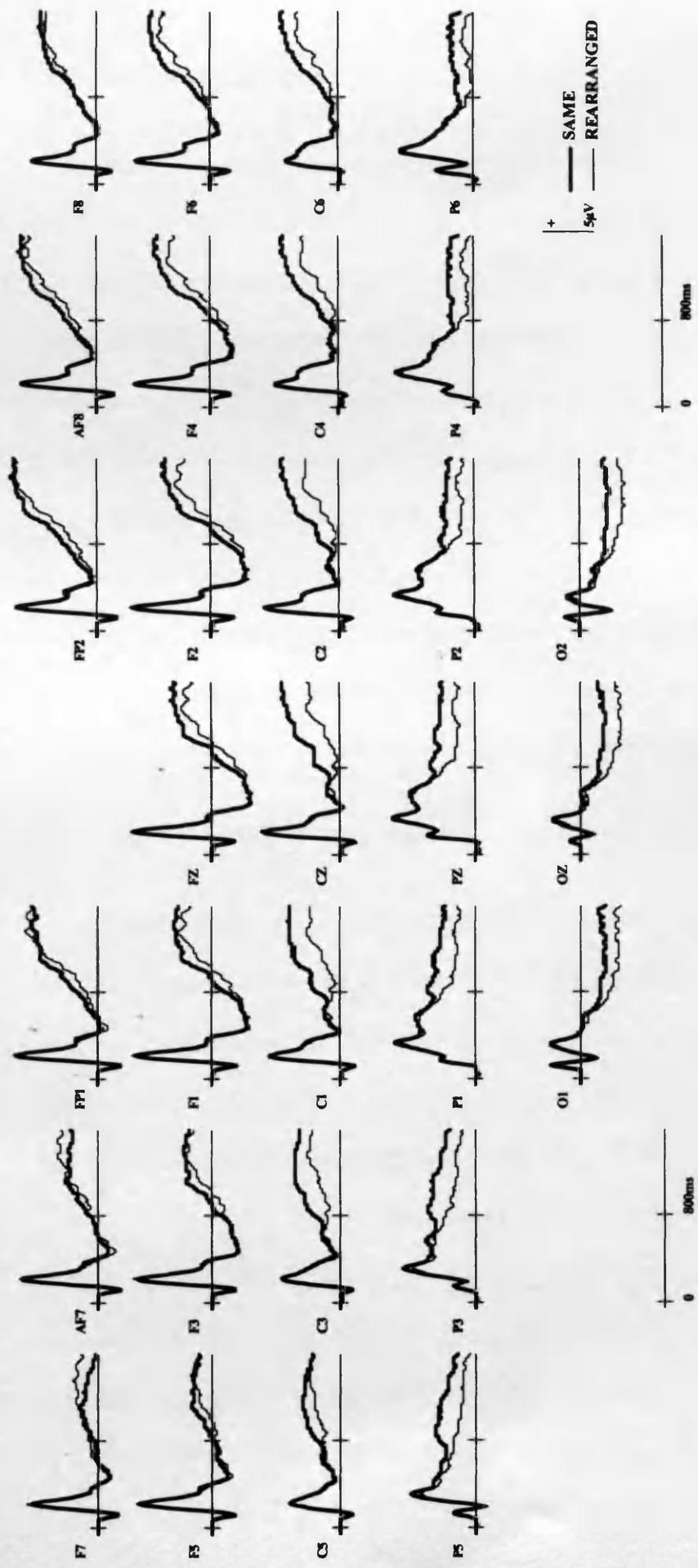


Figure 11. Grand average ERPs for the recognised (SAME) and REARRANGED response categories for associative recognition. Electrodes shown as in Figure 10.

Associative recognition

Figure 11 (p162) shows the grand average SAME and REARRANGED waveforms for associative recognition, again from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 46 (9) SAME and 42 (11) REARRANGED. The waveforms appear to diverge somewhat later than in item recognition; the earliest difference is only apparent from around 750 ms when the ERPs for SAME pairs became more positive than those for REARRANGED pairs over central and parietal sites. This deflection initially appears to have a left-sided distribution. From 1100 ms onwards, a positive same/rearranged difference also becomes apparent over right frontal sites. Nevertheless the most prominent effects remain over central and parietal sites, where they tend to develop a right-sided asymmetry as the epoch progresses.

Rationale for the ERP analyses

The principle aim of the analyses was to compare early mid-frontal, left parietal and late right frontal old/new effects (the putative ERP correlates of familiarity, recollection, and task-directed, post-retrieval decision processes, respectively) in item and associative recognition. Preliminary analyses (see "General Methods" chapter for details) indicated that the following latency regions best reflected the development of the ERP effects over time: 250-450 ms, 450-850 ms, 850-1100 ms and 1100-1900 ms. The mean amplitude (relative to the 104 ms prestimulus baseline) for each latency region was submitted to within-task magnitude ANOVAs to assess the presence of reliable ERP modulations in item and associative recognition. Between-task magnitude and topographic ANOVAs were conducted on the difference (and rescaled

difference) waveforms for each task to confirm any quantitative and qualitative disparity between the ERP correlates of item and associative recognition.

Precise details of the ERP analysis strategy for this and the other experiments can be found in the “General Methods” chapter.

Item recognition

The earliest old/new differences were observed at 248 ms (as shown by preliminary t-tests) over anterior (F2, F4, F6, FP2, AF4 and AF8) electrodes. Therefore, although main effects of response category in the Main, Central and Midline 250-450 ms ANOVAs (Table 3, p166) indicate that OLD waveforms were generally more positive than NEW waveforms, these magnitude differences appear to have a frontal focus (Figure 12, A, p168). Targeted t-tests confirmed that the modulation was robust over frontal [$t(22) = 3.31, p < 0.01$], but not over parietal [$t(22) = 1.51, n.s.$] sites, suggesting that it represents an early mid-frontal effect that extended to the central location. However, a response category by site interaction [$F(1.1, 24.8) = 8.06, p < 0.01$] in the subsidiary ANOVA of the left hemisphere, which followed the three-way interaction in the Main ANOVA, demonstrated that the effect had a slight right-sided asymmetry.

The widespread positivity of OLD waveforms continued into the 450-850 ms latency period, as shown by main effects of response category in all three initial ANOVAs. Subsidiary analyses investigating the three-way interaction in the Main ANOVA confirmed the presence of a robust left parietal old/new effect [$t(22) = 3.39, p < 0.01$] (Figure 12, B). Meanwhile, a main effect of response

category [$F(1,22) = 8.62, p < 0.01$] in the subsidiary ANOVA of frontal sites most likely reflects the early bilateral onset of the late right frontal effect.

By 850-1100 ms, a targeted t-test following the main effect of response category in the Main ANOVA indicated that the left parietal old/new effect was in decline [$t(22) = 1.73, n.s.$]. Moreover, the subsidiary analysis of parietal sites, investigating the response category, location and site interaction in the Main ANOVA produced a response category by site interaction [$F(1.2,25.9) = 5.08, p < 0.05$]. This finding demonstrated that posterior old/new differences had become focused over inferior electrodes. Over frontal sites, in contrast, robust widespread old/new differences persisted. These anterior effects were reflected by the two-way interaction in the Midline ANOVA and the response category, hemisphere and location interaction in the Main ANOVA [a subsidiary analysis of frontal electrodes produced a main effect of response category – $F(1,22) = 7.80, p < 0.05$].

The foregoing findings likely reflected the continuing bilateral onset of the late right frontal effect in the third time window (Figure 12, C). Accordingly, the interaction involving response category, hemisphere and location in the Main 1100-1900 ms ANOVA indexed the established late right frontal component. Subsidiary analyses revealed significant old/new differences over the right frontal hemisphere [$t(22) = 2.72, p < 0.05$] (Figure 12, D). Meanwhile, non-robust negative-going parietal old/new differences were greatest over superior sites: a subsidiary analysis of the posterior location following the interaction involving response category, location and site in the Main ANOVA produced a response category by site interaction [$F(1.3,29.5) = 7.72, p < 0.01$].

Associative recognition

Same/rearranged ERP differences were first observed at electrode PO7 at 784 ms post-stimulus onset. From around 800 ms, these differences were also evident over left parietal (P7, P5, P3) electrodes, and thereafter rapidly became widespread across the scalp. The extended distribution was reflected by main effects of response category in the Main, Central and Midline 850-1100 ms ANOVAs (Table 3). The critical question of whether the left parietal effect (Figure 12, C) was robust was addressed by targeted t-tests of left and right parietal hemispheres (collapsed across site). These analyses revealed significant ERP effects over both hemispheres [left parietal – $t(22) = 5.03$, $p < 0.001$; right parietal – $t(22) = 2.92$, $p < 0.05$], but the differences appeared slightly larger over the left hemisphere (Figure 13, C, p172).

Between 1100 and 1900 ms, main effects of response category in the Main, Central and Midline ANOVAs again indicated widespread positive ERP effects. For this time period, the principle questions of interest, namely the reliability of persistent left parietal activation and the late right frontal effect, were addressed through targeted t-tests of left and right parietal and frontal hemispheres. Significant same/rearranged differences were apparent over both left [$t(22) = 3.72$, $p < 0.01$] and right [$t(22) = 2.94$, $p < 0.05$] parietal hemispheres and appeared to be of equivalent magnitude (see Figure 13, F). These results illustrate a slowly declining left parietal effect in conjunction with a right-sided central/posterior positive activation: the subsidiary ANOVAs investigating the three-way interaction in the Central ANOVA revealed a response category by site interaction over the left hemisphere [$F(1.2,26.9) = 12.70$, $p = 0.001$], and a main effect of response category over the right hemisphere [$F(1,17) = 17.30$, p

< 0.001]. Importantly, however, right frontal same/rearranged differences were also robust [$t(22) = 3.00, p < 0.05$] (Figure 12, D).

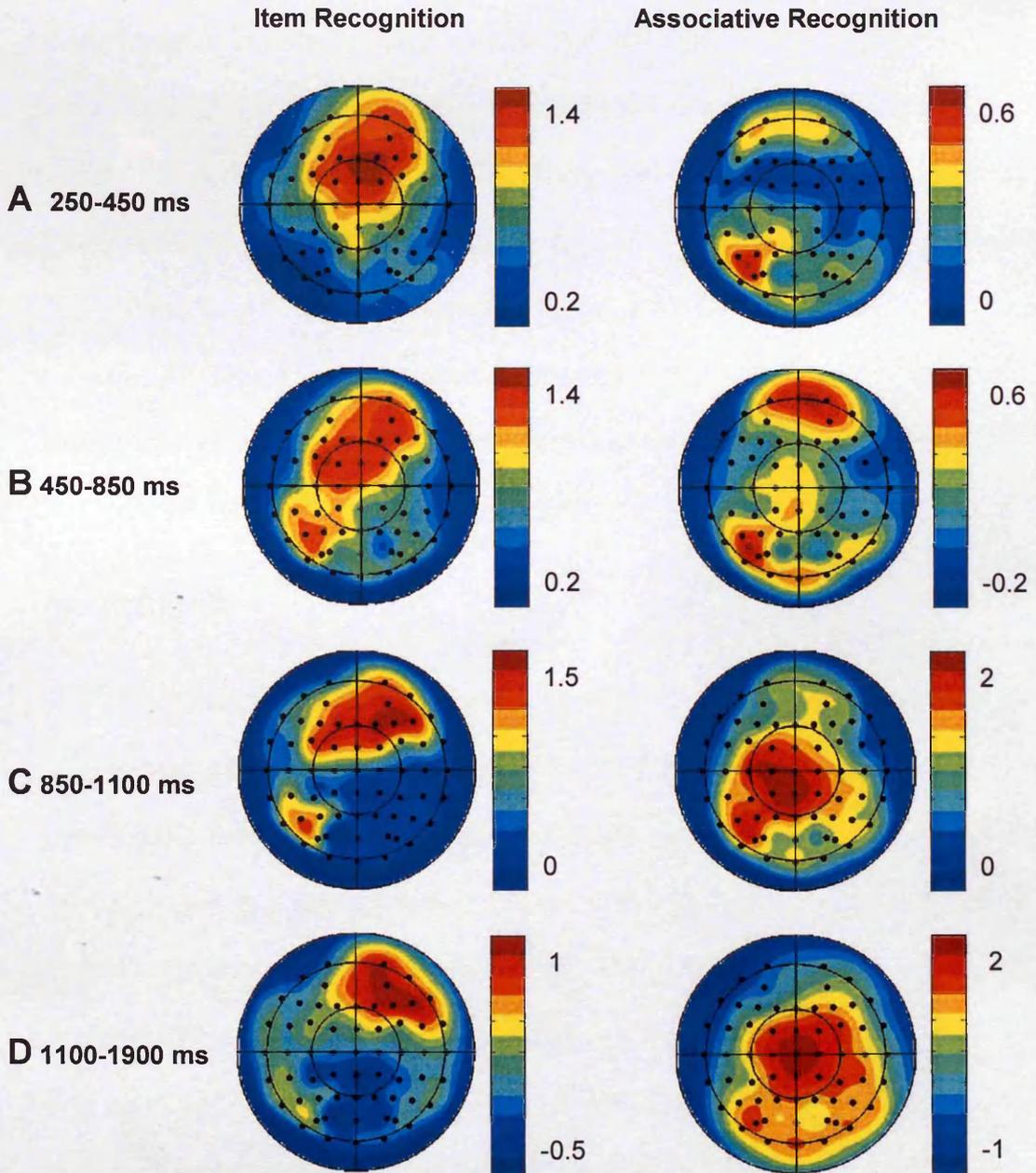


Figure 12. Topographic maps illustrating the scalp distribution of ERP effects for item and associative recognition in Experiment 1. Panel A illustrates the 250-450 ms latency region; B – 450-850 ms; C – 850-1100 ms; and D – 1100-1900 ms. Each map is shown as if looking down on the top of the head with anterior sites towards the top of the page. The scale bar to the right of each map indicates the voltage range (μV).

Topographic analyses

Within-task topographic Main (frontal and parietal locations), Central and Midline ANOVAs were conducted to assess qualitative differences in the ERP effects found in item and associative recognition across latency regions. The precise details of these analyses are described in the “General Methods” chapter. For item recognition, significant old/new effects were found in all four latency regions, consequently three topographic comparisons were conducted (250–450 ms vs. 450–850 ms, 450–850 ms vs. 850–1100 ms and 850–1100 ms vs. 1100–1900 ms). For associative recognition, robust ERP effects were only present from 850 ms onwards; therefore a single topographic comparison (850–1100 ms vs. 1100–1900 ms) was performed.

Item recognition

The Main 250–450 ms vs. 450–850 ms ANOVA produced an epoch, hemisphere and location interaction [$F(1,22) = 5.89, p < 0.05$] that reflected the progression from a mid-frontal effect in the first latency period to a left parietal effect in the second latency period (Figure 12, A and B). The 450–850 ms vs. 850–1100 ms comparison failed to produce any significant results, indicating that the distributions of ERP effects in these time windows were similar (Figure 12, B and C). The Main 850–100 ms vs. 1100–1900 ms ANOVA gave rise to an epoch by hemisphere interaction [$F(1,22) = 5.36, p < 0.05$] that marked the increasingly right-sided asymmetry of ERP effects (particularly over frontal sites) in the later time window (Figure 12, D).

Associative recognition

The Main 850-1100 ms vs. 1100-1900 ms ANOVA produced an epoch by hemisphere interaction [$F(1,22) = 4.31, p = 0.05$] that reflected the increasingly right-sided asymmetry in the later latency period (Figure 12, D). A similar progression over central sites was confirmed by an epoch by hemisphere interaction [$F(1,22) = 5.90, p < 0.05$] in the Central ANOVA.

Summary of the ERP effects elicited separately by item and associative recognition

As anticipated, item recognition produced the putative ERP correlate of familiarity, the early mid-frontal effect, from approximately 250 ms. The left parietal index of recollection was evident between 450 and 850 ms. More unexpectedly, from around 1100 ms, robust bilateral frontal old/new differences adopted a distinct right-sided asymmetry. In associative recognition, reliable same/rearranged differences were only apparent from around 850 ms onwards. Here, parietal positive-going activity, which initially exhibited a left-sided focus and likely represented the left parietal index of recollection, was elicited in conjunction with simultaneously onsetting widespread, generally right-sided, activation. From 1100 ms onwards, this activation was robust over right frontal sites, but was maximal at the Cz electrode (mean = $2.50 \pm 2.84 \mu\text{V}$).

Item vs. associative recognition

Robust ERP effects were present throughout the recording epoch in item recognition; therefore between-task magnitude analyses were conducted on the difference waveforms for each time window. In contrast, associative recognition

failed to produce any significant modulations until 800 ms post-stimulus onset. As between-task topographic comparisons are conducted to confirm distributional differences in any robust ERP effects present, these were only performed for the two later latency periods.

Table 4. Results of the between-task magnitude and topographic comparisons of difference waveforms.

Latency Region	Magnitude	Topographic
250-450ms		
TxL	$F(1,22)=4.55, p<0.05$	Not performed
TxS	$F(1.2,27.2)=6.02, p<0.05$	
TxHxS	$F(1.3,28.1)=4.95, p<0.05$	
450-850ms		
T	$F(1,22)=5.38, p<0.05$	Not performed
850-1100ms		
<i>Additional analyses</i>		No significant results
<i>T(c)</i>	$F(1,22)=7.36, p<0.05$	
<i>T(m)</i>	$F(1,22)=5.13, p<0.05$	
1100-1900ms		
T	$F(1,22)=4.50, p<0.05$	$F(1,22)=9.66, p<0.01$ $F(1.4,30.8)=4.22, p<0.05$
TxL	$F(1,22)=8.61, p<0.01$	
TxS	$F(1.4,29.9)=4.03, p<0.05$	
<i>Additional analyses</i>		$F(1.1,24.5)=11.80, p<0.01$ $F(1.7,38.2)=7.18, p<0.01$
<i>T(c)</i>	$F(1,22)=10.44, p<0.01$	
<i>TxS(c)</i>	$F(1.1,24.2)=13.23, p=0.001$	
<i>T(m)</i>	$F(1,22)=13.21, p=0.001$	
<i>TxL(m)</i>	$F(1.7,38.0)=6.99, p<0.01$	

The presence of the early mid-frontal effect in item recognition, but not in associative recognition, (Figure 13, A, p172) was confirmed by the post hoc t-test of frontal sites [$t(22) = 2.78, p < 0.05$] conducted to investigate the task by location interaction in the Main 250-450 ms magnitude ANOVA (Table 4). Between 450 and 850 ms, a main effect of task in the Main ANOVA indicated that ERP effects were generally more positive-going in item recognition than in associative recognition. However, a targeted t-test of left parietal sites was not

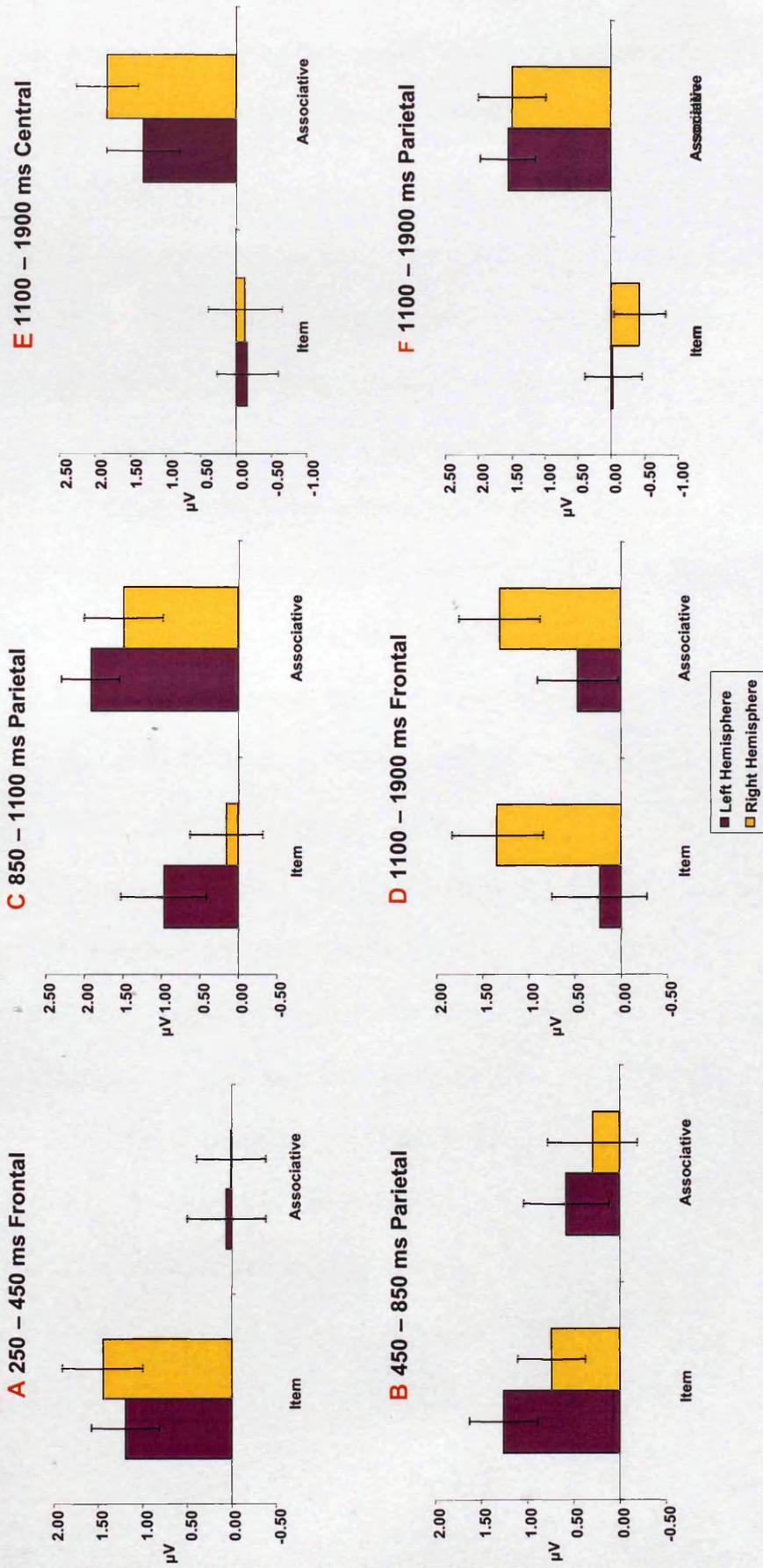


Figure 13. Mean amplitudes of ERP effects for item and associative recognition. The left hemisphere is collapsed across F1, F3 and F5 (frontal), C1, C3 and C5 (central), and P1, P3 and P5 (parietal); the right hemisphere is collapsed across F2, F4 and F6 (frontal), C2, C4 and C6 (central), and P2, P4 and P6 (parietal). In all the graphs in the experimental chapters the error bars represent the standard error of the mean.

significant [$t(22) = 1.13$, n.s.]. Although the left parietal effect was only robust in item recognition during this epoch, visual inspection of the data suggests that it was onsetting in associative recognition (Figure 12, B and Figure 13, B).

Similarly, the lack of any significant between-task differences in the Main 850-1100 ms magnitude ANOVA most likely reflects the continuing presence of the declining left parietal effect in item recognition (Figure 13, C), in conjunction with its robust homologue in associative recognition. Between-task magnitude (but not topographic) differences were, however, apparent over central and midline sites, where main effects of task indexed the increased amplitude of ERP activity in associative recognition. The late right frontal effects elicited by item and associative recognition appeared to be of similar magnitude (Figure 13, D). Accordingly, post hoc t-tests investigating the task by location interaction in the Main 1100-1900 ms ANOVA did not reveal any significant between-task differences over frontal sites [$t(22) = 0.24$, n.s.]. Over parietal electrodes, however, a significant between-task difference [$t(22) = 2.96$, $p < 0.05$] reflected the continued (left and right) posterior positivity in associative recognition, but not in item recognition (Figure 13, F). The more central/posterior distribution of effects in associative recognition was indicated by interactions involving task and location in the Main and Midline 1100-1900 ms topographic ANOVAs. Moreover, two-way interactions in the Central magnitude and topographic ANOVAs indicated the presence of centrally-distributed positive components only in associative recognition (Figure 13, E).

Summary of differences in the ERP effects elicited by item and associative recognition

The main between-task differences were the presence of the early mid-frontal ERP correlate of familiarity only in item recognition, and the appearance of a central/posterior positive-going component in associative recognition. The left parietal index of recollection appeared to have a different time course in the two tasks (it onset later and had a longer duration in associative recognition than in item recognition), but significant posterior between-task magnitude differences were only observed in the 1100-1900 ms latency period. Finally, the late right frontal index of post-retrieval monitoring processes appeared equivalent in both tasks.

Discussion

The ERP findings provide strong evidence that the neural correlates of item and associative recognition are dissociable, indicating that memory for items and memory for associations rely on different underlying processes. Significant between-task differences were apparent during the early (250-450 ms) and late (1100-1900 ms) phases of retrieval; specifically, a late central/posterior component was elicited by associative recognition, whereas an early mid-frontal old/new effect was produced by item recognition. This latter finding is consistent with the familiarity interpretation of the modulation, as familiarity is typically characterised as a basis for item recognition, but not for associative recognition. However, as will be discussed in subsequent sections, there were also commonalities; that late right frontal index of post-retrieval

decision processes was equivalent in item and associative recognition, and left parietal effects in both tasks reflected a shared reliance on recollection.

Behavioural findings

The comparable accuracy (as measured by Pr) in item and associative recognition is consistent with previous studies (e.g. Hockley, 1994). The emphasis on the association between the words at encoding (i.e. generating a single sentence containing both words in a study pair) likely facilitated associative recognition whilst leaving item recognition apparently unchanged (Hockley & Cristi, 1996). Nevertheless, the tasks were not performed in an identical fashion, with the adoption of a more conservative decision criterion in item recognition suggesting that there may be an underlying difference in the way the tasks were executed. Moreover, consistent with dual process theory (e.g. Yonelinas, 1997), the increased proportion of remember responses in associative recognition indicates a greater contribution of recollection, whereas the increased proportion of know responses in item recognition suggests an increased reliance on familiarity (but see "General Discussion" chapter for an alternative interpretation of the RKG data).

The most interesting feature of the RT data was the observation that whilst there was no latency difference between hits and correct rejections in item recognition, associative correct rejections were slower than associative hits. This RT difference in associative recognition could be interpreted in two ways. One possible explanation is that correct rejections were being produced by default following the non-recollection of a rearranged pair. An alternative interpretation is provided by the recall-to-reject hypothesis (Rotello & Heit,

2000; Rotello et al., 2000), which proposes that both the study pairs contributing to a rearranged test pairing must be recalled for an associative correct rejection to occur. The recall-to-reject hypothesis would therefore predict that, since associative hits are made on the basis of the recollection of a single study pairing, RTs to associative correct rejections should be longer than RTs to associative hits. These two accounts will be discussed with reference to the electrophysiological data in the "General Discussion" chapter.

Dissociating item and associative recognition: early mid-frontal and late central/posterior effects

The first significant difference in the ERP correlates of item and associative recognition was the appearance of an early mid-frontal effect in item recognition, but not in associative recognition. The remember/know results indicate that the contribution of familiarity was greater to item recognition than to associative recognition; therefore, inconsistent with Duarte and colleagues' (2004) recollection account, the appearance of the early mid-frontal effect only in the item task appears to support the assertion that the modulation indexes familiarity.

In associative recognition, the final (1100-1900 ms) epoch was dominated by a central/posterior component that, although it appeared maximal over the vertex, had a slight right-sided asymmetry. This positive-going effect closely resembles modulations seen in previous associative recognition ERP studies (Donaldson & Rugg, 1998; Van Petten et al., 2002). Donaldson and Rugg employed a three-way comparison (same vs. rearranged vs. new word pairs) to demonstrate a late posterior voltage gradation between same, new

and rearranged pairings from around 900 ms onwards; same waveforms remained more positive than new waveforms, which, in turn, were more positive than rearranged waveforms. It has previously been suggested that this late posterior negativity to rearranged pairs may be related to the late posterior negative slow wave (LPN) observed in source recognition studies (see "ERPs, Recognition Memory and Ageing" chapter). Accordingly, the late central/posterior positivity in the current experiment may chiefly represent a negative voltage shift to rearranged pairs, rather than a positive shift to same pairs. The component could therefore reflect the additional processing, such as the maintenance of attribute conjunctions (i.e. word-word associations) required to make a same/rearranged judgement (c.f. Johansson & Mecklinger, 2003).

Commonalities between item and associative recognition: left parietal and late right frontal effects

Both item and associative recognition appeared to elicit robust left parietal ERP effects. Although the onset of the associative recognition modulation was delayed and its duration was longer than the item recognition component (850-1900 ms in associative recognition vs. 450-850 ms in item recognition), their scalp distributions appeared similar (Figure 12, B and C, p168). Moreover, a targeted t-test comparing the mean left parietal voltage between 450 and 850 ms in item recognition ($1.26 \pm 1.79\mu\text{V}$) and between 850 and 1100 ms in associative recognition ($1.91 \pm 1.82\mu\text{V}$) demonstrated that the magnitude of the effects was comparable [$t(22) = 1.15$, n.s.]. Therefore, similar to the RT data, the delay in the onset of the associative recognition ERP

modulation may simply reflect the extended time taken to read two words instead of one.

Assuming that the left parietal effect indexes successful recollection, its similar magnitude in both tasks is consistent with the dual-process prediction that recollection should contribute to both item and associative recognition (Yonelinas, 1997, 2002). However, as the remember/know data from the current experiment indicates that the contribution of recollection was greater in the associative task, it might be anticipated that the left parietal effect should be larger in associative recognition. The reason for the unexpected voltage equivalence is not immediately transparent.

Late right frontal effects of similar magnitude were also apparent in item and associative recognition; therefore, post-retrieval evaluative processing appears to have been employed to an equivalent degree in both tasks. Although this result is not consistent with the pre-experimental prediction that only associative recognition should produce a late right frontal effect, the component has been reported in other item recognition tasks (e.g. Allan & Rugg, 1997; Düzel et al., 1997; Schloerscheidt & Rugg, 1997; Rugg et al., 1998b). Many of the foregoing paradigms possess some degree of complexity; for example, making a remember/know judgement or interleaving item recognition trials with a more demanding task. In the current experiment, the right frontal effect in item recognition does not reflect the RKG judgements because these were not made during the ERP recording, but may index the randomized presentation of item and associative recognition trials. Alternatively, as the encoding task promoted the association between the word pairs rather than the individual words themselves, the right frontal effect in item recognition

may reflect the post-retrieval operations required to ascertain the presence of a single word within a learned association.

Summary

Experiment 1 clearly demonstrates that the mnemonic processes underlying item and associative recognition can be dissociated using event-related potentials: First, the putative index of familiarity, the early mid-frontal effect is present in item recognition, but not in associative recognition. Second, the late time window shows a central/posterior positive-going modulation only in associative recognition. This component may be related to the retrieval of the encoded associations between the members of a word pair. However, similar left parietal effects were present for both associative and item recognition, suggesting a common reliance on recollection.

Having identified similarities and differences in the ERP correlates of item and associative recognition in young adults, Experiment 2 will extend the comparison to include older adults. As the current experiment contained a timing error, its basic design (with a number of modifications including the resolution of the timing issue) will be repeated using a new group of young participants, as well as a group of older adults. The specific aims of Experiment 2 are, firstly, to replicate the findings of Experiment 1 in young adults; then, more importantly, to examine the effect of ageing on the electrophysiological indices of the retrieval of item and associative information.

Chapter 7

Experiment 2

Introduction

Behavioural studies have indicated that as people grow older their capacity for recollection diminishes, whilst their ability to remember that something is familiar remains relatively unaffected (e.g. Hay & Jacoby, 1996; Jacoby et al., 1996; Jennings & Jacoby, 1997; Jacoby, 1999; Benjamin & Craik, 2001). Accordingly, elderly people experience more difficulty in remembering details of the source or context in which an item was encountered than in remembering the item itself (e.g. McIntyre & Craik, 1987; Schacter et al., 1991), and associative recognition tasks consistently demonstrate increased ageing deficits compared to item recognition tasks (e.g. object/location and object/colour associations, Chalfonte & Johnson, 1996; word/nonword, word/word and word/font associations, Naveh-Benjamin, 2000; and word/word associations, Castel & Craik, 2003).

ERP investigations of the effects of ageing on episodic memory have indicated that the neural correlates of episodic retrieval change with age (for a review, see Friedman, 2000). Nevertheless, relatively few ERP experiments have been conducted in this field to date, and the results remain somewhat equivocal. Consistent with the dual process account of age-related episodic memory impairment, item recognition and exclusion studies have demonstrated a severely reduced or absent left parietal index of recollection in older participants (Dywan et al., 2002; Morcom & Rugg, 2004). However, in source memory studies where recollection is promoted, left parietal age invariance has been reported (Mark & Rugg, 1998; Trott et al., 1999; Wegesin et al., 2002; but see Li et al., 2004). Likewise, the late right frontal index of post-retrieval evaluative operations has shown an age-related decline in some studies (Trott et al., 1999; Wegesin et al., 2002), whilst in others, similar late right frontal magnitudes and distributions have been observed in young and older adults (Mark & Rugg, 1998; Li et al., 2004; Morcom & Rugg, 2004).

In contrast, although only two studies have considered early frontal ERP effects in relation to ageing, their findings appear to concur. Wegesin and colleagues (2002) reported that an early medial prefrontal effect in young adults had an equivalent magnitude, but a more right-sided distribution, in older adults. Similarly, Morcom and Rugg (2004) reported early (300-500 ms) frontal effects in both young and older adults that were more right-sided in the elderly. The paucity of findings relating to early right frontal activity in older adults mean that little attention has been paid to its functional significance. However, if, despite its different topography, the early right frontal effect represents the older adults' homologue of the early mid-frontal putative index of familiarity in young adults,

the foregoing results would be consistent with the dual process view that elderly adults are relatively unimpaired at familiarity-based remembering.

Finally, three source memory studies (Trott et al., 1997; Wegesin et al., 2002; Li et al., 2004) have demonstrated a central negative-going old/new effect only in older adults, from about 800 ms post-stimulus. The functional significance of this modulation also remains unclear, but it may reflect older people's engagement of additional (possibly compensatory) processes to assist in the retrieval of source information (Wegesin et al., 2002; Li et al., 2004).

The principle aim of the current experiment is to examine the effects of ageing on the ERP components elicited separately by item and associative recognition; in addition, it will allow a direct contrast between the neural correlates of both tasks in each age group. The design closely resembles that of Experiment 1, with item and associative retrieval tasks being randomly intermixed; in Experiment 2, however, a confidence rating will also be required on each trial. In line with previous behavioural and ERP studies, and in accordance with the dual process view that older adults rely more on familiarity than on recollection, we made several predictions: First, that the age-related performance deficit would be increased in associative recognition compared to item recognition. Second, that the left parietal index of recollection should be severely reduced in older adults in item recognition. Third, that the left parietal effect may be less attenuated in older adults in the recollection-promoting associative recognition task. Fourth, since accurate same/rearranged judgements require memory for context (c.f. source memory), that older adults should produce a central negativity in associative recognition. And finally, if the familiarity interpretation of early frontal components is correct, that an early

frontal effect of an equivalent magnitude, but not necessarily equivalent distribution, as the early mid-frontal effect in young adults, should be elicited by item recognition in older people.

Methods

Participants

21 young adults (12 male; mean age 20.8 years, range 18-23), who differed from those in Experiment 1, and 19 older participants (9 male; mean age 69.8 years, range 65-78) took part in the experiment. The data from two participants (one young, one older) was excluded because of excessive eye movement; another young participant was excluded because of technical difficulties; and a further young participant was too tired to complete the experiment effectively. 18 participants remained in each group (young – 10 male, mean age 20.7 years, range 18-23; older – 8 male, mean age 69.8 years, range 65-78).

Neuropsychological tests

The results of the neuropsychological tests (see “General Methods” chapter for details) are shown in Table 5 (below). The groups were matched on years of education, health ratings and BDI scores. However, the older participants had higher IQ scores, whereas the young group performed better on the WMS-R immediate and delayed paired-associates subscales.

Table 5. Characteristics of the participants in Experiment 2 (mean \pm SD)

	Young	Older	p-value
Age (years)	20.7 \pm 1.8	69.8 \pm 4.5	<0.001
Gender	10/18 male	8/18 male	
Education (years)	15.4 \pm 1.7	14.4 \pm 4.0	n.s.
BDI	7.4 \pm 4.9	6.6 \pm 4.2	n.s.
Health	4.0 \pm 0.6	3.9 \pm 0.6	n.s.
IQ (WASI)	112 \pm 7	123 \pm 9	<0.001
WMS-R			
<i>Logical memory I</i>	47.6 \pm 9.3	45.6 \pm 6.2	n.s.
<i>Logical memory II</i>	31.1 \pm 7.3	28.2 \pm 5.5	n.s.
<i>Paired associates I</i>	25.1 \pm 6.9	19.5 \pm 6.4	<0.05
<i>Paired associates II</i>	7.5 \pm 1.2	6.4 \pm 1.7	<0.05
<i>Letter number sequencing</i>	13.3 \pm 2.9	12.2 \pm 2.9	n.s.
MMS		29.5 \pm 0.6	

Stimulus materials and procedure

The “General Methods” chapter describes the stimulus materials, procedure, and the ERP recording and analysis. The procedure in the current experiment differed from that employed in Experiment 1 as follows. First, participants were no longer required to restrict their blinking, therefore the exclamation mark was replaced by a central fixation mark (+). This change arose because 5 elderly participants who piloted the previous experimental design had great difficulty restricting their blinking. The additional secondary task load was therefore greater in the elderly compared with the young, introducing a potential confound to the between-group comparison (Wasman et al., 1970).

Second, in the current experiment, the study pairings only appeared on the screen for 1500 ms, whereas previously the display time was infinite. The older adults in the behavioural pilot tended to take longer to generate sentences in the study phase than the young adults in the previous ERP experiment. If

older adults were to consistently adopt a more leisurely approach to learning the word pairs than young adults, this might introduce another potential confound to any between-group comparison. Limiting the presentation time of each study word pair therefore aimed to encourage the older adults not to prolong the encoding task. This measure resulted in a 582 ms reduction in mean study RT of the elderly participants in the current experiment compared to the pilot.

Third, a trial-by-trial confidence judgement replaced the post-experiment remember/know/guess (RKG) procedure. The reason behind this change was threefold: A trial-by-trial decision should provide a more accurate rating for each stimulus than a post-experimental measure. In addition, some older adults in the ERP pilot appeared to have trouble comprehending the RKG instructions, and a separate behavioural pilot suggested that they found the instructions on how to use a confidence scale more straightforward. Moreover, it was hoped that separation of the trials according to confidence, would allow an ERP comparison between high (confidence rating = 5) and low (confidence rating = 4-2) confidence trials. However, as with the remember/know judgements, very few participants produced enough trials in the low confidence condition, so this analysis could not be performed.

Fourth, the pre- and post-stimulus fixation crosses were replaced with blank screens. The post-stimulus change aimed to minimise perceptual ERP activity which had appeared towards the end of the retrieval epochs in the previous experiment. The logic behind the pre-stimulus change, similarly, was to provide a baseline measure during which perceptual input was highly restricted.

The final modification was to ask participants to complete a post-experimental questionnaire (see "Appendix C"). This element was introduced to assess the participants' subjective experience of the study and test tasks, and thereby to gain more insight into how each task was performed by each age group.

Results

Behavioural

The performance data are summarised in Table 6 (below). The hits and correct rejections ANOVA produced main effects of task [$F(1,34) = 11.76, p < 0.01$], response category [$F(1,34) = 11.65, p < 0.01$], and age [$F(1,34) = 16.86, p < 0.001$]. Accuracy was greater for item recognition and correct rejection judgements overall, and the young participants' performance was superior to that of the elderly. These main effects were moderated by various interactions including one involving task, response category and age [$F(1,34) = 27.76, p < 0.001$]. Subsidiary t-tests indicated that the older group produced fewer correct rejections than the young group in associative recognition [$t(34) = 6.54, p < 0.001$], but fewer hits than the young group in item recognition [$t(34) = 3.67, p = 0.001$].

The discriminability (Pr) analysis produced main effects of task [$F(1,34) = 11.76, p < 0.01$] and age [$F(1,34) = 16.86, p < 0.001$], and an interaction involving task and age [$F(1,34) = 23.10, p < 0.001$]. Consistent with the hits and correct rejections analysis, discriminability overall was poorer in the associative task and in the older group. Independent t-tests revealed that the age-related

decline in performance was robust in associative recognition [$t(34) = 4.99, p < 0.001$], and marginal in item recognition [$t(34) = 2.01, p = 0.053$].

Table 6. Mean performance data (\pm S.D.) for Experiment 2.

	Item Recognition		Associative Recognition	
	Young	Older	Young	Older
<u>Accuracy</u>				
Hits	0.76 \pm 0.07	0.66 \pm 0.09	0.83 \pm 0.12	0.82 \pm 0.11
Correct Rejections (CR)	0.90 \pm 0.09	0.93 \pm 0.05	0.86 \pm 0.09	0.61 \pm 0.14
Confident Hits (rating = 5)	0.62 \pm 0.14	0.54 \pm 0.26	0.77 \pm 0.17	0.67 \pm 0.27
Confident CR (rating = 5)	0.36 \pm 0.23	0.47 \pm 0.30	0.50 \pm 0.20	0.33 \pm 0.29
Pr	0.66 \pm 0.12	0.59 \pm 0.10	0.69 \pm 0.18	0.43 \pm 0.14
Br	0.26 \pm 0.19	0.17 \pm 0.11	0.49 \pm 0.21	0.68 \pm 0.16
<u>RT(ms)</u>				
Hits	1459 \pm 347	1841 \pm 281	1688 \pm 331	2151 \pm 261
CR	1506 \pm 360	1672 \pm 279	2096 \pm 374	2594 \pm 279
<u>Study RT(ms)</u>	Young 3282 \pm 1114		Older 6670 \pm 3528	

The bias (Br) ANOVA revealed a main effect of task [$F(1,34) = 81.55, p < 0.001$], modulated by an interaction involving task and age [$F(1,34) = 10.90, p < 0.01$]. Overall, participants were more conservative in item recognition than in associative recognition, and the older group were more liberal than the young group on the associative task [$t(34) = 2.97, p < 0.01$].

For the confidence analyses, ratings of 5 were classed as high confidence; all other ratings were considered low confidence. The confidence ANOVA produced main effects of task [$F(1,34) = 15.50, p < 0.001$] and response category [$F(1,34) = 65.22, p < 0.001$]. Participants were more confident in associative recognition than in item recognition, and gave higher ratings to hits than to correct rejections. However, these main effects were

modulated by various interactions including a task, response category and age interaction [$F(1,34) = 8.94, p < 0.01$]. This interaction reflected the fact that although generally both groups were more confident about hits than about correct rejections, in item recognition, the older adults were equally confident for both response-types.

Importantly for the ERP comparison, there was no main effect of age in the original three-way confidence ANOVA, and post hoc t-tests on high confidence hit and correct rejection responses confirmed there was no significant age difference in either recognition task (all p values > 0.05). In view of the performance difference between the age groups, particularly in associative recognition, the proportion of trials on which a response based on weak memory or guessing occurred might have been expected to be higher in the older group. Such a difference would dilute the magnitude of the elderly participants' ERP effects, thus potentially producing misleading ERP ageing differences (Rugg & Morcom, 2004). The age-invariance in confidence suggests that this confound should not arise. The confidence data further indicate that no between-group differences in memory strength exists. Any memory strength disparity between young and older participants might differentially influence post-retrieval evaluative operations (Henson et al., 2000).

The test RT data produced main effects of task [$F(1,34) = 324.88, p < 0.001$], response category [$F(1,34) = 32.29, p < 0.001$], and age [$F(1,34) = 15.60, p < 0.001$], which were modulated by a task, response category and age interaction [$F(1,34) = 5.89, p < 0.05$]. Associative recognition responses were slower than item recognition responses, and correct rejections were slower than hits. However, subsidiary analyses investigating the three-way interaction

showed that although in associative recognition, the older group were globally slower than the young group [main effect of age – $F(1,34) = 21.87, p < 0.001$], in item recognition, there was a significant age difference for hits [$t(34) = 3.64, p = 0.001$], but not for correct rejections [$t(34) = 1.55, n.s.$].

Finally, despite the attempt to curtail the older adults' study RTs, they still took more time than the young group over the sentence generation task [$t(34) = 3.89, p < 0.001$]. Mann-Whitney tests on the post-experimental questionnaire responses (see "Appendix C" for the post-experimental questionnaire results) indicated that the older group found it harder to produce sentences than the young group [$U = 84.5, z = 2.61, p < 0.01$], and, despite their additional training (see "General Methods" chapter), did so less often [$U = 103, z = 1.98, p < 0.05$]. Moreover, when older adults resorted to using other methods during encoding, they reported using more shallow encoding methods than the young adults, who tended to make more use of imagery and other associative techniques.

Summary of behavioural data

The discriminability measures showed that the older participants performed well above chance ($Pr = 0$) on both tasks. Nevertheless, the elderly were less accurate than the young in associative recognition, and marginally impaired in item recognition. The older adults' more liberal response bias in associative recognition reflected an age-related decrease in associative correct rejections, and further suggested that the manner in which the elderly and young participants performed the task was different. Overall, both sets of participants produced similar confidence ratings, particularly in associative recognition, suggesting that, despite their performance deficit, the older groups'

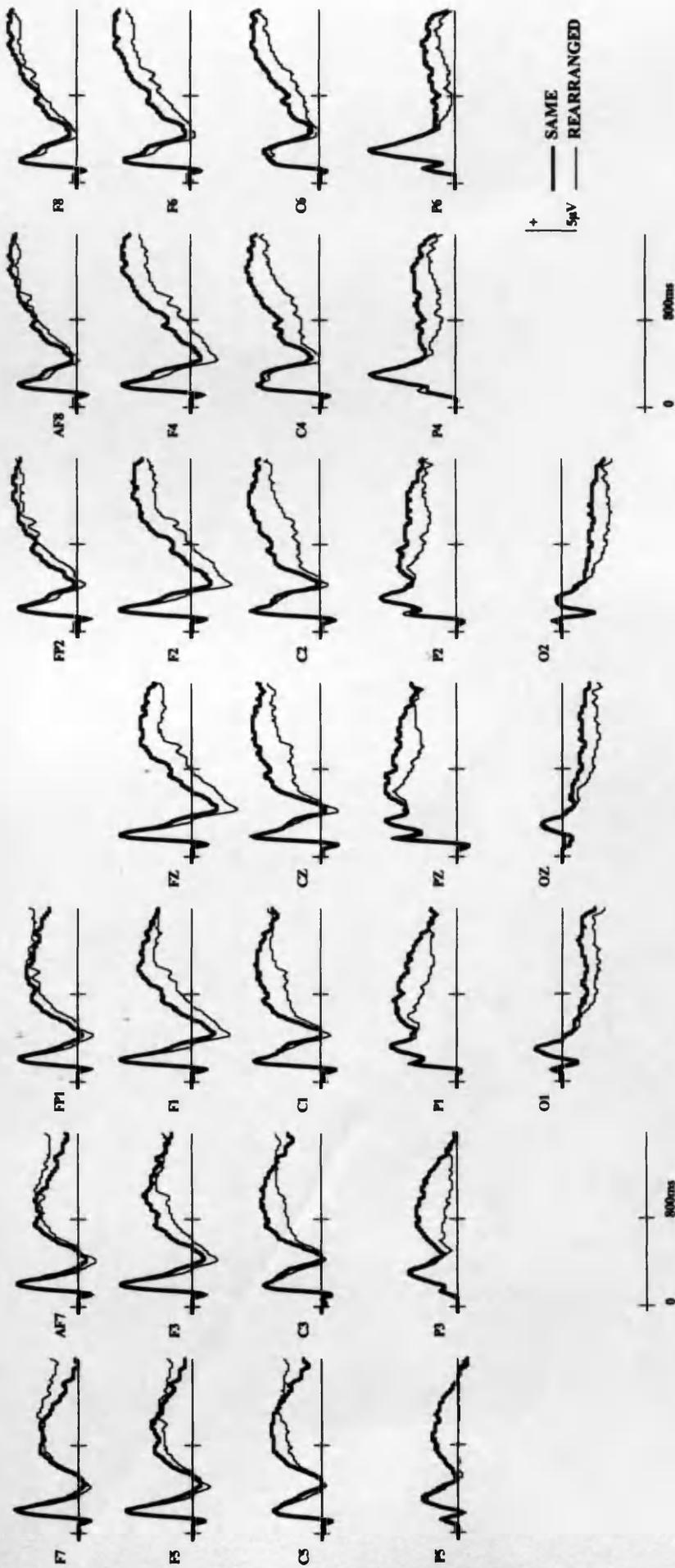
memory was not impoverished compared to the younger group. Finally, consistent with general slowing theory (see "Episodic Memory and Ageing" chapter), the older participants were generally slower than the young participants during retrieval.

Event-related potentials

Young group

Item recognition

Figure 14 (p191) shows the grand average OLD and NEW waveforms for item recognition from 30 EEG electrode sites. The mean number of trials (\pm S.D.) contributing to the ERPs was 40 (8) OLD and 48 (11) NEW. The waveforms diverge from approximately 360 ms post-stimulus onset, with the ERPs for OLD words becoming more positive than those for NEW words. This positive modulation, which is most evident over central and parietal sites, exhibits a left-sided asymmetry and declines from around 800 ms. Over frontal sites there is limited evidence of an early (400-600 ms) divergence between OLD and NEW waveforms, which becomes more prominent from approximately 700 ms. Initially, this component is bilateral, but its distribution clearly becomes right-sided from 1000 ms. A right-sided negative-going old/new difference appears over central and parietal sites at a similar latency, and persists until approximately 1700 ms post-stimulus onset.



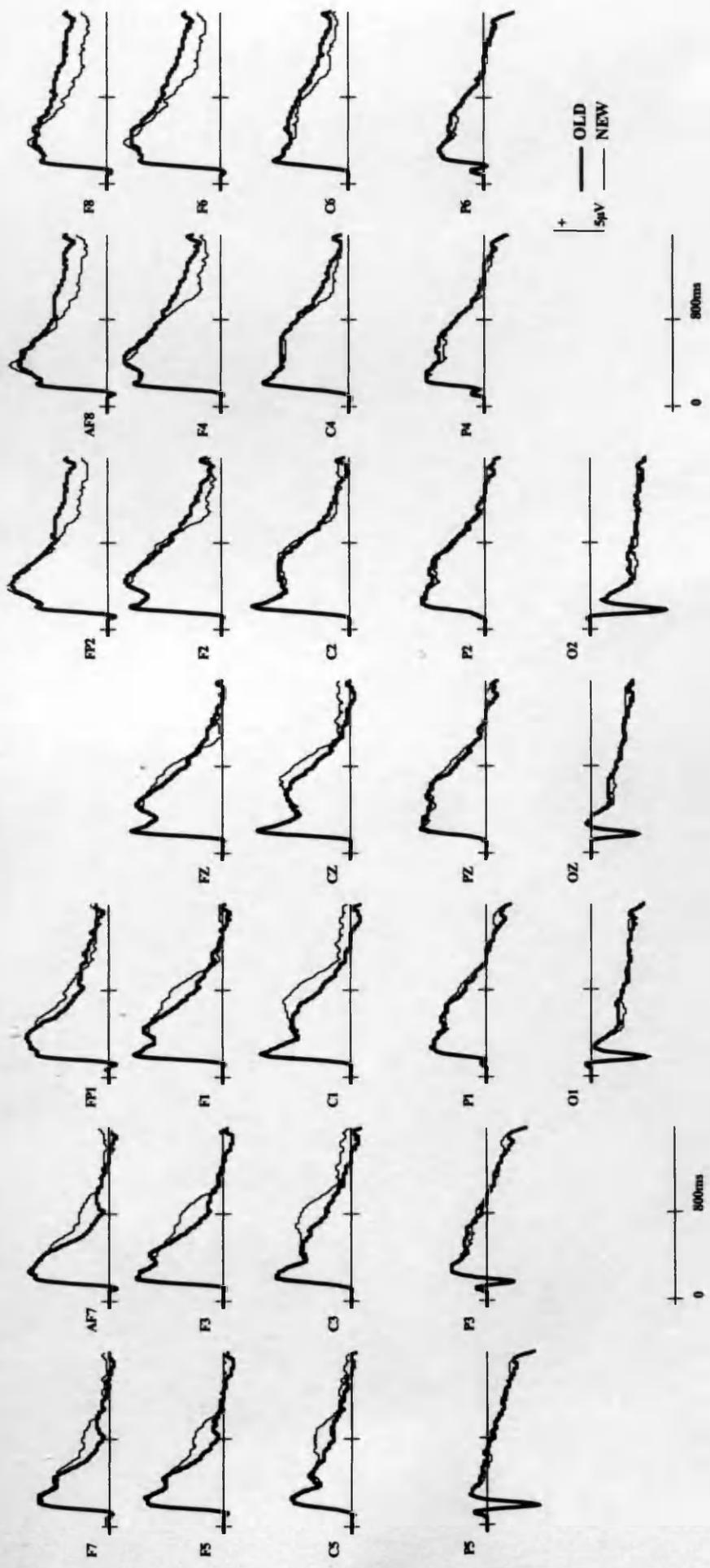


Figure 16. Grand average ERPs for the recognised (OLD) and NEW response categories for item recognition. Electrodes are shown as in Figure 10.

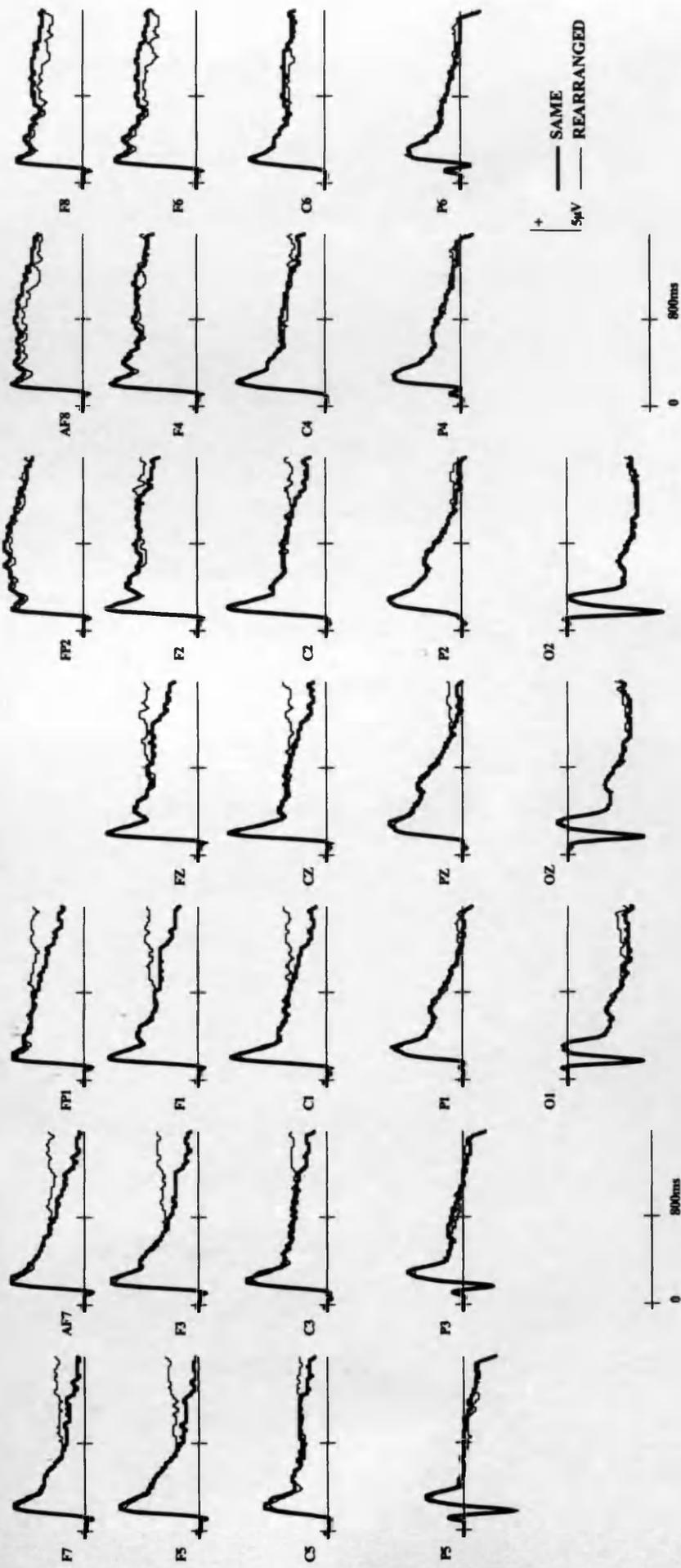


Figure 17. Grand average ERPs for the recognised (SAME) and REARRANGED response categories for associative recognition. Electrodes are shown as in Figure 10.

Associative recognition

Figure 15 (p192) shows the grand average SAME and REARRANGED waveforms for associative recognition, again from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 44 (9) SAME and 44 (9) REARRANGED. The waveforms appear to diverge from around 300 ms post-stimulus onset, with the ERPs for SAME pairings becoming more positive than those for REARRANGED pairings over frontal electrodes. At approximately 500 ms, the same/rearranged positivity extends to central and temporo-parietal sites; it appears to have a left-sided distribution and persists until around 1400 ms. Although the frontal positivity adopts a right-sided asymmetry from about 1100 ms onwards, the maximum amplitude of this modulation seems to be over central and temporo-parietal sites. Finally, a negative same/rearranged difference onsets at around 1000 ms over left prefrontal sites.

Older group

Item recognition

Figure 16 (p193) shows the grand average OLD and NEW waveforms for item recognition from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 36 (7) OLD and 50 (7) NEW. The waveforms diverge from about 500 ms post-stimulus onset, with the ERPs for OLD words becoming more negative than those for NEW words over left frontal electrodes. This negative shift extends to central electrodes and lasts until around 1000 ms. Meanwhile, a short-lived positivity is evident over parietal electrodes between approximately 500 and 700 ms. Towards the end of the epoch (from 800 ms

onwards), a positive-going old/new difference is maximal over right frontal and prefrontal sites.

Associative recognition

Figure 17 (p194) shows the grand average SAME and REARRANGED waveforms for associative recognition, again from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 45 (8) SAME and 31 (10) REARRANGED. The waveforms diverge from around 900 ms onwards, with the ERPs for SAME pairings becoming negative with respect to REARRANGED pairings over left prefrontal, left frontal and left central electrodes.

Rationale for the ERP analyses

The ERP analyses aimed to investigate between-task and ageing differences in the ERP correlates of item and associative recognition. Preliminary analyses and visual inspection led to four latency periods (300-500 ms, 500-900 ms, 900-1200 ms and 1200-1900 ms) being selected for both groups of participants. In the first instance, within-task magnitude ANOVAs were performed to assess the reliability of the ERP correlates of item and associative recognition in young and older adults. On this occasion, the appearance of ERP modulations over prefrontal electrodes, particularly in older adults, led to additional prefrontal ANOVAs [response category (hits vs. correct rejections) by hemisphere (left vs. right) by site (F7/F8 vs. AF7/AF8 vs. FP1/FP2)] being conducted for all four latency regions. To compare the ERP correlates of item and associative recognition in each age group, between-task magnitude and topographic comparisons were conducted separately for the young and older participants. Finally, to investigate age-related differences in

the ERP correlates of item and associative recognition, between-group magnitude and topographic analyses were performed on the difference (and rescaled difference) waveforms for each task. Once again, between-task and between-group magnitude and topographic analyses of prefrontal sites were also conducted.

Young Group

Item recognition

The earliest robust old/new differences were observed at 360 ms (as shown by preliminary t-tests) over left centro-parietal (CP3 and CP5) electrodes. Therefore, although main effects of response category in the Main, Central and Midline ANOVAs between 300 and 500 ms (Table 7, below) indicated that OLD waveforms were generally more positive than NEW waveforms, targeted t-tests of separate frontal and parietal locations showed that old/new differences were only robust over the posterior location [$t(17) = 3.00, p < 0.05$]. The positivities likely represent the onsetting left parietal effect, which reached its maximal value between 500 and 900 ms (Figure 18, A and B, p201): the subsidiary analyses that followed the response category, hemisphere and location interaction in the Main 500-900 ms ANOVA demonstrated a significant effect only over the left parietal hemisphere [$t(17) = 2.62, p < 0.05$]. Meanwhile, the investigations of the response category, location and site interaction in this latency period failed to reveal any significant results.

By 900-1200 ms, the left parietal effect was declining (Figure 18, C), and the main effect of response category over prefrontal electrodes and three-way interaction in the Main ANOVA appeared to reflect the bilateral onset of frontal components, even though subsidiary analyses investigating the interaction did not produce any significant results. From 1200 ms onwards, these old/new differences adopted a more right-sided distribution. However, the subsidiary analyses following the three-way interaction in the Main ANOVA once again failed to reveal any significant results, and a targeted t-test of right frontal electrodes confirmed that the late right frontal effect (Figure 18, D) was not statistically reliable [$t(17) = 1.12$, n.s.].

Associative recognition

The earliest robust amplitude differences in associative recognition were observed at around 300 ms over left prefrontal, and left and midline frontal (FT7, AF3, F3, F1 and Fz) electrodes. Between 300-500 ms, the interaction involving response category, location and site (Table 7) suggested the presence of an early mid-frontal effect (Figure 18, A). This interpretation was confirmed by a main effect of response category [$F(1,17) = 6.50$, $p < 0.05$] in the subsidiary ANOVA of frontal sites.

By 500-900 ms, main effects of response category in all four initial ANOVAs demonstrated that the magnitude differences had become more widespread. The interaction involving response category, hemisphere and location in the Main analysis appeared to reflect the presence of a left parietal effect that had not been evident in the previous latency region. However, although the same/rearranged difference appeared larger over the left parietal

hemisphere (Figure 19, B, p202), subsidiary analyses produced a main effect of response category over the parietal location [$F(1,17) = 10.63, p < 0.01$], but no posterior response category by hemisphere interaction.

The extensively-distributed magnitude differences persisted into the 900-1200 ms latency region, but here the main effect of response category in the Main ANOVA was modulated by a four-way interaction. Subsidiary ANOVAs revealed main effects of response category over parietal [$F(1,17) = 24.72, p < 0.001$] and right frontal [$F(1,17) = 8.61, p < 0.01$] sites, reflecting the summation of persistent parietal activity with the right frontal effect (Figure 18, C). During this time period, however, the same/rearranged differences were maximal over right central sites. Post hoc t-tests, conducted to investigate the response category by hemisphere interaction in the Central ANOVA, confirmed the effect was more robust over the right hemisphere [right central – $t(17) = 4.03, p < 0.01$; left central – $t(17) = 2.87, p < 0.05$].

A similar pattern of effects continued into the 1200-1900 ms latency period with some subtle differences. The subsidiary analyses following the response category, hemisphere and site interaction in the Main ANOVA revealed a main effect of response category over the right hemisphere [$F(1,17) = 8.50, p = 0.01$] and a response category by site interaction over the left hemisphere [$F(1.5,25.7) = 8.44, p < 0.01$]. These findings confirmed the right-sided asymmetry of the magnitude differences (Figure 18, D). Furthermore, the investigations of the response category, hemisphere and location interaction revealed a marginally significant same/rearranged difference over right frontal sites [$t(17) = 2.35, p = 0.062$]. However, although a main effect of response

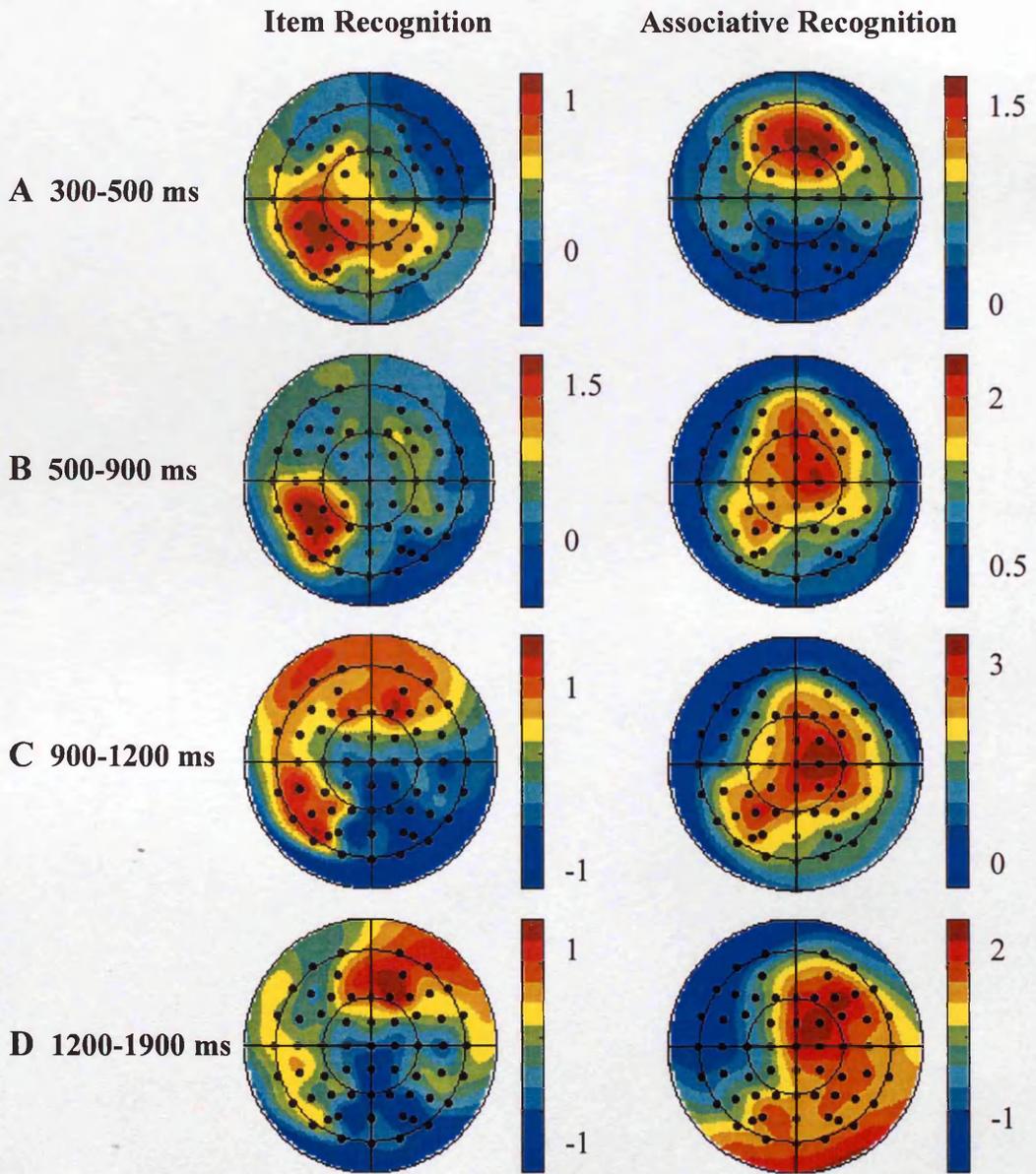


Figure 18. Topographic maps illustrating the scalp distribution of ERP effects for the young group in Experiment 2. Panel A illustrates the 300-500 ms latency region; B – 500-900 ms; C – 900-1200 ms; and D – 1200-1900 ms. The maps are shown as in Figure 12.

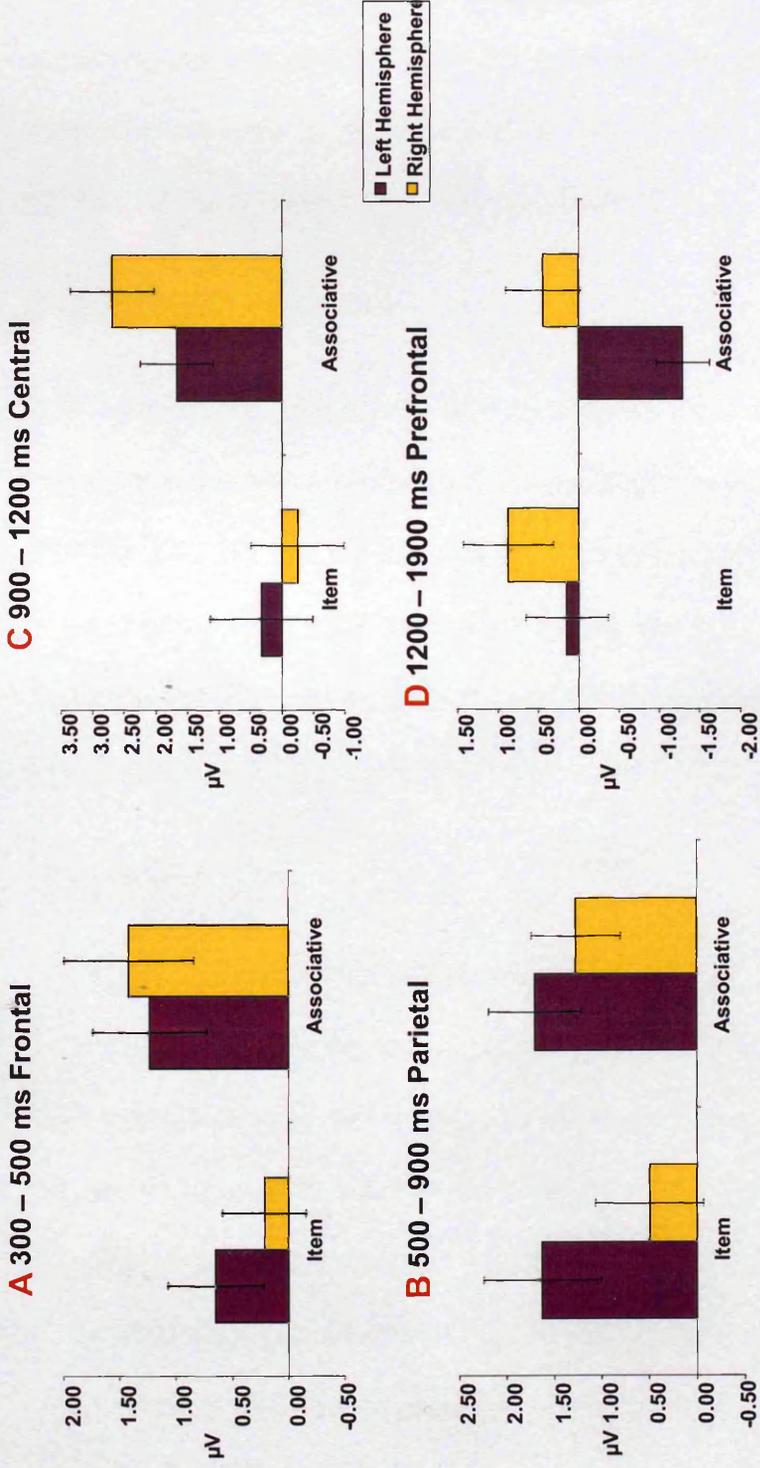


Figure 19. Mean amplitudes of selected ERP effects in the young group for item and associative recognition. The left hemisphere is collapsed across F1, F3 and F5 (frontal), C1, C3 and C5 (central), P1, P3, and P5 (parietal), and F7, AF7 and FP1 (prefrontal); the right hemisphere is collapsed across F2, F4 and F6 (frontal), C2, C4, and C6 (central), P2, P4, and P6 (parietal), and F8, AF8, and FP2 (prefrontal).

category over the parietal location [$F(1,17) = 7.83, p < 0.05$] reflected extensive posterior differences, a targeted t-test revealed that left parietal differences were no longer robust [$t(17) = 1.64, n.s.$]. Finally, a post hoc t-test of the left prefrontal hemisphere [$t(17) = 3.95, p < 0.01$] conducted to investigate the response category by hemisphere interaction in the Prefrontal ANOVA confirmed the presence of a negative-going effect.

Topographic analyses

As robust ERP effects were present in item and associative recognition throughout the epoch, three sets of topographic analyses (300-500 ms vs. 500-900 ms, 500-900 ms vs. 900-1200 ms and 900-1200 ms vs. 1200-1900 ms) were conducted for each task. These analyses included additional prefrontal ANOVAs [epoch (latency period 1 vs. latency period 2), hemisphere (left vs. right), and site (F7/F8 vs. AF7/AF8 vs. FP1/FP2)].

Item recognition

The Main 300-500 ms vs. 500-900 ms ANOVA produced an interaction involving epoch, hemisphere, location and site [$F(1.8,30.0) = 4.13, p < 0.05$]. This interaction reflected a frontal shift from an early non-robust left-sided old/new difference to a bilateral distribution, and a parietal shift in the reverse direction (Figure 18, A and B). The adoption of a more anterior distribution by the third latency period (Figure 18, C) was confirmed by an epoch and location interaction [$F(1,17) = 6.14, p < 0.05$] in the Main 500-900 ms vs. 900-1200 ms ANOVA. In the final (900-1200 ms vs. 1200-1900 ms) comparison, interactions involving epoch, hemisphere and site [$F(1.6,26.7) = 4.00, p < 0.05$] in the Main ANOVA, and epoch and hemisphere [$F(1,17) = 4.56, p < 0.05$] in the Prefrontal

ANOVA were principally due to the increased right-sided asymmetry in the 1200-1900 ms latency period (Figure 18, C and D).

Associative recognition

Between 300-500 ms and 500-900 ms, the evolution of the ERP effects from a frontal distribution towards an increasingly central/posterior distribution (Figure 18, A and B) was confirmed by interactions involving epoch and location [$F(1,17) = 6.20, p < 0.05$] in the Main ANOVA, and epoch and site [$F(1.2,19.9) = 9.00, p < 0.01$] in the Central ANOVA. The following (500-900 ms vs. 900-1200 ms) comparison produced an epoch by site interaction [$F(1.8,31.3) = 6.48, p < 0.01$] in the Prefrontal ANOVA, suggesting that frontal effects were more anterior in the earlier latency period (Figure 18, B and C). An interaction involving epoch, hemisphere and site [$F(1.4,24.3) = 10.24, p < 0.01$] in the Main 900-1200 vs. 1200-1900 ms ANOVA confirmed the increased right-sided asymmetry over frontal and parietal locations in the fourth latency period. Finally, an epoch by hemisphere interaction [$F(1,17) = 10.45, p < 0.01$] in the 900-1200 vs. 1200-1900 ms Prefrontal ANOVA reflected the evolution of the late negative-going modulation over left prefrontal sites (Figure 18, D).

Summary of the ERP effects elicited by item and associative recognition in young adults

In contrast to the results of Experiment 1, an early mid-frontal effect appeared robust in associative recognition, but not in item recognition, where the predominant feature during the 300-500 ms latency period was a left parietal effect that became maximal between 500 and 900 ms. Late frontal old/new effects onset bilaterally before developing into a non-reliable right

frontal modulation. In associative recognition, the early mid-frontal effect persisted into the 500-900 ms time window, where onsetting parietal effects appeared maximal over the left hemisphere. The robust parietal activity continued throughout the epoch, but from 900 ms onwards, parietal, central and frontal same/rearranged differences all became increasingly right-sided. Finally, a negative-going modulation appeared over left prefrontal electrodes between 1200 and 1900 ms.

Item vs. associative recognition

Robust ERP effects were present throughout the recording epoch, therefore between-task magnitude and topographic analyses could be conducted on all four time windows. Post hoc t-tests exploring the task by location interaction in the Main 300-500 ms magnitude ANOVA (Table 8, below) demonstrated robust differences in the ERP effects elicited by item and associative recognition over frontal sites [$t(17) = 2.53, p < 0.05$] (Figure 19, A). Importantly, task by location interactions in the Main and Midline topographic analyses (Table 8), confirmed the more anterior distribution of the old/new effects in associative recognition.

Between 500 and 900 ms, the lack of significant results in both magnitude and topographic ANOVAs indicated that the size and distribution of the left parietal effect was similar in item and associative recognition (Figure 19, B). By 900-1200 ms, main effects of task in the Main, Central and Midline magnitude ANOVAs suggested that associative recognition modulations were globally more positive-going than item recognition modulations; however, a targeted t-test of right frontal sites revealed no significant between-task

differences [$t(1,17) = 0.98$, n.s.]. Meanwhile, three-way interactions in the Central magnitude and topographic ANOVAs confirmed that associative recognition produced more positive-going central effects than item recognition. This between-task difference was particularly prominent over the right hemisphere (Figure 19, C), as shown by a main effect of task [$F(1,17) = 10.08$, $p < 0.01$] in the subsidiary magnitude ANOVA of right central sites.

Table 8. Results of the between-task magnitude and topographic comparisons in the young group.

Latency Region	Magnitude	Topographic
300-500ms TxL <i>Additional analyses</i> TxL(m) T(pf)	$F(1,17)=7.89,p<0.05$ $F(2.1,35.8)=4.43,p<0.05$ $F(1,17)=6.58,p<0.05$	$F(1,17)=7.61,p<0.05$ $F(2.1,35.7)=4.19,p<0.05$
500-900ms	No significant results	No significant results
900-1200ms T <i>Additional analyses</i> T(c) TxH(c) TxS(c) TxHxS(c) T(m)	$F(1,17)=4.43,p=0.051$ $F(1,17)=6.09,p<0.05$ $F(1,17)=6.19,p<0.05$ $F(1.1,19.5)=7.87,p<0.01$ $F(1.3,21.7)=4.72,p<0.05$ $F(1,17)=8.45,p=0.01$	$F(1.2,20.1)=6.59,p<0.05$ $F(1.2,20.7)=4.42,p<0.05$
1200-1900ms <i>Additional analyses</i> TxH(c) TxS(c) TxHxS(c) T(m) T(pf)	$F(1,17)=9.53,p<0.01$ $F(1.1,19.0)=6.18,p<0.05$ $F(1.2,21.0)=4.13,p<0.05$ $F(1,17)=7.70,p<0.05$ $F(1,17)=3.32,p=0.086$	$F(1,17)=4.73,p<0.05$ $F(1.1,19.3)=5.76,p<0.05$

Similarly, the principle between-task magnitude differences in the 1200 - 1900 ms latency period were over right central sites. Subsidiary analyses exploring the three-way interaction in the Central magnitude ANOVA produced a main effect of task only over right central electrodes [$F(1,17) = 7.55$, $p < 0.05$].

The topographic analysis of the central location confirmed the right-sided asymmetry in associative recognition (Figure 18, D). Finally, although the main effect of task in the Prefrontal magnitude ANOVA only approached significance, a targeted t-test of the left hemisphere [$t(17) = 2.62, p < 0.05$] confirmed the presence of a late prefrontal negative-going effect only in associative recognition (Figure 19, D).

Summary of ERP differences between item and associative recognition in young adults

The between-task analyses confirmed that, contrary to the results of Experiment 1, the early mid-frontal ERP effect was more evident in associative recognition than in item recognition. Similar to Experiment 1, however, both tasks elicited equivalent left parietal indices of recollection between 500 and 900 ms, with the associative recognition modulation persisting until 1200 ms. During the later time windows, the distribution of the ERP effects elicited by associative recognition appeared to be more posterior than that elicited by item recognition, with the principle between-task magnitude differences occurring over right central sites. Although the right frontal effect was robust only in associative recognition (it was also reliable in item recognition in Experiment 1), once again no late between-task differences were observed over right frontal electrodes. Finally, a late left prefrontal negativity present in associative recognition was absent from the item task.

Older group

Item recognition

The earliest robust old/new differences were observed at 512 ms over left parietal (P5 and PO7) electrodes. Accordingly, subsidiary analyses following the three-way interaction in the Main 300-500 ms ANOVA (Table 9, below) did not produce any statistically significant results (all p values < 0.1).

The four-way interaction in the Main 500-900 ms ANOVA reflected a robust negative-going old/new difference over left frontal sites (Figure 20, B, p210). Subsidiary analyses investigating interactions involving hemisphere in the Main, Prefrontal and Central ANOVAs indicated that the modulation extended to left prefrontal and left central sites [main effects of response category – left frontal, $F(1,17) = 9.58$, $p < 0.01$, left prefrontal, $F(1,17) = 12.80$, $p < 0.01$; left central $t(17) = 2.72$, $p < 0.05$].

By 900-1200 ms, the left fronto-central effect had started to decline (Figure 20, C), and the four-way interaction in the Main ANOVA principally indexed a robust right frontal effect. A subsidiary ANOVA of right frontal sites gave rise to a main effect of response category [$F(1,17) = 6.82$, $p < 0.05$], and a response category by site interaction [$F(1.5,24.7) = 4.51$, $p < 0.05$] that reflected the increased magnitude towards the inferior (F6) electrode. This lateralized effect also extended to prefrontal sites: a subsidiary analysis investigating the three-way interaction in the Prefrontal ANOVA produced a main effect of response category [$F(1,17) = 9.14$, $p < 0.01$] over the right hemisphere.

Table 9. Results of the magnitude analyses in the older group for the critical ERP comparisons for item and associative recognition.

Latency Region	TASK	
	Item Recognition (OLD vs. NEW)	Associative Recognition (SAME vs. REARRANGED)
300-500ms RCxHxL RCxHxS RCxLxS RCxHxLxS	F(1.6,27.8)=3.91,p<0.05	F(1,17)=4.98,p<0.05 F(1.4,24.1)=4.71,p<0.05 F(1.9,32.1)=6.72,p<0.01
500-900ms RCxH RCxL RCxHxL RCxS RCxHxS RCxHxLxS <i>Additional analyses</i> RCxH(c) RCxS(c) RCxL(m) RCxH(pf) RCxS(pf) RCxHxS(pf)	F(1,17)=16.6,p=0.001 F(1,17)=5.17,p<0.05 F(1,17)=15.81,p=0.001 F(1.2,19.9)=4.92,p<0.05 F(1.9,32.9)=4.75,p<0.05 F(1.8,30.6)=12.20,p<0.001 F(1,17)=8.76,p<0.01 F(1.2,20.0)=6.19,p<0.05 F(1.7,28.7)=4.90,p<0.05 F(1,17)=18.18,p=0.001 F(1.8,30.7)=3.53,p<0.05 F(1.6,27.7)=3.75,p<0.05	F(1,17)=8.93,p<0.01 F(1.6,27.5)=7.71,p<0.01 F(1,17)=8.26,p<0.05
900-1200ms RCxH RCxHxL RCxHxS RCxHxLxS <i>Additional analyses</i> RCxS(c) RCxH(pf) RCxHxS(pf)	F(1,17)=17.07,p=0.001 F(1,17)=10.22,p<0.01 F(1.6,26.8)=3.85,p<0.05 F(1.7,29.3)=7.48,p<0.01 F(1,17)=14.91,p=0.001 F(1.5,25.7)=4.12,p<0.05	F(1,17)=4.61,p<0.05 F(1,17)=8.50,p=0.01 F(1.3,22.5)=7.43,p<0.01 F(1.1,19.1)=7.32,p<0.05 F(1,17)=12.99,p<0.01
1200-1900ms RC RCxH RCxHxL RCxS RCxHxLxS <i>Additional analyses</i> RC(c) RCxS(c) RC(m) RCxL(m) RCxH(pf)	F(1,17)=9.41,p<0.01 F(1,17)=9.01,p<0.01 F(1.4,23.9)=5.23,p<0.05 F(1.4,23.2)=5.74,p<0.05 F(1,17)=18.94,p<0.001	F(1,17)=6.61,p<0.05 F(1,17)=5.76,p<0.05 F(1,17)=11.17,p<0.01 F(1.2,20.1)=7.53,p=0.01 F(1.6,27.5)=11.67,p<0.001 F(1,17)=5.23,p<0.05 F(1.1,18.5)=12.42,p<0.01 F(1,17)=8.54,p=0.01 F(2.0,34.4)=5.02,p<0.05 F(1,17)=15.37,p=0.001

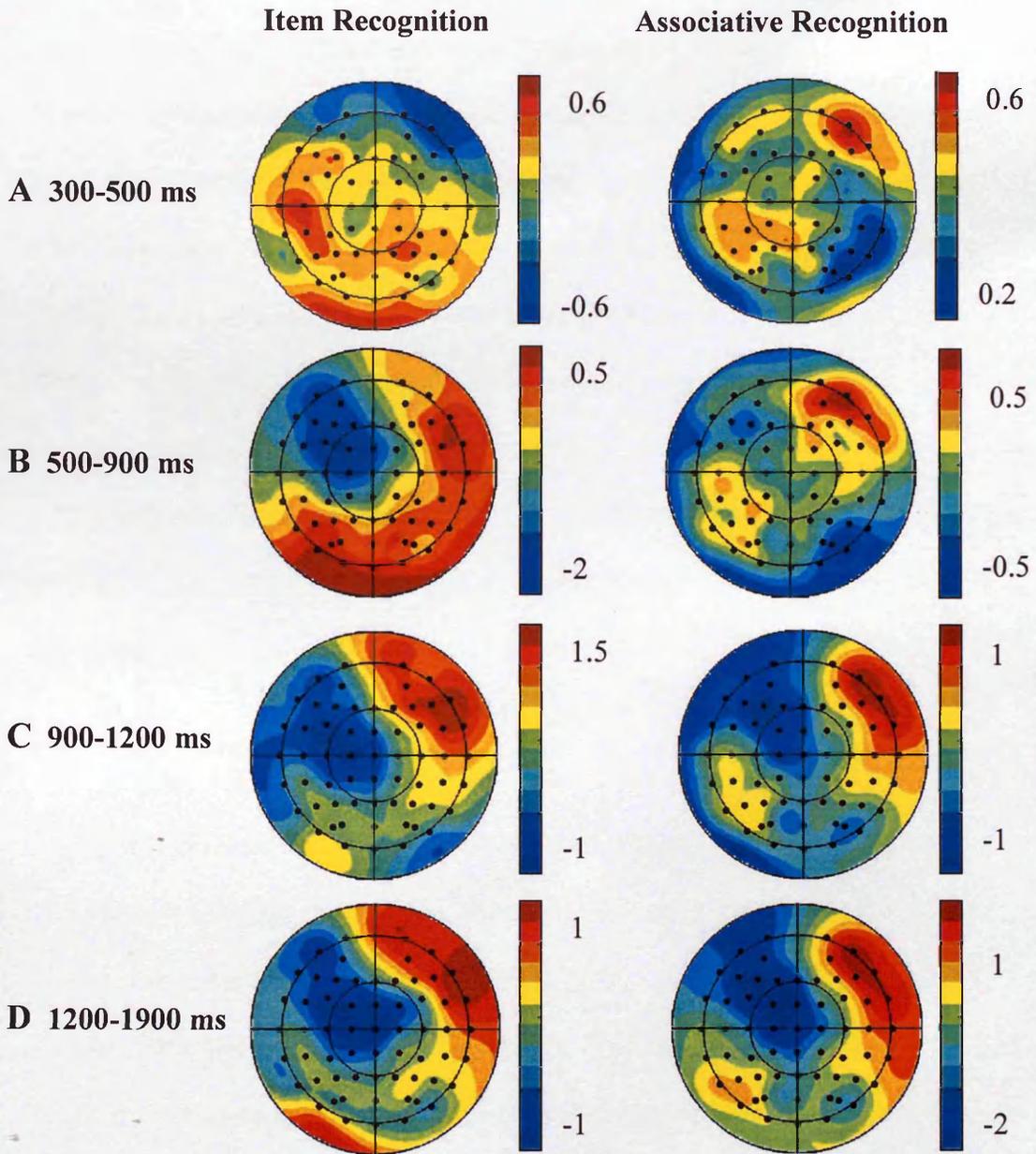


Figure 20. Topographic maps illustrating the scalp distribution of ERP effects for the older group in Experiment 2. Panel A illustrates the 300-500 ms latency region; B – 500-900 ms; C – 900-1200 ms; and D – 1200-1900 ms. The maps are shown as in Figure 12.

The lateralised right frontal effect persisted into the 1200-1900 ms latency period (Figure 20, D). This observation was confirmed by subsidiary analyses investigating the two- and four-way interactions in the Prefrontal and Main ANOVAs [right prefrontal – $t(17) = 3.08$, $p < 0.05$; right frontal – response category by site interaction, $F(1.3, 21.3) = 4.40$, $p < 0.05$].

Finally, although the preliminary analyses had suggested the presence of early old/new differences over left parietal electrodes, the 500-900 ms analyses failed to show any reliable effects over the posterior location. An ANOVA of frontal and parietal locations was therefore performed on a restricted (500-700 ms) period specifically to ascertain whether a short-lived parietal effect was present. This analysis produced an interaction involving response category, hemisphere, location and site [$F(1.9,31.8) = 8.66, p = 0.001$], and subsidiary ANOVAs revealed small, but robust, positive-going effects over left [$F(17) = 6.30, p < 0.05$], and right [$F(17) = 4.54, p < 0.05$], parietal sites (Figure 21, A, p215).

Associative recognition

The earliest robust same/rearranged differences were observed at around 900 ms over the F3 electrode. Accordingly, subsidiary analyses investigating interactions during the first two latency regions failed to demonstrate any robust ERP effects. The four-way interaction between 900 and 1200 ms reflected a significant negative-going magnitude shift over left frontal electrodes (Figure 20, C); a subsidiary analysis of the left frontal hemisphere revealed a main effect of response category [$F(1,17) = 11.05, p < 0.01$]. Moreover, a post hoc t-test of the left hemisphere investigating the two-way interaction in the Prefrontal ANOVA indicated that the modulation also extended to left prefrontal sites [$t(17) = 2.45, p = 0.05$].

Likewise, main effects of response category in the Main, Central and Midline 1200-1900 ms ANOVAs reflected an increasingly widespread, left-lateralized, negative-going component (Figure 20, C). Subsidiary investigations

of interactions in the Main and Prefrontal ANOVAs produced significant results over left frontal [main effect of response category – $F(1,17) = 34.14, p < 0.001$] and left prefrontal [$t(17) = 4.48, p < 0.001$] sites. Moreover, targeted t-tests of the central location confirmed that the modulation also extended to the left central hemisphere [$t(17) = 3.63, p < 0.01$].

Topographic analyses

As item recognition elicited robust ERP effects from 500 ms onwards in the older group, two within-task topographic comparisons were performed (500-900 ms vs. 900-1200 ms and 900-1200 ms vs. 1200-1900 ms). In associative recognition, as significant ERP effects were only observed from 900 ms onwards, a single comparison (900-1200 ms vs. 1200-1900 ms) was conducted.

Item recognition

Robust distributional differences were restricted to the 500-900 ms vs. 900-1200 ms comparison. Epoch by location interactions in the Main [$F(1,17) = 16.84, p = 0.001$] and Midline [$F(1.8,30.78) = 10.39, p = 0.001$] ANOVAs reflected the progression from a left-sided negative frontal effect in the first time window to a right-sided positive frontal effect in the second time window (Figure 20, A and B).

Associative recognition

The lack of significant interactions involving the factor of epoch confirmed that the late left fronto-central negativity was the sole ERP effect elicited by associative recognition in the older adults.

Summary of the ERP effects elicited by item and associative recognition in older adults

Between 500 and 900 ms, the predominant ERP effect elicited by item recognition was a left frontal negative-going modulation. This effect was temporally distinct from the later right frontal component that was apparent from 900 ms onwards. There was also evidence of some short-lived (500-700 ms) bilateral positive-going activity over parietal sites. The sole ERP modulation produced by associative recognition was a late left fronto-central negativity present from 900 ms onwards.

Item vs. associative recognition in older adults

As neither task elicited robust ERP modulations until 500 ms, between-task magnitude analyses were not conducted for the 300-500 ms latency region. Moreover, since robust ERP effects were only observed in associative recognition after 900 ms, between-task topographic comparisons were restricted to the 900-1200 ms and 1200-1900 ms latency regions. The absence of any significant findings in these topographic ANOVAs demonstrated that the ERP effects elicited by item and associative recognition in older adults were qualitatively similar.

The magnitude analyses revealed robust between-task voltage differences only in the 500-900 ms and 1200-1900 ms latency periods (Table 10). Two- and three-way interactions in the Main, Central and Prefrontal 500-900 ms ANOVAs indicated that the early left frontal negativity elicited by item recognition was absent in associative recognition (Figure 21, B, below). A subsidiary ANOVA of left frontal and left parietal sites produced a marginal

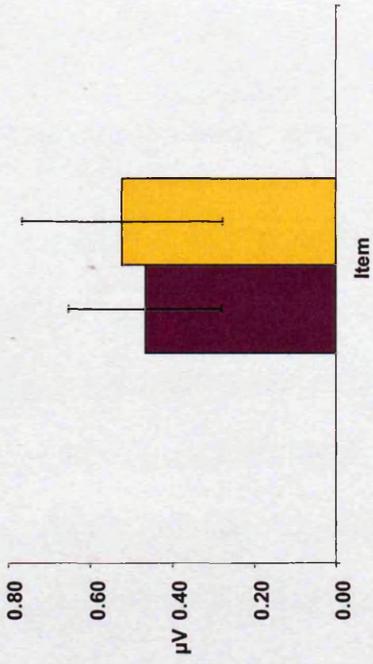
main effect of task [$F(1,17) = 4.29, p = 0.054$], and targeted t-tests showed that this result was principally due to differences over the left frontal scalp [$t(17) = 2.91, p < 0.05$]. Likewise, post hoc t-tests of the prefrontal and central locations demonstrated that between-task differences were left-lateralized [left prefrontal – $t(17) = 3.13, p < 0.05$; left central – $t(17) = 3.08, p < 0.05$].

Table 10. Results of the between-task magnitude comparisons in the older group.

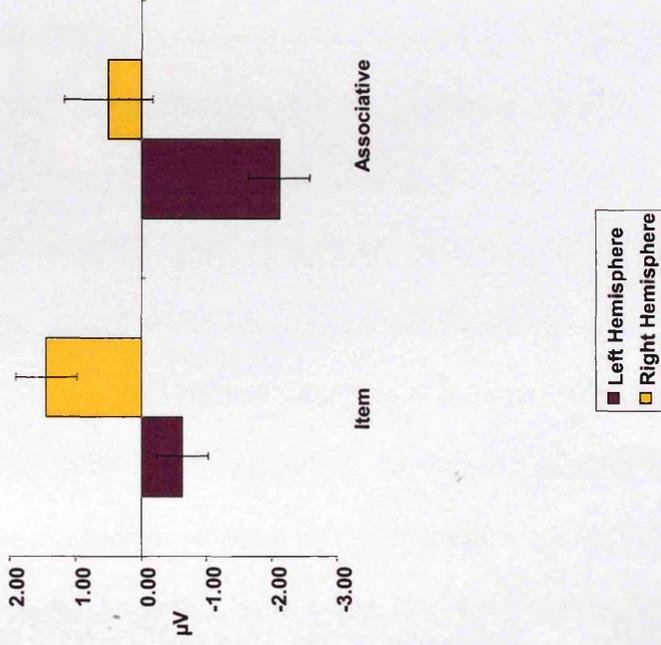
Latency Region	Magnitude
500-900ms	
TxH	$F(1,17)=10.21,p<0.01$
TxHxS	$F(1.8,30.0)=5.03,p<0.05$
<i>Additional analyses</i>	
<i>TxH(c)</i>	$F(1,17)=13.12,p<0.01$
<i>TxH(pf)</i>	$F(1,17)=7.04,p<0.05$
900-1200ms	No significant results
1200-1900ms	
<i>Additional analyses</i>	
<i>T(pf)</i>	$F(1,17)=5.45,p<0.05$

By 1200-1900 ms, the main effect of task over prefrontal electrodes reflected the presence of a late left prefrontal negativity in associative, but not in item, recognition (Figure 21, C). Targeted t-tests revealed a significant between-task difference only over the left prefrontal hemisphere [$t(17) = 3.00, p < 0.05$]. Interestingly, despite the presence of a reliable right frontal effect in item recognition alone, no between-task disparities were evident over right frontal electrodes.

A 500 – 700 ms Parietal



C 1200 – 1900 ms Prefrontal



B 500 – 900 ms Frontal

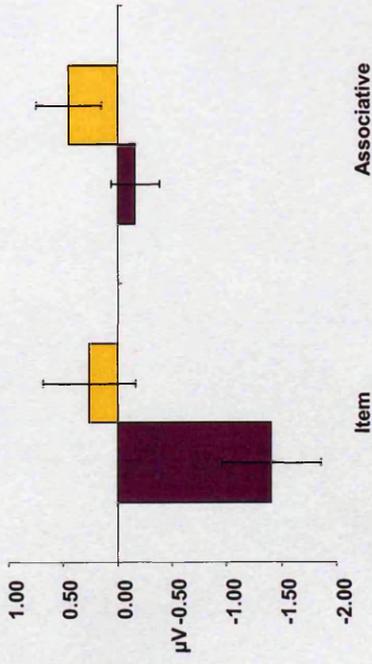


Figure 21. Mean amplitudes of selected ERP effects in the older group for item and associative recognition. The left hemisphere is collapsed across F1, F3 and F5 (frontal), P1, P3, and P5 (parietal), and F7, AF7 and FP1 (prefrontal); the right hemisphere is collapsed across F2, F4 and F6 (frontal), P2, P4, and P6 (parietal), and F8, AF8, and FP2 (prefrontal).

Summary of ERP differences between item and associative recognition in older adults

The left fronto-central negativity elicited by item recognition onset earlier than a similar component observed in associative recognition. Later in the epoch, however, despite the decline in the item recognition modulation, significant between-task differences were restricted to left prefrontal sites. Although the late right frontal effect was only reliable in item recognition, there was no between-task magnitude difference over right frontal electrodes. Likewise, parietal activation was equivalent in both tasks, even though a short-lived (500-700 ms) positivity was only robust in item recognition. Finally, the absence of any between-task topographic differences indicated that the ERP effects elicited by item and associative recognition in older adults were qualitatively similar.

Comparing young and older groups

All four latency periods were employed for magnitude age comparisons; however, as the older participants failed to produce any robust ERP effects in the earliest latency period, this was not used in the topographic comparison in either task. In associative recognition, the older participants only produced robust ERP effects from 900 ms onwards, therefore the topographic comparisons for the associative task were further restricted to the 900-1200 ms and 1200-1900 ms latency periods.

Item recognition

The absence of any significant interactions involving age in the 300-500 ms latency region suggested that the early ERP effects elicited by both groups were quantitatively similar. Between 500 and 900 ms, interactions involving the factor of hemisphere in the Main, Central and Prefrontal magnitude ANOVAs (Table 11, p219) indicated that age-related changes were greatest over the left hemisphere. Post hoc and targeted analyses of the left parietal [$t(34) = 2.34, p = 0.05$], left central [$t(34) = 2.73, p < 0.05$], left frontal [$t(34) = 2.80, p < 0.05$] and left prefrontal [$t(34) = 3.48, p < 0.01$] hemispheres confirmed the age-related reduction in the magnitude of the left parietal effect (Figure 22, B, p220), and the presence of a left fronto-central negativity only in the older participants (Figure 22, A). The increased frontal negativity in the older group was also demonstrated by an age by site interaction [$F(1.2, 39.8) = 4.20, p < 0.05$] in the subsidiary analysis of frontal sites that followed the age, location and site interaction in the Main ANOVA.

This last finding was not unexpected as parietal activity was only robust in the elderly between 500 and 700 ms. Nevertheless, a targeted t-test on this restricted latency region confirmed the left parietal age reduction [$t(34) = 2.77, p < 0.05$]. Finally, the left-sided asymmetry of the ageing effects was substantiated by two-way interactions in the Main, Central and Prefrontal 500-900 ms topographic analyses (Table 12, p221).

From 900 ms onwards, ERP activity tended to be more positive-going in young adults, although subsidiary investigations of the interactions in the Main ANOVA failed to reveal any significant findings. However, a subsidiary ANOVA

following the three-way interaction in the 900-1200 ms Prefrontal magnitude ANOVA produced a main effect of age over left prefrontal sites [$F(1,34) = 4.24$, $p < 0.05$]. This left-sided asymmetry, as confirmed by an age and hemisphere interaction in the Prefrontal topographic ANOVA, principally reflects the contrast between the declining left frontal effect in the older group and the bilateral frontal positive-going activation in the young group (Figure 22, C). Significantly, however, despite the presence of a robust right frontal effect only in older adults from 900 ms onwards, the age-related difference in right frontal and prefrontal activity was not reliable (both p values > 0.3).

Between 1200 and 1900 ms, the three-way interaction in the Main magnitude ANOVA appeared to principally reflect the increased laterality of right frontal activation in the older group (Figure 20, D vs. Figure 18, D). This interpretation was supported by an age by site interaction [$F(1.2,41.4) = 5.77$, $p < 0.05$] in the subsidiary investigation of the frontal location, and the three-way interaction in the Main topographic ANOVA.

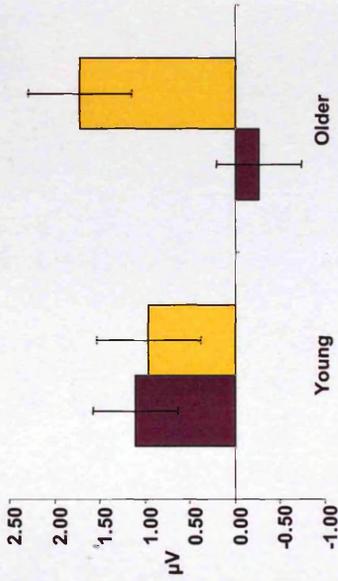
Associative recognition

Interactions involving the factor of age were observed in the Main and Midline 300-500 ms magnitude ANOVAs (Table 11). The subsidiary analysis of frontal sites produced a response category by site interaction [$F(1.3,43.4) = 6.53$, $p < 0.01$], confirming that early mid-frontal activity was only present in the young group (Figure 23, A, p223).

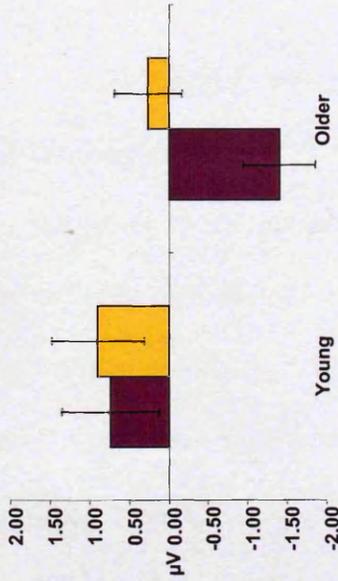
Table 11. Results of the magnitude age comparison for both item and associative recognition.

Latency Region	TASK	
	Item Recognition	Associative Recognition
300-500ms AxLxS <i>Additional analyses</i> AxL(m)	No significant results	F(1.5,49.5)=9.55,p=0.001 F(2.0,67.9)=5.32,p<0.01
500-900ms A AxH AxHxS AxLxS <i>Additional analyses</i> A(c) AxH(c) AxS(c) A(m) A(pf) AxH(pf)	F(1,34)=4.42,p<0.05 F(1,34)=9.89,p<0.01 F(1.5,49.6)=3.87,p<0.05 F(1.4,47.9)=4.32,p<0.05 F(1,34)=4.13,p=0.05 F(1,34)=7.26,p<0.05 F(1,34)=4.23,p<0.05 F(1,34)=10.95,p<0.01	F(1,34)=8.41,p<0.01 F(1,34)=5.96,p<0.05 F(1.2,39.4)=4.86,p<0.05 F(1,34)=6.39,p<0.05
900-1200ms A AxH AxS AxHxS AxLxS <i>Additional analyses</i> A(c) AxS(c) A(m) AxH(pf) AxHxS(pf)	F(1,34)=9.88,p<0.01 F(1.3,45.6)=4.05,p<0.05 F(1.4,46.6)=6.44,p<0.01 F(1,34)=6.60,p<0.05 F(2.0,66.6)=3.30,p<0.05	F(1,34)=14.28,p=0.001 F(1.4,47.1)=6.59,p<0.01 F(1.3,43.4)=4.16,p<0.05 F(1,34)=11.09,p<0.01 F(1.2,40.5)=14.79,p<0.001 F(1,34)=15.84,p<0.001
1200-1900ms A AxS AxLxS <i>Additional analyses</i> A(c) AxS(c) A(m) AxL(m)	F(1.3,43.8)=7.81,p<0.01	F(1,34)=10.98,p<0.01 F(1.6,53.8)=7.97,p<0.001 F(1.7,58.1)=4.61,p<0.05 F(1,34)=5.89,p<0.05 F(1.2,40.5)=16.77,p<0.001 F(1,34)=14.87,p<0.001 F(1.8,61.8)=3.92,p<0.05

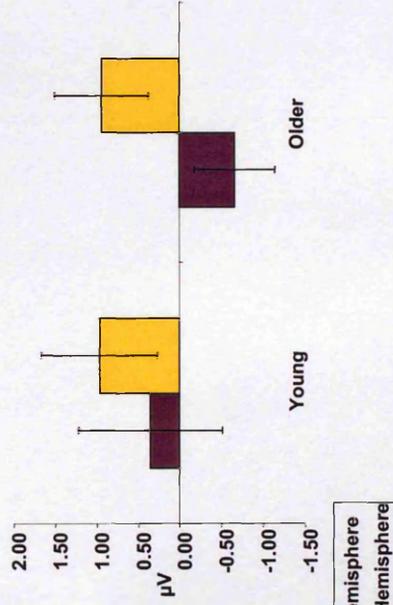
C 900 – 1200 ms Prefrontal



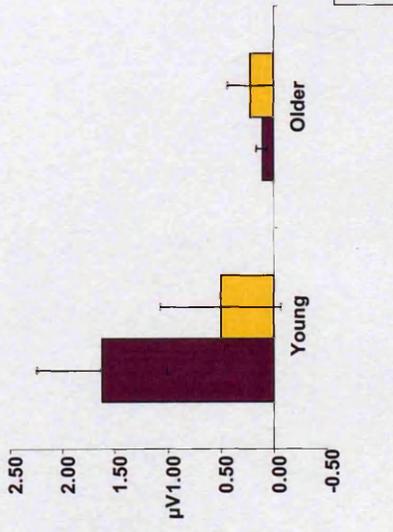
A 500 – 900 ms Frontal



D 1200-1900 Frontal



B 500 – 900 ms Parietal



■ Left Hemisphere
■ Right Hemisphere

Figure 22. Mean amplitudes of selected ERP effects in the young and older groups for item recognition. The left hemisphere is collapsed across F1, F3 and F5 (frontal), P1, P3, and P5 (parietal), and F7, AF7, and FP1 (prefrontal); the right hemisphere is collapsed across F2, F4 and F6 (frontal), and P2, P4, and P6 (parietal), and F8, AF8, and FP2 (prefrontal).

Table 12. Results of the topographic age comparison for both item and associative recognition.

Latency Region	TASK	
	Item Recognition	Associative Recognition
500-900ms AxH AxLxS <i>Additional analyses</i> AxH(c) AxH(pf)	F(1,34)=7.46,p=0.01 F(1.4,46.8)=4.70,p<0.05 F(1,34)=5.81,p<0.05 F(1,34)=7.94,p<0.01	No significant results
900-1200ms AxH AxS AxLxS <i>Additional analyses</i> AxS(c) AxH(pf)	F(1,34)=7.78,p<0.01 F(1.3,45.8)=7.23,p<0.01 F(1,34)=4.70,p<0.05	F(1.3,45.0)=6.72,p<0.01 F(1.4,46.1)=3.99,p<0.05 F(1.2,39.7)=14.80,p<0.001
1200-1900ms AxS AxLxS <i>Additional analyses</i> AxS(c) AxL(m)	F(1.3,42.7)=8.07,p<0.01	F(1.6,52.7)=8.08,p<0.01 F(1.7,57.3)=4.75,p<0.05 F(1.2,40.2)=17.15,p<0.001 F(1.8,61.8)=3.80,p<0.05

From 500 ms onwards, main effects of age in the Main, Central and Midline magnitude ANOVAs indicated that ERP activity was globally more positive-going in the young age group (although caution should be exercised over the interpretation of main effects as prima facie evidence of ageing differences, see Rugg & Morcom, 2004). Targeted t-tests of separate parietal hemispheres between 500 and 900 ms indicated the presence of a left parietal effect only in the young group [$t(34) = 2.29$, $p = 0.058$] (Figure 23, B).

A subsidiary analysis of frontal sites investigating the three-way interaction in the Main 900-1200 ms magnitude ANOVA produced a main effect of age [$F(1,34) = 7.01$, $p < 0.05$], and an age by site interaction [$F(1.2,40.7) = 9.19$, $p < 0.01$]. These results reflected the presence of the late left fronto-

central negativity in the older adults compared with the right frontal effect in the young adults (Figure 23, C). Over posterior sites, a main effect of age [$F(1,34) = 13.12, p = 0.001$] indicated that the parietal positivity, which reflected the prolonged left parietal effect in conjunction with a right-sided central/posterior activation in young adults (Figure 23, D), was absent in the elderly.

Distributional ageing differences were confirmed by interactions in the Main and Central topographic ANOVAs (Table 12).

The pattern of results in the 1200-1900 ms magnitude and topographic ANOVAs was similar to the above: a targeted t-test of left frontal sites showed that anterior differences indexed the presence of the left frontal negativity only in the older adults [$t(34) = 3.63, p < 0.01$] (Figure 23, E). In this time window, however, a main effect of age over parietal electrodes [$F(1,34) = 6.30, p < 0.05$] in the subsidiary analysis of the three-way interaction in the Main magnitude ANOVA principally appeared to reflect the late right-sided central/posterior positivity in the young adults. Meanwhile, an age by location interaction in the Midline topographic ANOVA suggested that age-related differences were maximal over central and frontal locations. Notably, however, a targeted t-test confirmed that the left prefrontal negativity observed in young adults, although visibly reduced (Figure 23, F), was not statistically different from that observed in the older group [$t(34) = 1.42, n.s.$].

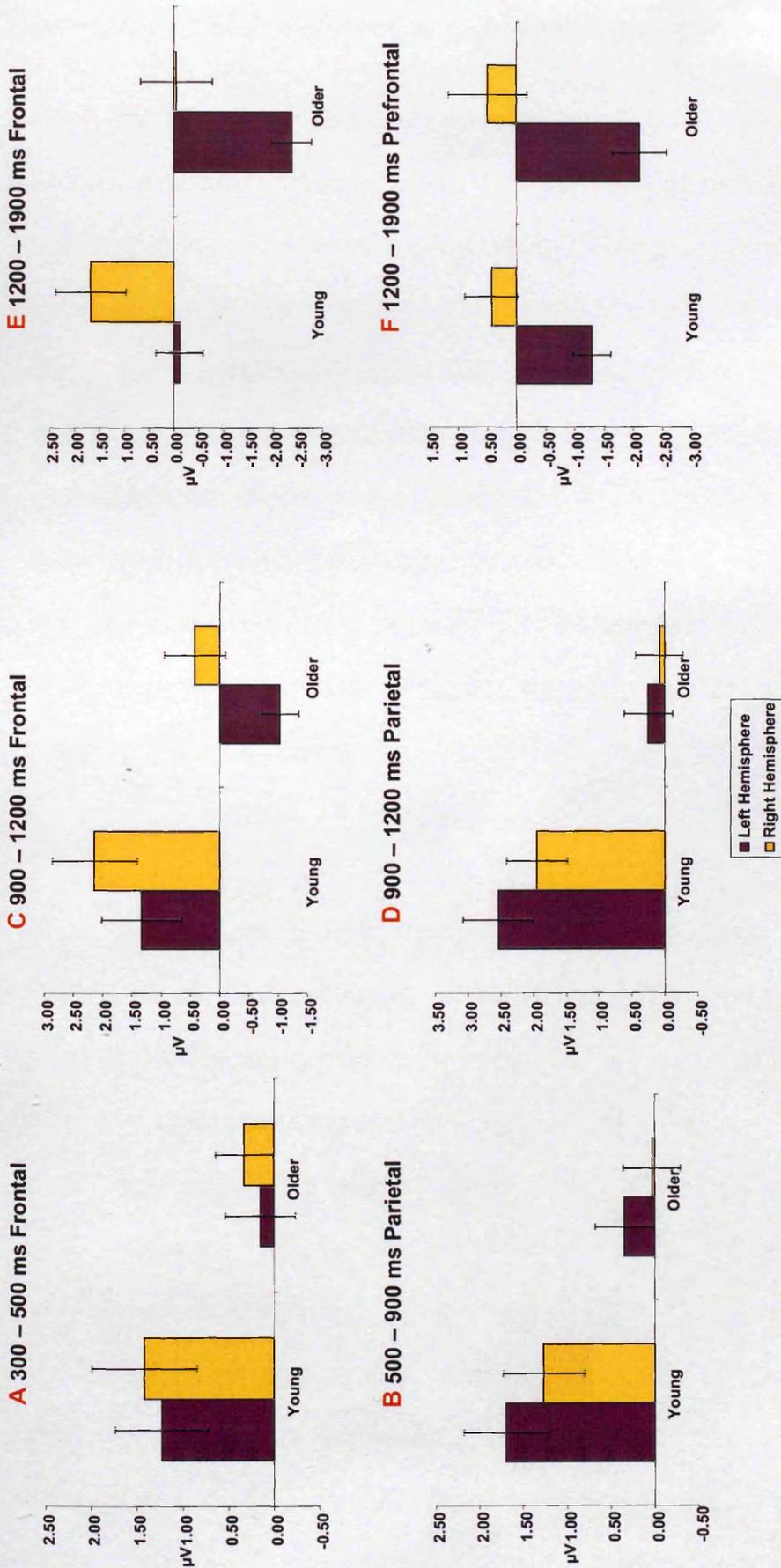


Figure 23. Mean amplitudes of selected ERP effects in the young and older groups for associative recognition. The left hemisphere is collapsed across F1, F3 and F5 (frontal), P1, P3, and P5 (parietal), and F7, AF7, and FP1 (prefrontal); the right hemisphere is collapsed across F2, F4 and F6 (frontal), P2, P4, and P6 (parietal), and F8, AF8, and FP2 (prefrontal).

Summary of ERP differences between young and older adults

The left parietal effect elicited by item recognition in young adults was severely reduced in the older group, who instead produced a left frontal negativity in the 500-900 ms latency region. Although a lateralized late right frontal effect was robust only in the elderly participants, the magnitude of the modulation was statistically equivalent in both age groups. In associative recognition, early mid-frontal, extended left parietal, and late right frontal and central/posterior effects were present only in young adults. In contrast, the older group produced a left frontal negativity from 900 ms that became more widespread as the epoch progressed. Interestingly, a late (1200-1900 ms) left prefrontal negativity in the young group did not differ significantly from that observed in the older group.

Discussion

The principle aim of Experiment 2 was to examine the effects of ageing on the ERP correlates of item and associative recognition. As anticipated, compared to the young participants, older adults demonstrated a severely reduced left parietal effect in item recognition, and produced a left-sided negativity in associative recognition. However, several findings ran contrary to our expectations: First, the left parietal effect was absent in older adults in associative recognition. Second, the older group produced a left-sided negativity for item recognition as well as for associative recognition. Third, on this occasion, the early mid-frontal effect was maximal in associative recognition in the young group, and no early frontal activity was evident in the older participants.

Behavioural findings

Although the older adults' performance on both tasks was well above chance, as predicted they were less able to discriminate between same and rearranged pairs than the young participants. Moreover, in item recognition, whilst the ageing deficit was reduced, the age difference in discriminability was still marginally significant. The increased age-related impairment in associative recognition also corresponds to the neuropsychological test results (Table 5) suggesting that the older adults' memory for word pairs (immediate and delayed) was disproportionately compromised. In particular, and consistent with previous studies (e.g. Castel & Craik, 2003), the elderly struggled to reject rearranged pairs, but whereas older adults typically also produce fewer hits than young adults in associative recognition, in the current experiment the hit rate was equivalent in both groups.

Although this proficient memory for same pairs suggests that the elderly participants benefited from the associative encoding instructions, they still took longer over the sentence generation task and found it more difficult than the young participants. This deficit was apparent despite the extra training given to older people and the measures taken to limit their response time at encoding. Indeed, the nature of the encoding task may make it particularly hard for older adults; integrating unrelated items requires a high level of self-initiated processing and places a large demand on their cognitive resources (Craik & Byrd, 1982; Craik, 1983; Smith et al., 1998).

Both groups appeared to be more confident about associative recognition than about item recognition. Dual process theory assumes that

recollection produces high confidence responses, but that familiarity supports a wide range of confidence responses (Yonelinas et al., 1996; Yonelinas, 1997, 2001b, 2002). The increased confidence ratings in associative recognition therefore appear to suggest that, as expected, this task promoted recollection-based responding in both age groups. In contrast, the behavioural data appears somewhat equivocal with regard to the assumption that the elderly rely more on familiarity as their capacity for recollection becomes impaired. Although a decreased correct rejection rate in associative recognition has been interpreted as showing an increased reliance on familiarity by older people (Light et al., 2002), no age-related differences in high confidence ratings were found in either item or associative recognition (but see "The left parietal index of recollection appears severely reduced or absent in older adults", below).

Consistent with general slowing theory (see "Episodic Memory and Ageing" chapter), the older adults' response times tended to be longer than those of the young adults in both retrieval tasks. Nevertheless, identical latency regions were selected for the ERP analyses in both groups; the preliminary paired t-tests indicated that, despite the age-related slowing, the same latency regions best reflected the development of the ERP effects in both young and older adults.

The ERP correlates of item and associative recognition in young adults

Surprisingly, the ERP results for the young adults in the current experiment were not entirely consistent with those from Experiment 1. Most significantly, the early mid-frontal effect was more prominent in associative

recognition than in item recognition. This finding appears to be more in accordance with suggestions that the modulation reflects recollection (Duarte et al., 2004), or operations specific to contextual retrieval (Donaldson & Rugg, 1998, Experiment 2), than with its interpretation as an index of familiarity. The reason for the discrepancy between the two experiments is unclear; however, their design differed in two ways. First, in the current experiment, the presentation time at encoding was restricted. Although this modification produced slightly shorter RTs in the young group on the sentence generation task, the difference was not significant ($p > 0.4$), and it therefore seems unlikely that this change would have affected the subsequent mid-frontal component.

Second, the introduction of a two-stage judgement to the test phase (i.e. the old/new or same/rearranged decision followed by a confidence rating) may have altered the time courses of the ERP waveforms. For example, the latency periods that appeared to best reflect the ERP components were delayed in the current experiment compared to Experiment 1. Moreover, in item recognition, the left parietal effect was apparent between 300 and 500 ms, whereas it was not evident until the second latency period in Experiment 1; similarly, in associative recognition, robust left parietal activity was present in the second, rather than the third, time window. This final observation indicates that the delay in the onset of the associative recognition left parietal effect in Experiment 1 was not simply, as suggested, a function of the extended time to read two words instead of one.

There were two other electrophysiological differences between Experiments 1 and 2. First, the right frontal effect in item recognition was no longer reliable in the current experiment. Second, the young adults produced a

late left prefrontal negative-going activation during the associative task. No such component was apparent in Experiment 1.

ERP differences between young and older adults

As the principle aim of the current experiment was to examine age-related changes in the ERP correlates of item and associative recognition, further discussion of any inter-experimental inconsistencies will be reserved for the "General Discussion" chapter. The following sections will therefore focus on electrophysiological differences and similarities between the young and older participants.

The left parietal index of recollection appears severely reduced or absent in older adults

Whilst item recognition elicited a robust left parietal effect in the young group, the bilateral posterior activation evident in older participants was severely reduced in magnitude and duration. This observation is consistent with a previous item recognition study (Morcom & Rugg, 2004) and suggests that elderly adults use recollection less than young adults. One way of reconciling the electrophysiological data with the confidence ratings, where the age-equivalence implies that recollection-based responding is similar in both groups, is to assume that the elderly participants' high confidence ratings may reflect a greater proportion of high confidence familiarity responses, whereas the young participants' high confidence ratings mainly reflect recollection. The wide range of confidence ratings supported by familiarity may include high confidence ratings (Yonelinas et al., 1996) and the current experiment does not

provide a distinction between high confidence familiarity and recollection (Yonelinas, 1997; 2001b; 2002).

Left parietal activity was also severely reduced in the elderly adults in associative recognition. This finding contradicts reports of left parietal age equivalence from previous recollection-promoting source memory paradigms. One possible explanation for this disparity is that whilst the ERP epoch in many source memory paradigms encompasses an initial old/new decision, with the secondary source judgement occurring subsequently, the contextual judgement in the current experiment forms the primary decision. Interestingly, the one source memory study that required a single-stage source judgement reported an age-related reduction in the left parietal effect (Li et al., 2004, although here right parietal activation was equivalent in both age groups). Moreover, an exclusion study that used a single target/non-target judgement to assess memory for temporal context, also reported a decrease in left parietal activation (Dywan et al., 2002). A second possibility is that the requirement to switch between the item and associative retrieval tasks reduced left parietal activation disproportionately in the older adults. Task-switching has been found to attenuate task-specific processing in young adults (Wilding & Nobre, 2001), and its electrophysiological signature has been shown to endure until about 1250 ms post-stimulus onset (Werkle-Bergner et al., 2005).

Left-sided negativities in older adults

The predominant ERP effect elicited by item recognition between 500 and 900 ms in older adults was a negative-going left frontal component that was temporally and topographically distinct from the late right frontal effect.

Negative-going modulations have been observed in older adults in previous ERP source memory studies (Trott et al., 1999; Wegesin et al., 2002), however, these appeared to have a more central/posterior distribution and a later (post-800 ms) onset than the current component (but see Li et al. 2004, for evidence of a more frontally-distributed, earlier negative-going effect). Moreover, although the late left fronto-central negative component elicited by associative recognition was temporally more comparable to the previous source memory negativities, its anterior distribution was indistinguishable from that of the item recognition modulation in the current experiment.

What is the functional significance of these left fronto-central negativities? The CARA (Cortical Asymmetry of Reflective Activity) model (Nolde et al., 1998) proposes that while right prefrontal cortex (PFC) is implicated in simple episodic memory tasks, left PFC can be additionally activated when the task is more demanding. Accordingly, event-related fMRI studies of young adults have revealed greater left dorsolateral PFC activity for shallowly-encoded words compared to deeply-encoded words (Buckner et al., 1998), and increased left anterior and left ventrolateral PFC activity for retrieval of context compared to item retrieval (Rugg et al., 1999; and for a review, see Fletcher & Henson, 2001).

In the current experiment, increased effort was particularly evident in associative recognition: besides the age-related reduction in performance, the post-experimental questionnaire indicated that the elderly found it harder than the young to discriminate between same and rearranged pairs [Mann Whitney $U = 57$, $z = 3.57$, $p < 0.001$]. However, a small age-related performance deficit was also apparent in item recognition, and interestingly, similar negative-going

frontal ERP effects have been observed in older adults at longer lags on continuous recognition tasks as performance becomes impaired (Rugg et al., 1997; Swick & Knight, 1997). However, the poor spatial resolution of ERPs inevitably restricts their ability to dissociate different regions of prefrontal cortex. This methodological limitation means that, given the widespread distribution of the left fronto-central negativity, the possibility that the component is non-unitary in nature cannot be excluded. Accordingly, the late negativity in associative recognition may also reflect retrieval of context; the young group in the current experiment produced a late left prefrontal negativity in associative recognition, whose magnitude did not differ statistically from that of the older adults.

Frontal and central positive-going modulations in young and older adults

The lack of robust early frontal ERP effects in the elderly is inconsistent with previous reports of early modulations of equivalent magnitude, but with different distributions, in young and older adults (Wegesin et al., 2002; Morcom & Rugg, 2004). Moreover, with the age-related reduction in the left parietal effect supporting the dual process prediction that recollection in the older participants would be compromised, familiarity might be expected to form their primary basis for retrieval in both item and associative recognition. Accordingly, the absence of any early right frontal activation in older adults appears to run counter to its interpretation as an ERP index of familiarity. Alternatively, given the late onset of robust ERP effects in older adults in the current experiment, it is possible that the high task-switch load may have disproportionately

attenuated their early components. The requirement to switch between tasks has been shown to elicit positive-going frontal and prefrontal correct rejection waveforms from 250 ms post-stimulus (Werkle-Bergner et al., 2005).

In associative recognition, the central/posterior positivity present in young adults was absent in older adults, and the late right frontal effect was significantly reduced. The latter finding suggests that the post-retrieval monitoring processes elicited by associative recognition in young adults are reduced in the elderly (c.f. Trott et al., 1999; Wegesin et al., 2002). In item recognition, in contrast, the magnitude of the right frontal component was statistically equivalent in both age groups, but its distribution was more lateralised in the elderly. However, as Figure 20 (p191) shows, the increased lateralization appears to reflect component overlap; specifically, the conjunction of residual left-sided frontal negativity with the late right frontal effect. Accordingly, in item recognition, post-retrieval monitoring processes appear to be elicited to a similar degree in both groups (c.f. Mark & Rugg, 1998; Li et al., 2004; Morcom & Rugg, 2004).

Summary

The principle age-related differences in the neural correlates of item and associative recognition were the severe reduction or absence of the left parietal index of recollection, and the appearance of left fronto-central negative-going modulations (early in item recognition; late in associative recognition) in the elderly participants. This pattern of left frontal activation combined with late right frontal activation, particularly evident in item recognition, is compatible with evidence from haemodynamic imaging showing increasingly bilateral frontal

activation in older adults during episodic retrieval tasks (Bäckman et al., 1997; Cabeza et al., 1997a; Madden et al., 1999; Cabeza et al., 2002). Finally, associative recognition failed to elicit a late central/posterior modulation in the elderly, and there was no sign of the early right frontal activation that may represent the ERP correlate of familiarity in older adults. This absence of early frontal activity and the severe reduction of the left parietal effect in older adults may, however, simply reflect the disproportionate attenuation of the elderly adults' ERPs by the high task-switch load within each test block. The following chapter addresses this question by presenting an experiment in which the requirement to switch between retrieval tasks at random intervals was removed.

Chapter 8

Experiment 3

Introduction

Experiments 1 and 2 demonstrated a clear dissociation between the ERP correlates of item and associative recognition in young adults, and indicated that these correlates change with age. The most notable differences in older adults were the severe reduction or absence of the left parietal index of recollection in both tasks, the appearance of left fronto-central negative-going modulations that onset earlier in item recognition than in associative recognition, and the absence of the central/posterior positivity in associative recognition. Moreover, in contrast to two recent ERP ageing studies (Wegesin et al., 2002; Morcom & Rugg, 2004), the elderly adults in Experiment 2 failed to exhibit any early frontal activation in either task.

Robust age-related reductions in left parietal activation are not reported universally. It is therefore possible that some aspect of the experimental design,

such as the requirement to switch between item and associative recognition at random intervals, may have contributed to the attenuation of left parietal and early frontal components in the elderly participants in Experiment 2.

Behaviourally, task switching typically leads to increased error rates and longer response times in young adults; these task-switch costs are considered to reflect the executive control processes involved in initiating a new task set, inhibiting a previous task set, or keeping track of the current appropriate task (Posner, 1980; Rogers & Monsell, 1995; Wylie & Allport, 2000; and for a review, see Monsell, 2003). As executive control processes are thought to be subserved by the frontal lobes (Aron et al., 2004), the frontal lobe hypothesis of cognitive ageing (Moscovitch & Winocur, 1995; West, 1996) would predict that any impact of task-switching should be increased in the elderly (for evidence in support of this argument, see Kramer et al., 1999).

Electrophysiologically, task switching has been shown to attenuate the ERP indices of retrieval orientation (Wilding & Nobre, 2001), and to produce an early (250 ms) onsetting bilateral frontal slow wave (Werkle-Bergner et al., 2005) in young adults. As these results reflect changes in the morphology of correct rejection waveforms, it is likely that task switching will also impact on the neural correlates of retrieval success (as measured by contrasting hit and correct rejection waveforms). Moreover, according to the frontal lobe hypothesis, any such changes may be disproportionately greater in older adults.

The current experiment therefore aims to examine the possibility that the ERP ageing differences reported in Experiment 2 may reflect the differential impact of task switching on young and older adults, rather than changes in

mnemonic processes per se. Accordingly, the task-switch costs will be reduced by blocking the retrieval tasks. This manipulation is expected to improve both item and associative recognition accuracy, and, as task-switch costs are increased in older adults (Kramer et al., 1999), the performance enhancement should be greater in the elderly.

Improving the older groups' performance will address another potential confound inherent in the results of Experiment 2, where age-related behavioural deficits mean that any ERP ageing differences may simply reflect an increase in subjective task difficulty on the part of the older adults (Rugg and Morcom, 2004). However, as previous ERP ageing studies have demonstrated that age-related differences in left parietal and central negative-going modulations persist when young and older adults performance is equated (Li et al., 2004; Morcom & Rugg, 2004), it is anticipated that the ERP effects observed in a performance-enhanced older group should be highly similar to those reported in Experiment 2.

Methods

Participants

19 young (9 male; mean age 19.7 years, range 17-27) and 19 older (8 male; mean age 70.9 years, range 65-77) participants took part in the experiment. The data from one young participant was excluded because of technical difficulties, and one older participant was removed because they did not have enough artifact-free trials in all critical categories. 18 participants remained in each group (young – 9 male, mean age 19.8 years, range 17-27; older – 8 male, mean age 70.8 years, range 65-77).

Neuropsychological tests

Table 13. Characteristics of the participants in Experiment 3 (mean \pm SD)

	Young	Older	p-value
Age (years)	19.8 \pm 2.3	70.8 \pm 4.3	<0.001
Gender	9/18 male	8/18 male	
Education (years)	14.7 \pm 1.7	13.8 \pm 4.0	n.s
BDI	5.3 \pm 4.1	4.8 \pm 2.7	n.s
Health	4.0 \pm 0.8	4.3 \pm 0.5	n.s
IQ (WASI)	115 \pm 8	122 \pm 7	<0.01
WMS-R			
<i>Logical memory I</i>	49.6 \pm 6.7	42.7 \pm 8.7	<0.05
<i>Logical memory II</i>	32.4 \pm 5.9	25.5 \pm 7.1	<0.01
<i>Paired associates I</i>	24.9 \pm 6.2	16.9 \pm 6.3	<0.001
<i>Paired associates II</i>	7.2 \pm 1.5	5.1 \pm 2.2	<0.01
<i>Letter number sequencing</i>	14.2 \pm 2.9	12.7 \pm 2.6	n.s
MMS		29.2 \pm 0.9	

The neuropsychological tests (Table 13) show the groups to be matched on years of education, health ratings and BDI scores. However, the older participants produced higher IQ scores, and the young group performed better on the WMS-R logical memory I and II, and immediate and delayed paired associates subscales. This profile is slightly different from that reported in Experiment 2, insofar as the memory deficit of the current older group extended beyond the paired associates tests.

Stimulus materials and procedure

The procedure in the current experiment differed from that employed in Experiment 2 in one respect; the retrieval tasks were blocked during the test phase, rather than randomly interleaved. Consequently, for half of the participants, the first 16 trials of each test block were equal portions of randomly intermixed old and new single words (item recognition); for the remaining

participants, the first 16 test trials consisted of equal portions of randomly intermixed same and rearranged pairs (associative recognition).

Results

Behavioural

The performance data are summarised in Table 14 (below). The hits and correct rejections data produced a main effect of age [$F(1,34) = 19.28, p < 0.001$], which reflected greater overall accuracy in the young group. The analysis also revealed an interaction involving task, response category and age [$F(1,34) = 7.74, p < 0.01$]. In associative recognition, the older group produced fewer correct rejections [$t(34) = 3.76, p = 0.001$] than the young group, but in item recognition, the hit rate was reduced in the elderly [$t(34) = 3.26, p < 0.01$].

The discriminability (Pr) analysis produced a main effect of age [$F(1,34) = 19.28, p < 0.001$] demonstrating that the elderly performed less well than the young adults at both item and associative recognition. The bias (Br) ANOVA gave rise to a main effect of task [$F(1,34) = 17.12, p < 0.001$] indicating that all participants were more conservative in item recognition.

The confidence data was divided into high and low confidence responses as previously. Main effects of task [$F(1,34) = 12.51, p = 0.001$] and response category [$F(1,34) = 86.77, p < 0.001$] in the high confidence data showed that participants were more confident about associative recognition than item recognition, and gave higher ratings to hits than to correct rejections. However, task by age [$F(1,34) = 22.58, p < 0.001$] and task by response category by age [$F(1,34) = 14.01, p = 0.001$] interactions indicated that, on this

occasion, the older group tended to be less confident than the young group about associative correct rejections [$t(34) = 2.56, p = 0.031$].

Table 14. Mean performance data (\pm S.D.) for Experiment 3.

	Item Recognition		Associative Recognition	
	Young	Older	Young	Older
<u>Accuracy</u>				
Hits	0.85 \pm 0.09	0.73 \pm 0.12	0.91 \pm 0.07	0.85 \pm 0.10
Correct Rejections (CR)	0.90 \pm 0.10	0.88 \pm 0.07	0.91 \pm 0.09	0.76 \pm 0.15
Confident Hits (rating = 5)	0.64 \pm 0.21	0.56 \pm 0.25	0.70 \pm 0.24	0.61 \pm 0.27
Confident CR (rating = 5)	0.30 \pm 0.19	0.39 \pm 0.29	0.52 \pm 0.29	0.30 \pm 0.29
Pr	0.75 \pm 0.13	0.61 \pm 0.14	0.81 \pm 0.13	0.61 \pm 0.15
Br	0.38 \pm 0.29	0.31 \pm 0.14	0.49 \pm 0.18	0.59 \pm 0.21
<u>RT(ms)</u>				
Hits	1504 \pm 397	1594 \pm 310	1728 \pm 312	2016 \pm 272
CR	1571 \pm 296	1678 \pm 334	2117 \pm 284	2390 \pm 289
<u>Study RT(ms)</u>	Young 4235 \pm 2159		Older 5922 \pm 2132	

The test RT ANOVA produced main effects of task [$F(1,34) = 241.03, p < 0.001$], response category [$F(1,34) = 38.80, p < 0.001$], and age [$F(1,34) = 4.38, p < 0.05$], which were modulated by interactions involving task and age [$F(1,34) = 8.87, p < 0.01$], and task and response category [$F(1,34) = 49.57, p < 0.001$]. Associative recognition responses were slower than item recognition responses, correct rejections were slower than hits, and the elderly were slower than the young, but only in associative recognition [$t(34) = 3.15, p < 0.01$].

Once again, older adults were slower than young adults on the sentence generation encoding task [$t(34) = 2.36, p < 0.05$]. Mann Whitney tests on the post-experimental questionnaire responses (see "Appendix C") indicated that whilst, unlike Experiment 2, there was no age difference in the subjective

experience of task difficulty [$U = 110$, $z = 1.77$, $p = 0.076$], the sentences generated by the elderly participants tended to be more detailed than those produced by the young [$U = 88$, $z = 2.47$, $p < 0.05$].

Summary of behavioural data in Experiment 3

As predicted, the blocked design of Experiment 3 improved performance in both age groups. In associative recognition, the mean discriminability rose from 0.69 to 0.81 [$t(34) = 2.40$, $p < 0.05$] in young adults, and from 0.42 to 0.61 [$t(34) = 3.86$, $p < 0.001$] in older adults. In item recognition, the young participants' mean discriminability likewise rose from 0.66 to 0.75 [$t(34) = 2.13$, $p < 0.05$], but the older participants showed a less pronounced increase, from 0.59 to 0.61 [$t(34) = 0.52$, n.s.]. Therefore, instead of showing the anticipated increased improvement compared to the young, the elderly group's item recognition performance was similar to that of their counterparts in the task-switching version. This unexpected result may partly reflect the neuropsychological scores, which indicate that the current older participants were impaired on their memory for facts (WMS-R Logical Memory I and II), whereas those in Experiment 2 were not. Alternatively, the older adults' increased speed of responding in item recognition (here, contrary to Experiment 2, there was no age-related slowing in item recognition) may have compromised their accuracy. This explanation appears unlikely, however, as the main RT reduction in the current older group compared to that in Experiment 2 occurred in item hits, whereas the decrease in accuracy occurred in item correct rejections.

Behavioural comparison of the young adults in Experiment 2 and the older adults in Experiment 3

In the current experiment, the young group continued to outperform the older group in both item and associative recognition; however, the performance of the young adults in Experiment 2 (Table 6, p187) and the elderly participants in Experiment 3 (Table 14) was very similar. Separate ANOVAs of the hits and correct rejections, and the discriminability and bias measures of these two participant groups did not produce any significant results involving the factor of age (highest F value = 3.36, $p = 0.075$). Replication of the ERP effects produced by the previous elderly group by the current high-performing older participants will therefore confirm that the electrophysiological ageing changes reported in Experiment 3 were not simply a function of an age-related performance deficit.

Event-related potentials

Young group

Item recognition

Figure 24 (p243) shows the grand average OLD and NEW waveforms for item recognition from 30 EEG electrode sites. The mean number of trials (\pm S.D.) contributing to the ERPs was 45 (8) OLD and 48 (11) NEW. The waveforms appear to diverge from approximately 250 ms post-stimulus onset, with the ERPs for OLD words becoming more positive than those for NEW words over frontal electrodes. This difference appears to exhibit a bilateral distribution and lasts until around 650 ms. Over parietal sites, meanwhile, a

positive-going old/new difference, present between 380 and 850 ms, is maximal over the left hemisphere. A second frontal positivity onsets at around 800 ms and becomes increasingly right-sided as the epoch progresses.

Associative recognition

Figure 25 (p244) shows the grand average SAME and REARRANGED waveforms for associative recognition, again from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 44 (13) SAME and 49 (6) REARRANGED. The waveforms appear to diverge from around 400 ms post-stimulus onset, with the ERPs for SAME pairings becoming more positive than those for REARRANGED pairings mainly over central and parietal sites. The voltage difference initially appears to exhibit a left-sided asymmetry, particularly over central sites, but becomes more bilateral and then right-sided as the epoch progresses. Over frontal electrodes, a long-lasting bilateral positivity onsets at 700 ms and persists until around 1600 ms.

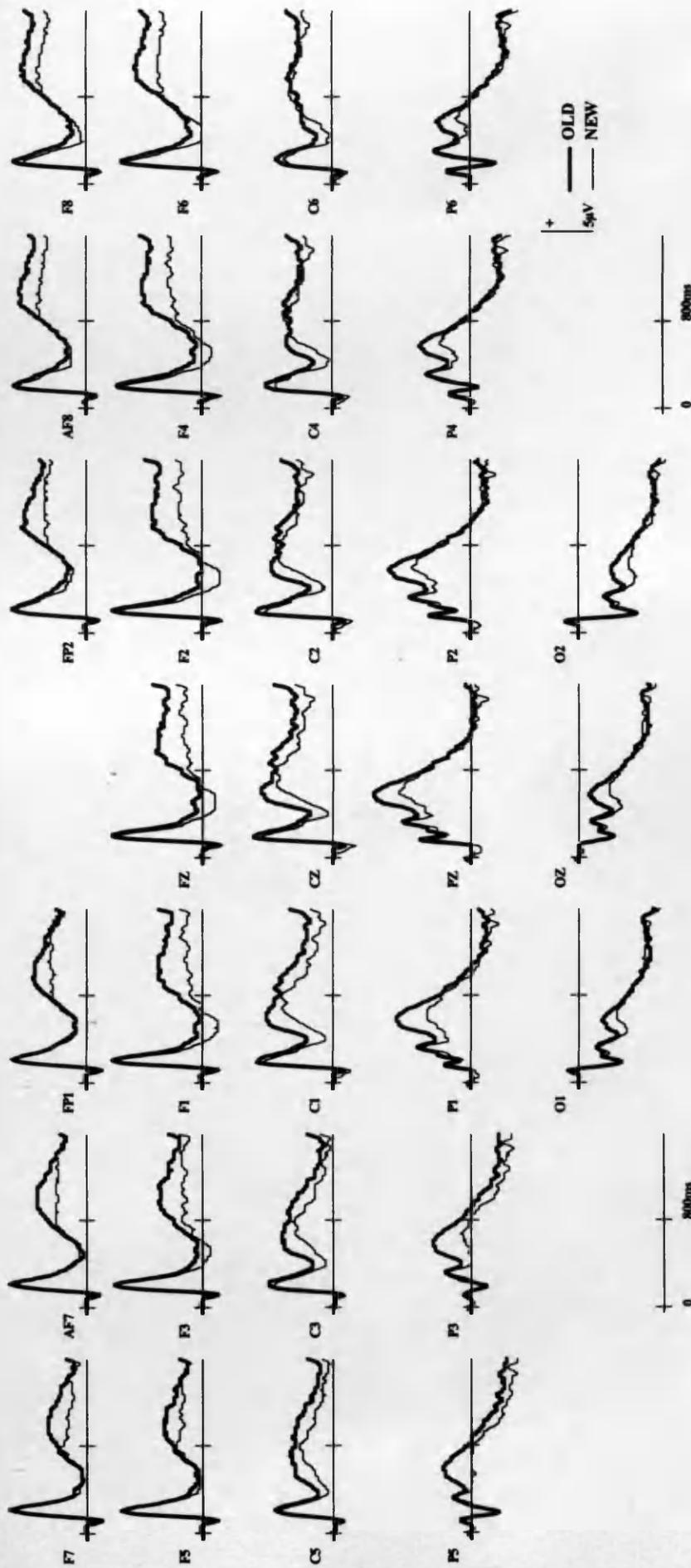


Figure 24. Grand average ERPs for the recognised (OLD) and NEW response categories for item recognition. Electrodes are shown as in Figure 10.

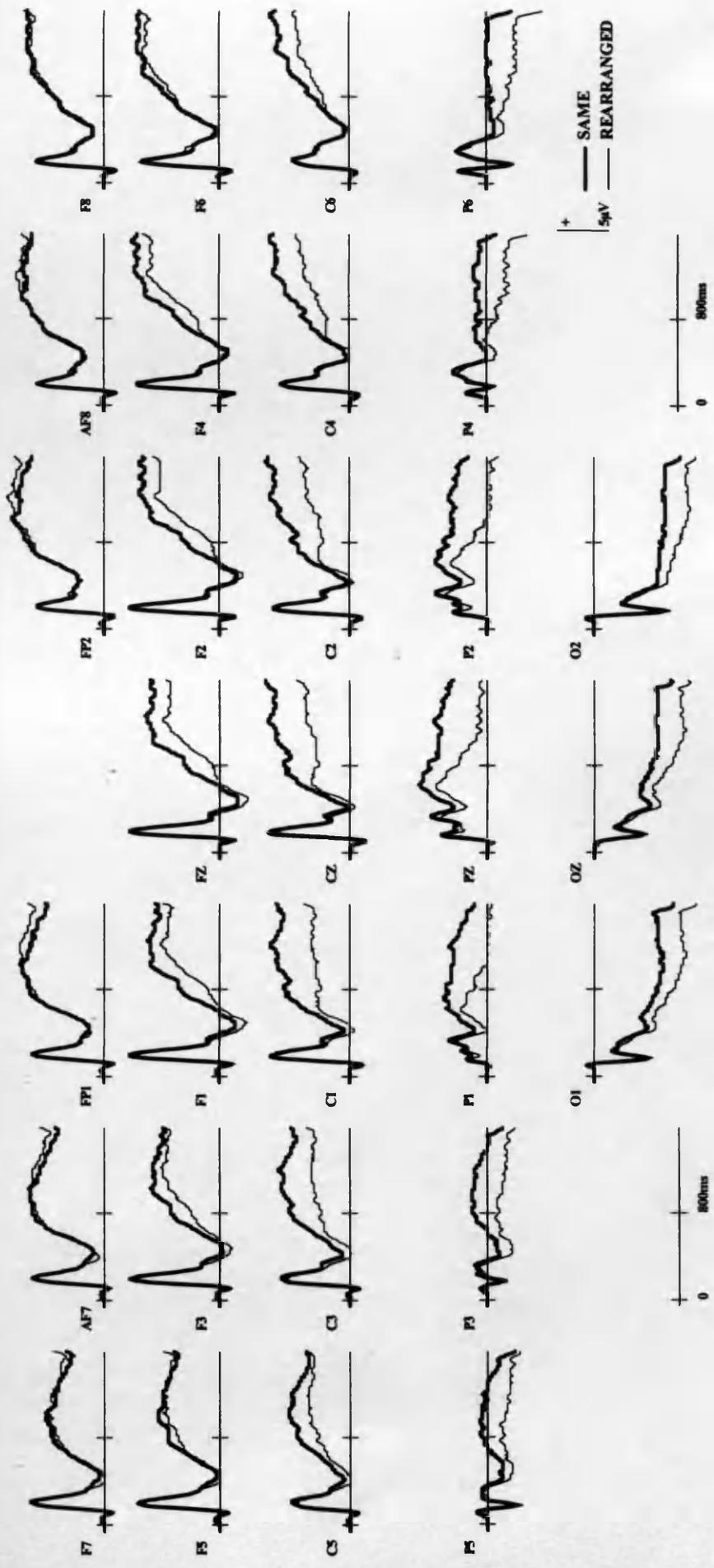


Figure 25. Grand average ERPs for the recognised (SAME) and REARRANGED response categories for associative recognition. Electrodes are shown as in Figure 10.

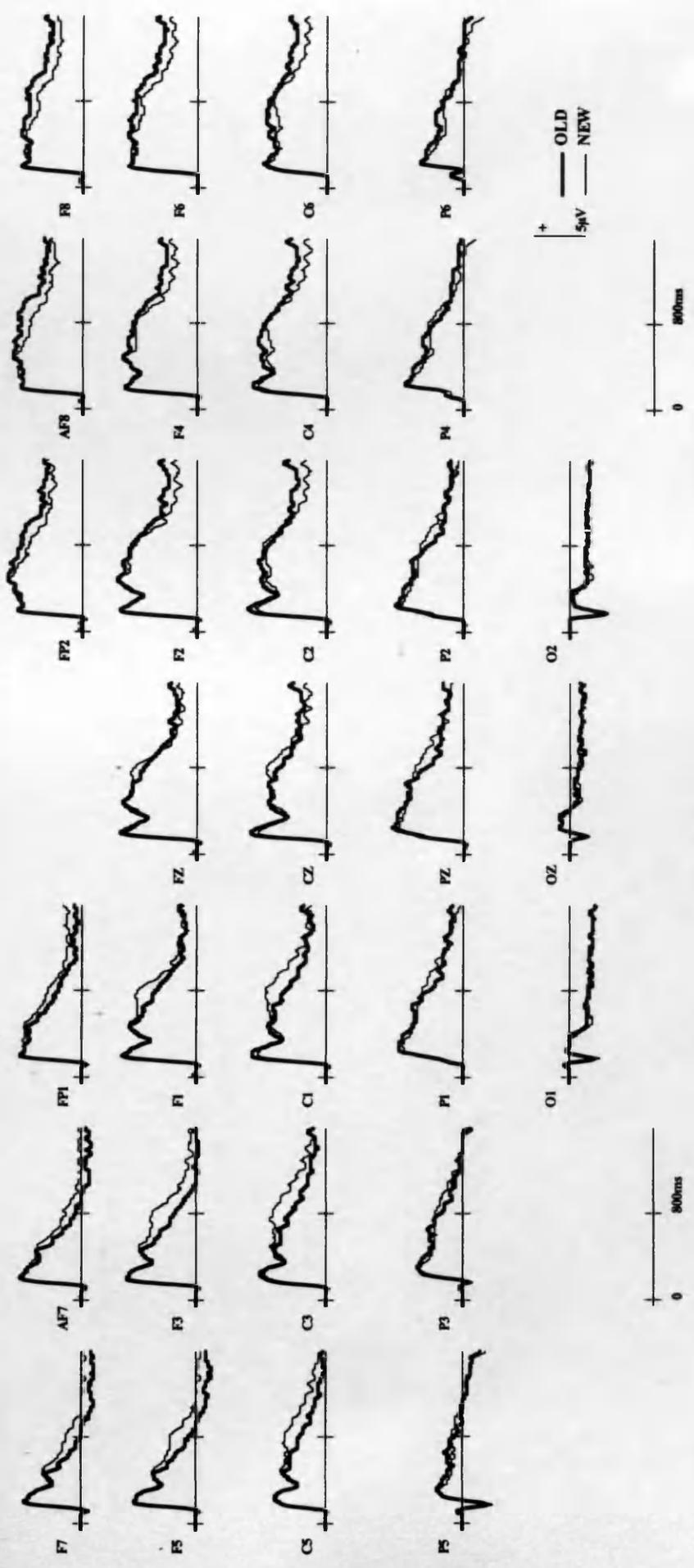


Figure 26. Grand average ERPs for the recognised (OLD) and NEW response categories for item recognition. Electrodes are shown as in Figure 10.

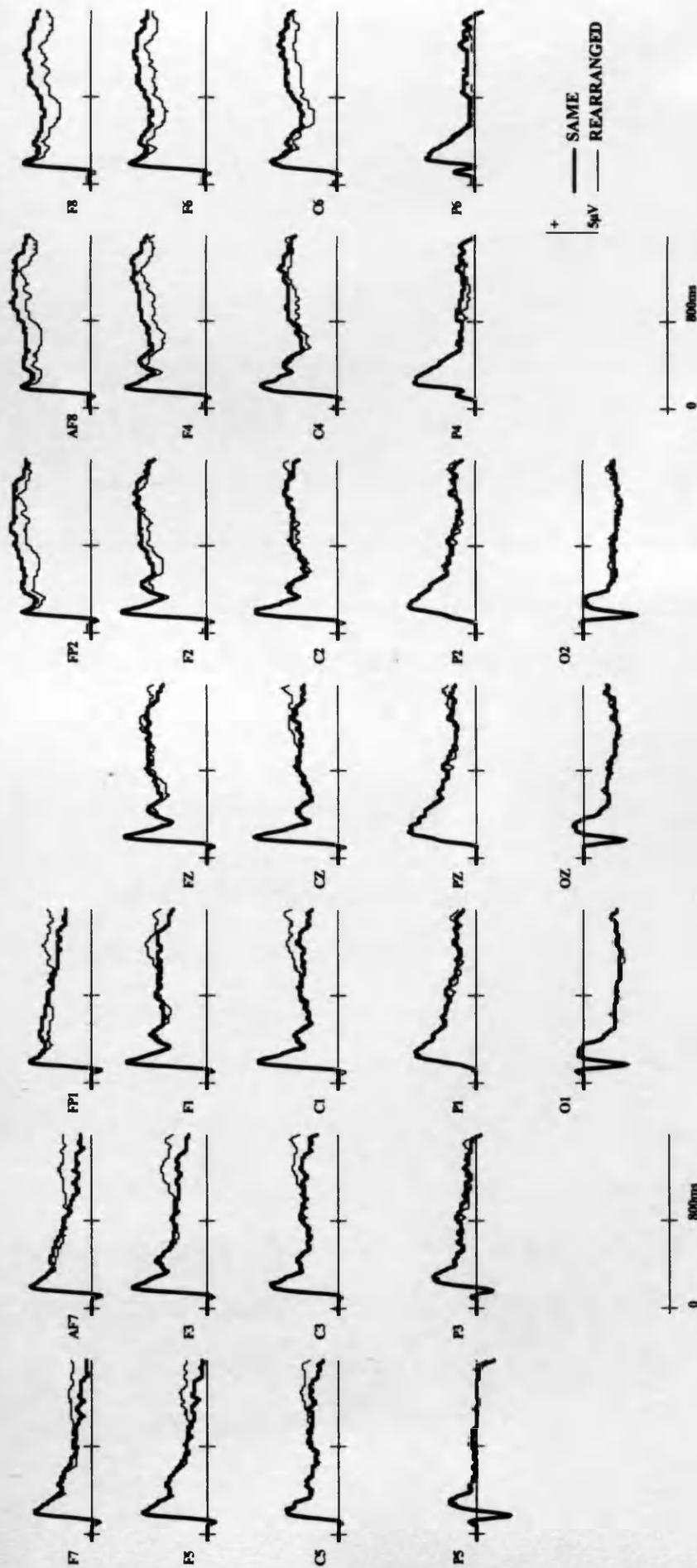


Figure 27. Grand average ERPs for the recognised (SAME) and REARRANGED response categories for associative recognition. Electrodes are shown as in Figure 10.

Older group

Item recognition

Figure 26 (p245) shows the grand average OLD and NEW waveforms for item recognition from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 38 (12) OLD and 46 (11) NEW. The waveforms diverge from about 500 ms post-stimulus onset, with the ERPs for OLD words becoming more negative than those for NEW words over left frontal and left central electrodes. This negative shift lasts until around 1200 ms.

Simultaneously, a positive-going shift, which extends to central sites from 1000 ms, appears over right frontal and prefrontal sites and persists until the end of the recording epoch.

Associative recognition

Figure 27 (p246) shows the grand average SAME and REARRANGED waveforms for associative recognition, again from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 41 (13) SAME and 35 (12) REARRANGED. The earliest same/rearranged difference is apparent around 300 ms post-stimulus onset, with SAME waveforms becoming more positive than REARRANGED waveforms over right prefrontal and right frontal sites. This modulation extends towards right central sites as the epoch progresses. Meanwhile, from around 1000 ms onwards, SAME waveforms become more negative-going than REARRANGED waveforms over left prefrontal, left frontal, and left central sites.

Rationale for the ERP analyses

The ERP analyses aimed to identify the neural correlates of item and associative recognition in young and older adults when the retrieval tasks were blocked, and to investigate ageing changes in these correlates. Preliminary analyses led to four latency periods (200-400 ms, 400-800 ms, 800-1200 ms and 1200-1900 ms) being selected for the young group, and four slightly later latency periods (300-500 ms, 500-900 ms, 900-1200 ms and 1200-1900 ms) being chosen for the older group. Due to the appearance of ERP modulations over prefrontal electrodes in the older group, additional Prefrontal ANOVAs (see Experiment 2) were conducted for the within-task, between-task and between-group magnitude and topographic comparisons for each latency region.

Young group

Item recognition

The earliest robust old/new differences were observed at 176 ms over right frontal (F8 and FT8) electrodes. Main effects of response category in the Main, Central and Midline 200-400 ms ANOVAs (Table 15, p249) demonstrated widespread positive-going differences between OLD and NEW waveforms. A subsidiary analysis of frontal sites, investigating the three-way interaction in the Main ANOVA, revealed a main effect of response category [$F(1,17) = 8.56, p < 0.01$]. This result reflected a robust early mid-frontal effect (Figure 28, A, p250). The slight right-sided asymmetry of this modulation was confirmed by subsidiary analyses investigating interactions in the Prefrontal ANOVA [main effect of response category – right prefrontal, $F(17) = 4.57, p < 0.05$].

Table 15. Results of the magnitude analyses in the young group for the critical ERP comparisons for item and associative recognition.

Latency Region	TASK	
	Item Recognition (OLD vs. NEW)	Associative Recognition (SAME vs. REARRANGED)
200-400ms RC RCxHxL RCxS <i>Additional analyses</i> RC(c) RC(m) RCxH(pf) RCxHxS(pf)	F(1,17)=8.37,p=0.01 F(1,17)=7.95,p<0.05 F(1.2,20.9)=7.38,p<0.01 F(1,17)=7.56,p<0.05 F(1,17)=7.79,p<0.05 F(1,17)=5.97,p<0.05 F(2.0,33.8)=3.87,p<0.05	No significant results
400-800ms RC RCxHxL RCxS RCxLxS <i>Additional analyses</i> RC(c) RCxH(c) RCxS(c) RC(m)	F(1,17)=19.97,p<0.001 F(1,17)=5.11,p<0.05 F(1.2,21.1)=7.29,p=0.01 F(1.7,28.7)=6.67,p<0.01 F(1,17)=14.23,p<0.01 F(1,17)=4.47,p=0.05 F(1,17)=14.87,p=0.001	F(1,17)=13.17,p<0.01 F(1.2,21.1)=13.89,p=0.001 F(1,17)=8.58,p<0.01 F(1,17)=8.25,p<0.05 F(1.2,19.9)=12.85,p=0.001 F(1,17)=15.73,p=0.001
800-1200ms RC RCxL RCxS RCxLxS <i>Additional analyses</i> RC(c) RCxS(c) RC(m) RCxL(m) RC(pf)	F(1,17)=8.70,p<0.01 F(1,17)=6.34,p<0.05 F(1.5,25.6)=9.66,p<0.01 F(1,17)=4.65,p<0.05 F(1.8,30.6)=6.30,p<0.01 F(1,17)=6.12,p<0.05	F(1,17)=19.20,p<0.001 F(1,17)=4.64,p<0.05 F(1.3,22.3)=18.01,p<0.001 F(1.7,28.4)=5.51,p<0.05 F(1,17)=20.01,p<0.001 F(1.2,21.0)=27.76,p<0.001 F(1,17)=23.09,p<0.001
1200-1900ms RC RCxH RCxL RCxHxL RCxS RCxLxS <i>Additional analyses</i> RC(c) RCxS(c) RC(m) RCxL(m)	 F(1,17)=8.68,p<0.01 F(1.7,28.7)=5.24,p<0.05	F(1,17)=9.22,p<0.01 F(1,17)=8.55,p<0.01 F(1,17)=9.36,p<0.01 F(1.2,20.1)=9.46,p=0.01 F(1,17)=13.41,p<0.01 F(1.2,20.1)=18.88,p<0.001 F(1,17)=16.44,p=0.001 F(2.0,34.1)=3.21,p=0.053

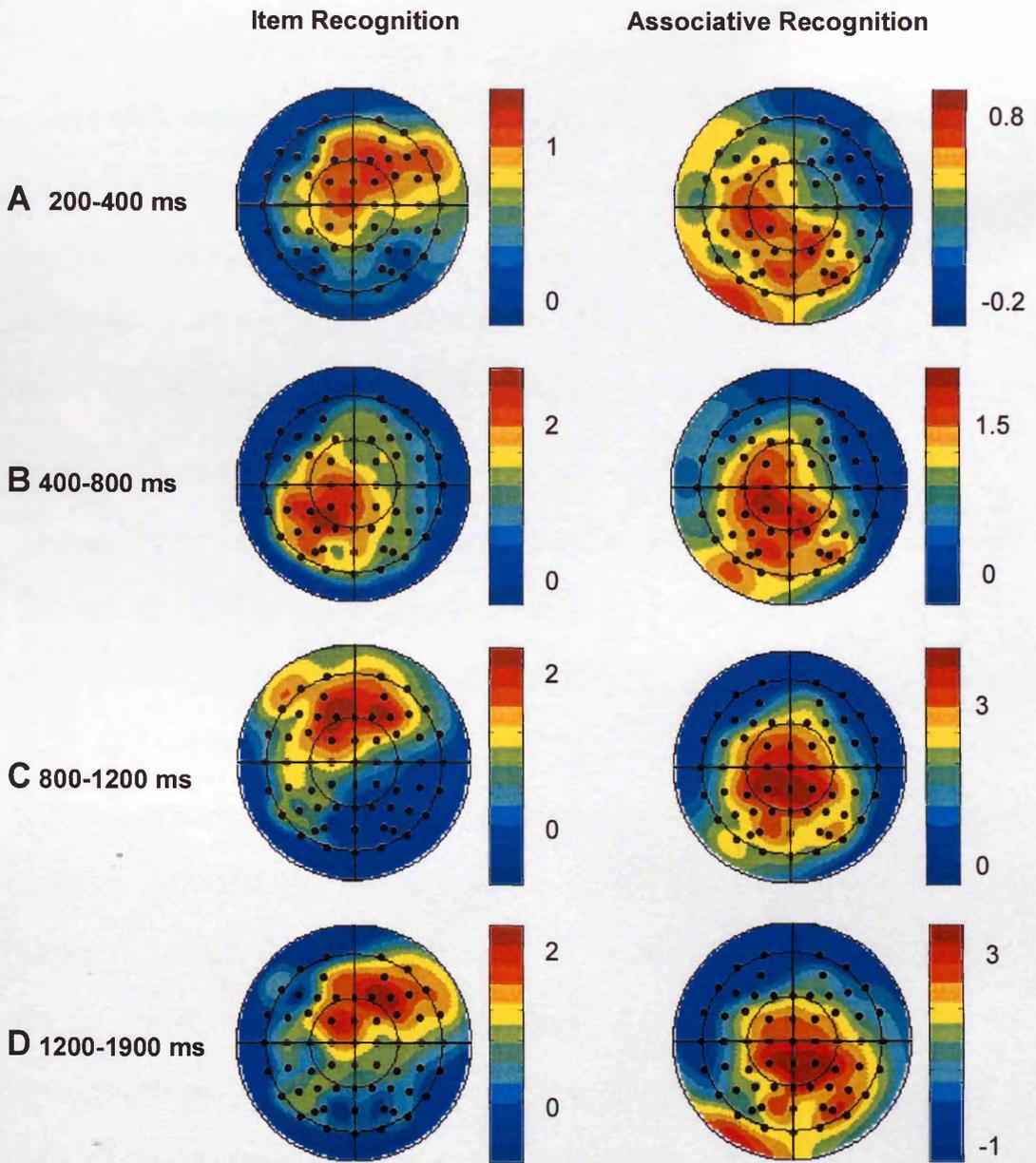


Figure 28. Topographic maps illustrating the scalp distribution of ERP effects for the young group in Experiment 3. Panel A illustrates the 200-400 ms latency region; B – 400-800 ms; C – 800-1200 ms; and D – 1200-1900 ms. The maps are shown as in Figure 12.

Between 400 and 800 ms, main effects of response category in the Main, Central and Midline ANOVAs demonstrated continued widespread, positive-going old/new differences. Subsidiary analyses following the three-way interactions in the Main ANOVA confirmed the persistence of the frontal

activation [main effect of response category – $F(1,17) = 7.90, p < 0.05$; response category by site interaction – $F(1.3,22.9) = 12.66, p = 0.001$], and the presence of a left parietal effect [parietal sites – response category by hemisphere interaction $F(1,17) = 7.91, p < 0.05$]. The response category by hemisphere interaction in the Central ANOVA indicated that the left parietal effect also extended to the central location (Figure 28, B).

By 800-1200 ms, the left parietal effect was in decline, and the interactions in the Midline and Main ANOVAs reflected bilateral frontal activity (Figure 28, C) that visually appeared distinct from the earlier mid-frontal effect (Figure 24). Subsidiary analyses investigating the three-way interaction in the Main ANOVA revealed a main effect of response category [$F(1,17) = 15.64, p = 0.001$] and a response category by site interaction [$F(1.5,25.6) = 11.12, p = 0.001$]. From 1200 ms onwards, the presence of a significant late right frontal effect (Figure 28, D) was confirmed by the subsidiary analysis of the right frontal hemisphere [$t(17) = 3.54, p < 0.01$] investigating the response category, hemisphere and location interaction in the Main ANOVA. The subsidiary frontal ANOVA that followed the interaction involving response category, location and site also corroborated the robustness of anterior old/new differences [main effect of response category – $F(1,17) = 5.70, p < 0.05$; response category by site interaction – $F(1.4,23.3) = 6.86, p < 0.01$].

Associative recognition

The earliest robust same/rearranged differences were observed at around 410 ms over left centro-parietal (CP3) and midline parietal (Pz) electrodes. Main effects of response category in the Main, Central and Midline

400-800 ms ANOVAs (Table 15) indicated that same/rearranged differences were widespread during this latency region. Targeted t-tests of the parietal location confirmed the presence of robust modulations over both left [$t(17) = 4.03, p < 0.01$] and right [$t(17) = 3.18, p = 0.01$] parietal hemispheres. However, a response category by hemisphere interaction in the Central ANOVA demonstrated the left-sided asymmetry of this centro-parietal effect (Figure 28, B).

During the 800-1200 ms latency period, although the same/rearranged differences were widespread, visually they appeared focused over central and posterior sites (Figure 28, C). The bilateral distribution of these effects was confirmed by interactions involving response category and site in the Central ANOVA, and in the subsidiary analyses investigating the three-way interaction in the Main ANOVA [frontal – $F(1.4,24.0) = 21.61, p < 0.001$; parietal – $F(1.4,24.4) = 4.56, p < 0.05$]. These results reflected the increased positivity towards superior sites.

By 1200-1900 ms, the global right-sided asymmetry of the ERP effects was confirmed by the post hoc t-test of the right hemisphere [$t(17) = 3.90, p < 0.01$] investigating the response category by hemisphere interaction in the Main ANOVA. However, the marginal response category by location interaction in the Midline ANOVA demonstrated the continued focus of the same/rearranged differences over central and posterior sites [Cz – $t(17) = 3.34, p < 0.01$; Pz – $t(17) = 4.30, p < 0.001$; Oz – $t(17) = 4.79, p < 0.001$] (Figure 28, D), and a targeted t-test revealed that the late right frontal effect was not robust [$t(17) = 1.69, p > 0.2$]. Finally, the lack of significant results in the Prefrontal ANOVA

indicated that the late left-sided, negative-going modulation was not statistically reliable on this occasion.

Topographic analyses

For item recognition, as ERP effects were found in all four latency regions, three sets of topographic analyses were conducted (200-400 ms vs. 400-800 ms, 400-800 ms vs. 800-1200 ms and 800-1200 ms vs. 1200-1900 ms). In associative recognition, as robust ERP effects onset at around 400 ms, only two sets of topographic comparisons were performed (400-800 ms vs. 800-1200 ms and 800-1200 ms vs. 1200-1900 ms).

Item recognition

In the 200-400 ms vs. 400-800 ms comparison, epoch by hemisphere interactions in the Main [$F(1,17) = 7.36, p < 0.05$] and Prefrontal [$F(1,17) = 5.59, p < 0.05$] ANOVAs, and epoch by location [$F(1,17) = 7.28, p < 0.05$], and epoch by hemisphere by site [$F(1.5,25.1) = 3.90, p < 0.05$] interactions in the Main ANOVA confirmed the progression from the early mid-frontal effect in the first time window to a left parietal effect in the second time window (Figure 28, A and B). The following (400-800 ms vs. 800-1200 ms) comparison produced interactions involving epoch and location [$F(1,17) = 22.20, p < 0.001$], and epoch and site [$F(1.2,21.2) = 8.16, p < 0.01$] in the Main ANOVA, epoch and location [$F(1.5,24.7) = 13.11, p < 0.001$] in the Midline ANOVA, and epoch, hemisphere and site [$F(1.3,21.5) = 4.71, p < 0.05$] in the Prefrontal ANOVA. These results demonstrated the transition to a bilaterally-onsetting frontal component in the later latency region. Finally, the 800-1200 ms vs. 1200-1900 ms comparison gave rise to epoch by hemisphere interactions in the Main

[$F(1,17) = 6.30, p < 0.05$] and Prefrontal [$F(1,17) = 23.39, p < 0.001$] ANOVAs, and an epoch by hemisphere by site interaction in the Central ANOVA [$F(2.0,33.3) = 4.38, p < 0.05$]. These results reflected the right-sided asymmetry of frontal activity from 1200 ms.

Associative recognition

The absence of significant results in the 400-800 ms vs. 800-1200 ms ANOVAs indicated that the ERP effects elicited during these periods were qualitatively similar. The 800-1200 ms vs. 1200-1900 ms comparison produced interactions involving epoch and hemisphere [$F(1,17) = 7.59, p < 0.05$], epoch, hemisphere and site [$F(1.6,26.4) = 4.28, p < 0.05$], and epoch, location and site [$F(1.2,20.9) = 4.35, p < 0.05$] in the Main ANOVA, and epoch, hemisphere and site [$F(2.0,33.7) = 10.78, p < 0.001$] in the Central ANOVA. These findings confirmed the increasingly right-sided distribution from 1200 ms onwards.

Summary of the ERP effects elicited by item and associative recognition in young adults

The ERP components elicited by item recognition in Experiment 3 more closely resemble those in Experiment 1, than those in Experiment 2: an early mid-frontal effect was present during the first two latency periods, whilst the left parietal effect was robust between 400 and 800 ms. Moreover, a reliable late right frontal effect was evident from 1200 ms. The predominant feature in associative recognition was once again a central/parietal positivity, which was initially left-sided, but adopted a right-sided distribution from 1200 ms onwards. Unlike Experiment 2 (but similar to Experiment 1), associative recognition failed to produce early mid-frontal and late left prefrontal negative-going effects.

Finally, in contrast to both previous experiments, the right frontal index of post-retrieval processing was not robust.

Item vs. associative recognition - young

Magnitude analyses comparing the ERP effects elicited by item and associative recognition in young adults were conducted over all four latency regions. However, as associative recognition failed to elicit any robust effects between 200 and 400 ms, no between-task topographic analyses were conducted for this time period.

The presence of an early mid-frontal effect only in item recognition was confirmed by the investigation of the task, hemisphere and location interaction in the Main 200-400 ms magnitude ANOVA (Table 16, below). These subsidiary analyses indicated that early frontal between-task differences were robust, but only over the right hemisphere [$t(17) = 2.63, p < 0.05$]. The right-sided asymmetry of old/new differences during this latency period was confirmed by the subsidiary ANOVAs following the task, hemisphere and site interaction in the Main magnitude ANOVA. Here, the right hemisphere gave rise to a main effect of task [$F(1, 17) = 5.55, p < 0.05$], while the left hemisphere produced a task by site interaction [$F(1.2, 21.1) = 4.77, p < 0.05$]. The investigation of the three-way interaction in the Prefrontal magnitude ANOVA did not produce any significant results.

The magnitude of left parietal effects appeared equivalent in item and associative recognition. Subsidiary analyses investigating the three-way interaction in the Main 400-800 ms magnitude ANOVA were non-significant (all

p values > 0.1). The three-way interaction in the topographic ANOVA most likely reflected the more bilateral parietal activity in associative recognition.

Between 800 and 1200 ms, the main effect of task in the Prefrontal magnitude ANOVA and two-way interactions in the Main, Central and Midline magnitude ANOVAs reflected increased bilateral prefrontal activation in item recognition and increased bilateral central/posterior activation in associative recognition. Post hoc t -tests confirmed that between-task differences were robust over parietal sites [$t(17) = 3.07$, $p < 0.05$], and over mid [$t(17) = 2.95$, $p < 0.05$] and superior [$t(17) = 3.01$, $p < 0.05$] central sites. Task by location interactions in the Main and Midline topographic ANOVAs verified the distributional differences between the effects elicited by item and associative recognition.

The anterior/posterior distinction between the neural correlates of item and associative recognition persisted throughout the 1200-1900 ms latency period. Although there were no reliable between-task differences in the magnitude of the right frontal effect, the main effect of task in the Prefrontal magnitude ANOVA indicated the more positive-going prefrontal activation in item recognition. Moreover, the presence of a right posterior component only in associative recognition was confirmed by the post hoc t -test of right parietal sites [$t(17) = 3.07$, $p < 0.05$] conducted to investigate the three-way interaction in the Main magnitude ANOVA, and by the task, hemisphere and location interaction in the Main topographic ANOVA.

Table 16. Results of the between-task magnitude and topographic comparisons in the young group.

Latency Region	Magnitude	Topographic
200-400ms TxHxL TxHxS <i>Additional analyses</i> TxH(pf) TxHxS(pf)	$F(1,17)=10.78,p<0.01$ $F(1.5,25.5)=4.03,p<0.05$ $F(1,17)=10.20,p<0.01$ $F(1.9,32.5)=3.96,p<0.05$	Not performed
400-800ms TxHxL	$F(1,17)=6.22,p<0.05$	$F(1,17)=6.12,p<0.05$
800-1200ms TxL <i>Additional analyses</i> T(c) TxS(c) T(m) TxL(m) T(pf)	$F(1,17)=13.85,p<0.01$ $F(1,17)=7.82,p<0.05$ $F(1.1,18.9)=5.10,p<0.05$ $F(1,17)=7.66,p<0.05$ $F(2.0,33.8)=5.89,p<0.01$ $F(1,17)=5.03,p<0.05$	$F(1,17)=13.33,p<0.01$ $F(2.0,33.5)=6.45,p<0.01$
1200-1900ms TxL TxHxL <i>Additional analyses</i> TxS(c) TxL(m) T(pf)	$F(1,17)=8.41,p=0.01$ $F(1,17)=27.35,p<0.001$ $F(1.1,19.6)=5.92,p<0.05$ $F(2.1,35.6)=4.62,p<0.05$ $F(1,17)=9.27,p<0.01$	$F(1,17)=5.00,p<0.05$ $F(1,17)=22.62,p=0.001$ $F(2.1,35.1)=3.76,p<0.05$

Summary of ERP differences between item and associative recognition in young adults

Despite the disparity in the electrophysiological data between the blocked and randomized (task switching) versions of the experiment, the findings of the current between-task comparison were highly similar to those reported in the previous experimental chapters. Although both tasks exhibited left parietal effects of similar magnitude, the associative modulation had a longer duration than its item counterpart and appeared in conjunction with robust right-sided parietal activation. In later time windows, the distribution of

right-sided positive-going components appeared more central and posterior in associative recognition than in item recognition, but nevertheless there was no significant between-task difference in the magnitude of late right frontal activation. The main discrepancies between the blocked and randomized versions relate to the presence of the early mid-frontal effect in item recognition, but not in associative recognition, and the lack of robust late left prefrontal activation in associative recognition. However, although these findings were inconsistent with Experiment 2, they are comparable with the results of Experiment 1.

Older group

Item recognition

The earliest robust old/new differences were observed at around 500 ms over left frontal (F5) and right temporo-parietal (TP8) electrodes. Accordingly, the response category by hemisphere by location interaction in the Main 500-900 ms ANOVA, and the response category by hemisphere interaction in the corresponding Prefrontal ANOVA (Table 17, below) reflected the presence of a left frontal negativity (Figure 29, B, p 261). Subsidiary analyses confirmed that the modulation was robust [left frontal – $t(17) = 3.66$, $p < 0.01$; left prefrontal – $t(17) = 2.74$, $p < 0.05$]. Over the right hemisphere, meanwhile, a response category by site interaction [$F(1.4, 23.1) = 5.49$, $p < 0.05$] in the subsidiary analysis investigating the interaction involving response category, hemisphere and site in the Main ANOVA, demonstrated that right-sided positive old/new differences were greatest over inferior sites.

The persistence of the left frontal negativity during the 900-1200 ms latency region, and its spread to central sites (Figure 29, C), was confirmed by interactions involving response category, hemisphere and location (Main ANOVA), and response category and hemisphere (Prefrontal and Central ANOVAs). Subsidiary analyses confirmed that the modulation was robust over left frontal [$t(17) = 2.55, p < 0.05$] and left central [$t(17) = 2.65, p < 0.05$] sites, but not over the left prefrontal [$t(17) = 2.03, n.s.$] hemisphere. Investigations of the remaining three-way interactions in the Main ANOVA produced a main effect of response category [$F(1, 17) = 4.82, p < 0.05$] over the left hemisphere, and response category by site interactions over the right hemisphere [$F(1.7, 28.2) = 3.76, p < 0.05$] and over the parietal location [$F(1.4, 23.2) = 4.03, p < 0.05$]. These results confirm the robustness of the left-sided negativity in this latency period, and also demonstrate the presence of a non-robust, lateralised right-sided positivity.

The principle old/new difference between 1200 and 1900 ms was the presence of a robust right-sided positivity (Figure 29, D). Subsidiary analyses investigating the three-way interactions in the Main ANOVA revealed a main effect of response category [$F(1, 17) = 5.04, p < 0.05$] over the right hemisphere and a response category by site interaction [$F(1.8, 29.9) = 4.41, p < 0.05$] over the frontal location. Nevertheless, although targeted t-tests revealed that significant voltage differences were present over right parietal sites [$t(17) = 2.75, p < 0.05$], the late right frontal effect was not reliable [$t(17) = 1.60, p > 0.1, n.s.$].

Table 17. Results of the magnitude analyses in the older group for the critical ERP comparisons for item and associative recognition.

Latency Region	TASK	
	Item Recognition (OLD vs. NEW)	Associative Recognition (SAME vs. REARRANGED)
300-500ms <i>Additional analyses</i> RCxHxS(c) RC(pf) RCxH(pf)	No significant results	$F(1, 7, 29.7)=8.27, p<0.01$ $F(1, 17)=6.23, p<0.05$ $F(1, 17)=5.57, p<0.05$
500-900ms RCxH RCxHxL RCxHxS <i>Additional analyses</i> RCxH(c) RCxHxS(c) RC(pf) RCxH(pf)	$F(1, 17)=8.88, p<0.01$ $F(1, 17)=44.31, p<0.001$ $F(1.4, 23.1)=4.12, p<0.05$ $F(1, 17)=6.37, p<0.05$ $F(1, 17)=14.76, p=0.001$	$F(1, 17)=11.10, p<0.01$ $F(1, 17)=8.64, p<0.01$ $F(1.4, 23.4)=4.76, p<0.05$ $F(1, 17)=6.54, p<0.05$ $F(2.0, 33.7)=6.14, p<0.01$ $F(1, 17)=6.34, p<0.05$ $F(1, 17)=11.34, p<0.01$
900-1200ms RCxH RCxHxL RCxHxS RCxLxS <i>Additional analyses</i> RCxH(c) RCxS(c) RCxHxS(c) RCxH(pf)	$F(1, 17)=11.07, p<0.01$ $F(1, 17)=13.95, p<0.01$ $F(1.6, 27.5)=6.06, p=0.01$ $F(1.5, 26.3)=5.29, p<0.05$ $F(1, 17)=4.18, p=0.057$ $F(1, 17)=12.14, p<0.01$	$F(1, 17)=26.29, p<0.001$ $F(1, 17)=14.99, p=0.001$ $F(1.7, 28.5)=8.23, p<0.01$ $F(1, 17)=11.94, p<0.01$ $F(1.3, 21.9)=7.65, p<0.01$ $F(1.7, 28.6)=5.42, p<0.05$ $F(1, 17)=19.79, p<0.001$
1200-1900ms RCxH RCxHxL RCxHxS <i>Additional analyses</i> RCxH(c) RCxS(c) RCxH(pf)	$F(1, 17)=7.25, p<0.05$ $F(1, 17)=5.24, p<0.05$ $F(1.8, 31.0)=5.65, p<0.01$ $F(1, 17)=7.12, p<0.05$	$F(1, 17)=25.95, p<0.001$ $F(1, 17)=18.75, p<0.001$ $F(1.8, 30.3)=7.08, p<0.01$ $F(1, 17)=6.82, p<0.05$ $F(1.3, 22.6)=7.51, p<0.01$ $F(1, 17)=21.14, p=0.001$

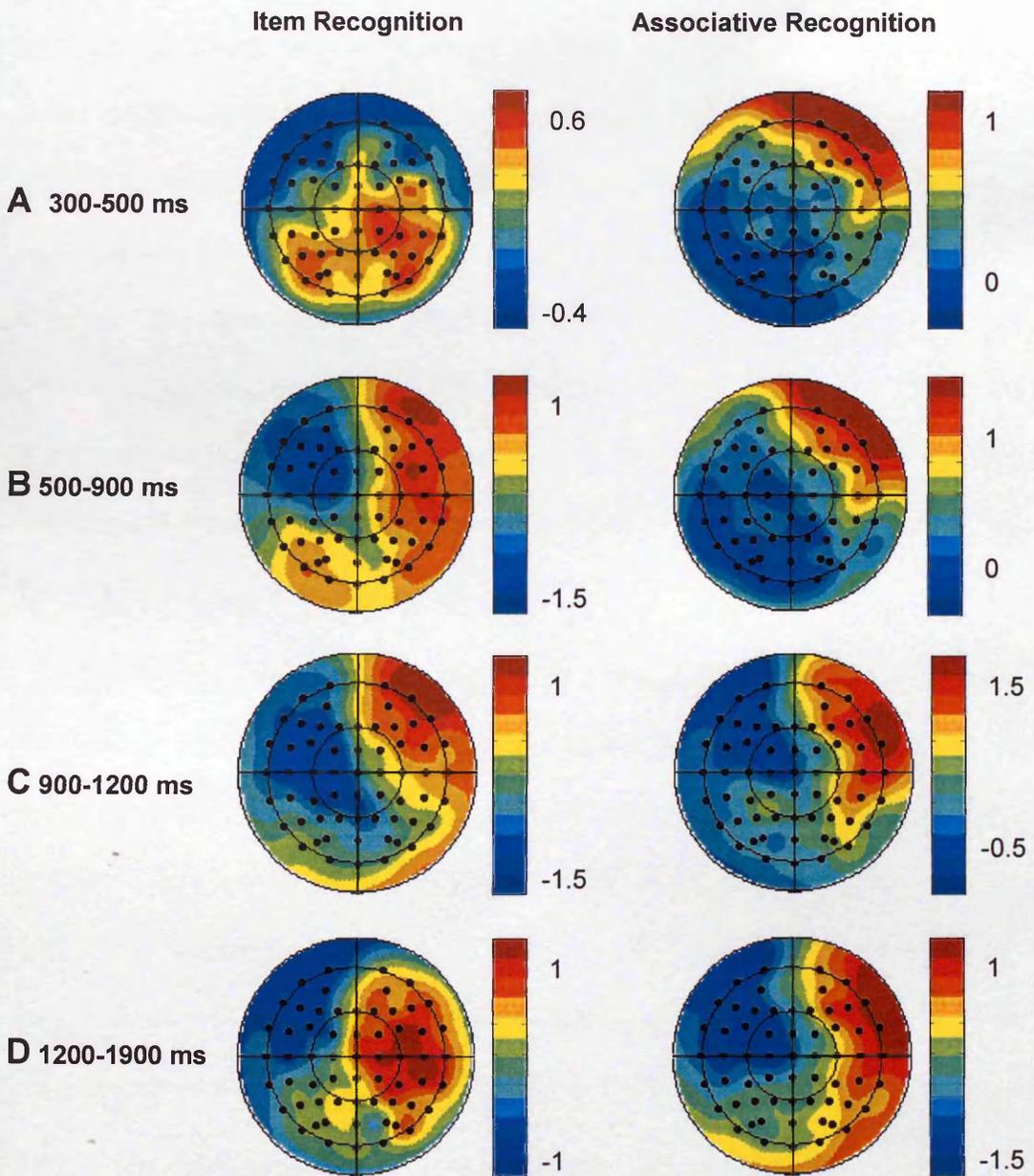


Figure 29. Topographic maps illustrating the scalp distribution of ERP effects for the older group in Experiment 3. Panel A illustrates the 300-500 ms latency region; B – 500-900 ms; C – 900-1200 ms; and D – 1200-1900 ms. The maps are shown as in Figure 12.

Associative recognition

The earliest same/rearranged differences were apparent at around 130 ms over the right frontal electrode FT8. However, although an additional 100-300 ms latency region was subjected to the same analyses as the other time

periods, no robust early ERP effects were revealed. Between 300-500 ms, however, the response category by hemisphere interaction in the Prefrontal ANOVA (Table 17) reflected a right prefrontal positive-going effect (Figure 29, A). Post hoc t-tests confirmed that same/rearranged differences were robust only over the right prefrontal hemisphere [$t(17) = 3.24, p = 0.01$]. Over right central sites, meanwhile, a response category by site interaction [$F(1.4,24.6) = 8.81, p < 0.01$] was revealed in the investigation of the three-way interaction in the Central ANOVA. This result confirmed the lateralised distribution of the early right-sided positivity.

The persistence of this modulation into the following latency period (Figure 29, B) was confirmed by subsidiary analyses exploring the interactions in the Prefrontal and Main 500-900 ms ANOVAs [right prefrontal – $t(17) = 3.76, p < 0.01$; right frontal – $t(17) = 2.69, p < 0.05$]. Moreover, a response category by site interaction [$F(1.5,25.4) = 8.07, p < 0.01$] in the analysis of the right hemisphere that followed the three-way interaction in the Central ANOVA demonstrated that the modulation once again extended to the central location.

The pattern of effects observed during the 900-1200 ms latency period was similar (Figure 29, C). Subsidiary analyses investigating two- and three-way interactions in the Main, Prefrontal and Central ANOVAs confirmed that the same/rearranged differences were robust over right prefrontal [$t(17) = 2.80, p < 0.05$] and right frontal [$t(17) = 2.51, p < 0.05$] sites. With response category by site interactions over the right hemisphere [frontal/parietal – $F(1.4,23.5) = 7.01, p < 0.01$; central – $F(1.7,28.6) = 5.42, p < 0.05$] again reflecting the lateralized distribution of the modulation.

From 1200 ms onwards, the right-sided positivity was in decline and the predominant ERP effect was a left fronto-central negativity that extended to prefrontal sites (Figure 29, D). Subsidiary analyses investigating interactions in the Main, Prefrontal and Central ANOVAs confirmed that these magnitude differences were robust [left frontal – $t(17) = 3.65$, $p < 0.01$; left prefrontal – $t(17) = 3.59$, $p < 0.01$; left central – $t(17) = 2.72$, $p < 0.05$].

Topographic analyses

As robust ERP effects were only found from 500 ms in item recognition, two sets of topographic analyses (500-900 ms vs. 900-1200 ms and 900-1200 ms vs. 1200-1900 ms) were performed. In associative recognition, robust modulations were found in all four latency regions, therefore three topographic comparisons (300-500 ms vs. 500-900 ms, 500-900 ms vs. 900-1200 ms and 900-1200 ms vs. 1200-1900 ms) were conducted.

Item recognition

The 500-900 ms vs. 900-1200 ms comparison revealed an epoch, location and site interaction [$F(1.3,21.7) = 4.20$, $p < 0.05$] in the Main ANOVA, and an epoch by location interaction [$F(2.0,33.6) = 3.59$, $p < 0.05$] in the Midline ANOVA. These results reflect the spread of the left-frontal negativity towards posterior sites in the later time window (Figure 29, B vs. C). The second (900-1200 ms vs. 1200-1900 ms) comparison produced epoch by location interactions in the Main [$F(1,17) = 10.18$, $p < 0.01$] and Midline [$F(1.9,32.8) = 4.03$, $p < 0.05$] ANOVAs, and epoch by site interactions in the Main [$F(1.3,22.9) = 4.82$, $p < 0.05$] and Central [$F(1.3,21.8) = 8.02$, $p < 0.01$] ANOVAs. These

results principally reflected the development of the right-sided central positivity from 1200 ms (Figure 29, D).

Associative recognition

The lack of any significant interactions in the first topographic comparison indicated that frontal positive-going effects in the 300-500 ms and 500-900 ms latency periods were qualitatively similar (Figure 29, A and B). The 500-900 ms vs. 900-1200 ms comparison produced epoch by location interactions in the Main $F(1,19) = 7.72, p < 0.05$ and Midline $[F(1.8,31.2) = 3.51, p < 0.05]$ ANOVAs, and an epoch by site interaction $[F(1.3,22.7) = 4.95, p < 0.05]$ in the Prefrontal ANOVA. These results principally reflect the more posterior distribution of the right-sided positivity between 900 and 1200 ms (Figure 29, C). The lack of robust topographic differences in the final (900-1200 ms vs. 1200-1900 ms) comparison suggests that the left fronto-central negativity, which was robust from 1200 ms, was onsetting in the previous time window (Figure 29, C and D).

Summary of the ERP effects elicited by item and associative recognition in older adults

Blocking the retrieval phase (and the concomitant performance improvement in associative recognition) did not produce an increase in the magnitude of left parietal activation in either task. However, associative recognition (but not item recognition) did elicit an early (from 300 ms) frontal positive-going modulation, which exhibited a right-sided asymmetry and extended to central sites as the epoch progressed. However, the late left fronto-central negativity was only robust from 1200 ms (c.f. from 900 ms in Experiment

2). Finally, in item recognition, the early left fronto-central negativity appeared to last longer in the blocked version (500-1200 ms c.f. 500-900 ms in Experiment 2), and to adopt a more posterior distribution in the later (900-1200 ms) time window.

Item vs. associative recognition - older

Magnitude analyses comparing the ERP effects elicited by item and associative recognition in older adults were performed for all four time windows. However, as item recognition failed to elicit any robust ERP effects between 300 and 500 ms, between-task topographic analyses were not conducted for this latency region.

Table 18. Results of the between-task magnitude and topographic comparisons in the older group.

Latency Region	Magnitude	Topographic
300-500ms Additional analyses <i>TxHxS(c)</i> <i>T(pf)</i>	$F(1.9, 31.9) = 3.87, p < 0.05$ $F(1, 17) = 6.22, p < 0.05$	Not performed
500-900ms <i>TxL</i> <i>TxHxL</i> Additional analyses <i>TxHxS(c)</i>	$F(1, 17) = 5.47, p < 0.05$ $F(1, 17) = 12.96, p < 0.01$ $F(1.9, 31.7) = 3.41, p < 0.05$	$F(1, 17) = 4.09, p < 0.059$ $F(1, 17) = 4.34, p = 0.053$ $F(1.9, 32.6) = 4.75, p < 0.05$
900-1200ms	No significant results	No significant results
1200-1900ms Additional analyses <i>T(c)</i> <i>TxS(c)</i> <i>T(m)</i>	$F(1, 17) = 5.66, p < 0.05$ $F(1.4, 24.0) = 7.09, p < 0.01$ $F(1, 17) = 6.06, p < 0.05$	$F(1.4, 24.3) = 6.70, p < 0.01$

The presence of an early right frontal positivity only in associative recognition was reflected by the main effect of task in the 300-500 ms

magnitude Prefrontal ANOVA (Table 18), with targeted t-tests confirming that the between-task difference was only robust over right prefrontal sites [$t(17) = 2.50, p < 0.05$]. Moreover, a task by response category interaction [$F(1.2,21.1) 4.69, p < 0.05$] in the subsidiary analysis of the right central hemisphere investigating the three-way interaction in the Central ANOVA indicated that the between-task differences were maximal over inferior sites.

Between 500 and 900 ms, the left frontal negativity elicited by item recognition was absent from associative recognition. Subsidiary analyses investigating three-way interactions in the Main and Central magnitude ANOVAs demonstrated that between-task differences were significant over left frontal [$t(17) = 2.88, p < 0.05$] and left central [main effect of task, $F(1,17) = 4.73, p < 0.05$] sites. Despite the presence of an early right frontal effect only in associative recognition, between-task differences were not robust over these electrodes. The different distributions of the effects elicited by item and associative recognition were confirmed by interactions in the 500-900 ms topographic analyses (Table 18).

In the 900-1200 ms time window, the effects elicited by item and associative recognition were quantitatively and qualitatively similar. However, from 1200 ms, the presence of the left fronto-central negativity in only associative recognition was demonstrated by the main effect of response category and two-way interaction in the Central magnitude ANOVA. Targeted t-tests confirmed that between-task differences were robust over the left central hemisphere [$t(17) = 2.40, p = 0.056$]. Finally, a task by site interaction in the Central topographic ANOVA confirmed that the distributions of the effects elicited by item and associative recognition were distinct.

Summary of ERP differences between item and associative recognition in older adults

The main between-task differences reported in Experiment 2 are replicated here; an early left fronto-central negativity was present in item recognition and a similar effect onset later in associative recognition. However, an additional ERP effect was evident in the current blocked experiment: specifically, an early right frontal positive-going effect elicited only by the associative task had not been apparent in the randomized version.

Comparing young and older groups

Four sets of between-group magnitude comparisons were performed: 200-400 ms (young) vs. 300-500 ms (older); 400-800 ms (young) vs. 500-900 ms (older); 800-1200 ms (young) vs. 900-1200 ms (older); 1200-1900 (young vs. older). The lack of robust ERP effects in the earliest latency period, in associative recognition in the young group and in item recognition in the older group, meant that topographic comparisons were restricted to the three later time windows.

Item recognition

The early mid-frontal effect was only present in young adults (Figure 30, A, p273). A subsidiary ANOVA of frontal sites investigating the three-way interaction in the Main 200-400/300-500 ms magnitude ANOVA (Table 19, p270) produced a main effect of age [$F(1,34) = 7.41, p = 0.01$]. Meanwhile, age-related differences in left fronto-central (Figure 30, B) and left parietal effects (Figure 30, C), suggested by age by hemisphere interactions in the Main and

Central 400-800/500-900 ms magnitude ANOVAs, were substantiated by post hoc and targeted t-tests [left frontal – $t(34) = 4.11$, $p < 0.001$; left central – $t(34) = 4.48$, $p < 0.001$; left parietal – $t(34) = 4.22$, $p < 0.001$]. Further confirmation that the young adults' left parietal effect was qualitatively different from the older adults' left fronto-central negativity was provided by age by hemisphere interactions in the Main and Central 400-800/500-900 ms topographic analyses (Table 20, p271).

A similar pattern of ageing differences was observed in the third time window. Here, however, age by hemisphere interactions in the Main and Central magnitude and topographic ANOVAs principally reflected the continuing presence of the left-sided negativity in the older adults. This interpretation was confirmed by post hoc and targeted t-tests of left frontal [$t(34) = 3.99$, $p < 0.001$] and left central [$t(34) = 3.71$, $p < 0.01$] hemispheres. Finally, the lack of significant findings in the 1200-1900 ms magnitude and topographic comparisons indicate that the magnitude and distributions of the young group's late right frontal effect and the older group's more posterior activation were equivalent.

Associative recognition

The earliest ageing ERP difference in associative recognition was the presence of a robust right frontal positivity only in older adults between 300 and 500 ms (Figure 31, A, p273). This observation was confirmed by the results of the subsidiary analyses investigating the two- and three-way interactions in the Prefrontal, Main and Central 200-400/300-500 ms magnitude ANOVAs (Table 19): First, the post hoc t-test of right prefrontal sites was significant [$t(34) =$

2.36, $p < 0.05$]. Second, an age by hemisphere interaction [$F(1,34) = 10.85$, $p < 0.01$] was revealed over the frontal location. And finally, age by site interactions were found over the right hemisphere [frontal/parietal – $F(1.4,46.7) = 6.46$, $p < 0.01$]; central – $F(1.3,45.4) = 7.19$, $p < 0.01$].

In the 400-800/500-900 ms comparison, left parietal activation was only present in young adults (Figure 31, B). Subsidiary and targeted analyses following the three-way interactions in the Main and Central magnitude ANOVAs revealed robust ageing differences over left parietal [$t(34) = 2.99$, $p = 0.01$] and left central [main effect of age – $F(1,17) = 7.76$, $p < 0.01$] sites, and age by site interactions over the right hemisphere [frontal/parietal – $F(1.4,47.5) = 13.98$, $p < 0.001$; central – $F(1.4,47.2) = 22.08$, $p < 0.001$]. Moreover, the persistence of the age-related increase in right prefrontal activation was confirmed by a post hoc t-test [$t(34) = 3.61$, $p < 0.01$] investigating the age by hemisphere interaction in the Prefrontal magnitude ANOVA. Qualitative differences between these components in young and older adults were confirmed by interactions in the Main, Central and Prefrontal topographic 400-800/500-900 ms ANOVAs (Table 20).

Table 19. Results of the magnitude age comparison for item and associative recognition.

Latency Region	TASK	
	Item Recognition	Associative Recognition
200-400/300-500ms AxHxL AxHxS <i>Additional analyses</i> <i>AxH(c)</i> <i>AxHxS(c)</i> <i>AxH(pf)</i>	$F(1,34)=5.27, p<0.05$	$F(1,34)=5.71, p<0.05$ $F(1.5,50.6)=4.18, p<0.05$ $F(1,34)=5.89, p<0.05$ $F(1.9,63.6)=6.56, p<0.01$ $F(1,34)=9.37, p<0.01$
400-800/500-900ms A AxH AxL AxHxL AxS AxHxS <i>Additional analyses</i> <i>A(c)</i> <i>AxH(c)</i> <i>AxS(c)</i> <i>AxHxS(c)</i> <i>A(m)</i> <i>A(pf)</i> <i>AxH(pf)</i>	$F(1,34)=14.26, p=0.001$ $F(1,34)=11.11, p<0.01$ $F(1.2,41.3)=9.33, p<0.01$ $F(1,34)=9.40, p<0.01$ $F(1,34)=10.39, p<0.01$ $F(1.2,39.5)=4.27, p<0.05$ $F(1,34)=11.89, p<0.01$ $F(1,34)=5.49, p<0.05$	$F(1,34)=9.90, p<0.01$ $F(1,34)=4.48, p<0.05$ $F(1,34)=8.14, p<0.01$ $F(1.2,41.2)=10.27, p<0.01$ $F(1.6,54.2)=5.27, p<0.05$ $F(1,34)=14.80, p=0.001$ $F(1.2,39.0)=15.16, p<0.001$ $F(1.9,65.5)=5.47, p<0.01$ $F(1,34)=6.94, p<0.05$ $F(1,34)=4.10, p=0.051$ $F(1,34)=14.11, p=0.001$
800-1200/900-1200ms A AxH AxHxL AxS AxHxS <i>Additional analyses</i> <i>A(c)</i> <i>AxH(c)</i> <i>AxS(c)</i> <i>A(m)</i> <i>AxH(pf)</i>	$F(1,34)=6.71, p<0.05$ $F(1,34)=10.87, p<0.01$ $F(1.4,46.3)=3.81, p<0.05$ $F(1,34)=4.36, p<0.05$ $F(1,34)=6.69, p<0.05$ $F(1,34)=8.33, p<0.01$	$F(1,34)=8.24, p<0.01$ $F(1,34)=7.25, p<0.05$ $F(1,34)=4.12, p=0.05$ $F(1.3,43.9)=17.14, p<0.001$ $F(1.7,56.5)=4.73, p<0.05$ $F(1,34)=10.96, p<0.001$ $F(1,34)=9.78, p<0.01$ $F(1.3,42.8)=33.75, p<0.001$ $F(1,34)=16.11, p<0.001$ $F(1,34)=11.08, p<0.01$
1200-1900ms A AxHxL AxS <i>Additional analyses</i> <i>A(c)</i> <i>AxS(c)</i> <i>A(m)</i> <i>AxL(m)</i> <i>AxH(pf)</i>	No significant results	$F(1,34)=9.09, p<0.01$ $F(1,34)=9.61, p<0.01$ $F(1.3,43.5)=10.00, p=0.001$ $F(1,34)=14.16, p=0.001$ $F(1.2,42.1)=26.09, p<0.001$ $F(1,34)=17.79, p<0.001$ $F(2.1,70.4)=3.52, p<0.05$ $F(1,34)=8.41, p<0.01$

Table 20. Results of the topographic age comparison for item and associative recognition.

Latency Region	TASK	
	Item Recognition	Associative Recognition
400-800/500-900ms		
AxH	$F(1,34)=10.67, p<0.01$	$F(1,34)=11.33, p<0.01$
AxL		$F(1,34)=4.64, p<0.05$
AxHxL		$F(1,34)=8.99, p<0.01$
AxS	$F(1.2,41.3)=10.07, p<0.01$	$F(1.2,40.9)=8.38, p<0.01$
AxHxS		$F(1.5,52.5)=5.80, p<0.01$
<i>Additional analyses</i>		
<i>AxH(c)</i>	$F(1,34)=9.30, p<0.01$	$F(1,34)=14.68, p=0.001$
<i>AxS(c)</i>	$F(1.2,39.7)=4.69, p<0.05$	$F(1.1,38.7)=13.82, p<0.001$
<i>AxHxS(c)</i>		$F(2.0,66.3)=6.07, p<0.01$
<i>AxH(pf)</i>	$F(1,34)=5.49, p<0.05$	$F(1,34)=14.54, p=0.001$
800-1200/900-1200ms		
AxH	$F(1,34)=11.55, p<0.01$	$F(1,34)=12.73, p=0.001$
AxHxL		$F(1,34)=7.39, p=0.01$
AxS		$F(1.3,43.3)=13.75, p<0.001$
AxHxS		$F(1.7,56.7)=6.49, p<0.01$
<i>Additional analyses</i>		
<i>AxH(c)</i>	$F(1,34)=6.87, p<0.05$	$F(1,34)=11.96, p=0.001$
<i>AxS(c)</i>		$F(1.3,43.1)=29.44, p<0.001$
<i>AxH(pf)</i>	$F(1,34)=7.92, p<0.01$	$F(1,34)=15.01, p<0.001$
1200-1900ms		
AxHxL		$F(1,34)=13.03, p=0.001$
AxS		$F(1.3,45.2)=8.65, p<0.01$
<i>Additional analyses</i>	No significant results	
<i>AxS(c)</i>		$F(1.2,43.0)=24.24, p<0.001$
<i>AxL(m)</i>		$F(2.1,70.9)=3.35, p<0.05$
<i>AxH(pf)</i>		$F(1,34)=12.15, p=0.001$

The continuing age-related decrease in parietal activation during the third time windows was confirmed by the subsidiary analysis of the parietal location [main effect of age – $F(1,34) = 10.41, p < 0.01$] that was conducted during the investigations of the two- and three-way interactions in the Main and Central magnitude ANOVAs. Moreover, significant results over the left hemisphere [left frontal – $t(34) = 2.72, p = 0.01$; left central – $t(34) = 4.60, p < 0.001$; left frontal/parietal – main effect of age, $F(1,34) = 13.36, p = 0.001$], in

addition to two- and three-way interactions in the Main and Central topographic ANOVAs, reflected the left asymmetry of the ageing differences. Moreover, the lack of robust age-related differences over right frontal and right prefrontal electrodes indicated that right frontal activation was equivalent in both age groups (Figure 31, C).

Finally, the 1200-1900 ms magnitude comparison demonstrated the presence of the left frontal negativity only in older adults (Figure 31, D). Subsidiary analyses investigating the three-way interaction in the Main magnitude ANOVA produced a marginally significant left frontal age difference [$t(34) = 2.27, p = 0.06$], and a main effect of age over the parietal location [$F(1,34) = 14.90, p < 0.001$]. This latter finding, in conjunction with the main effect of age in the Central magnitude ANOVA, reflects the widespread central/posterior positive modulation that was only present in the young adults (Figure 28, D). Interactions in the topographic analyses confirmed the age-related distributional differences between these late ERP effects. Finally, post hoc t-tests investigating the age by hemisphere interaction in the Prefrontal ANOVA failed to find any significant age differences over left prefrontal sites.

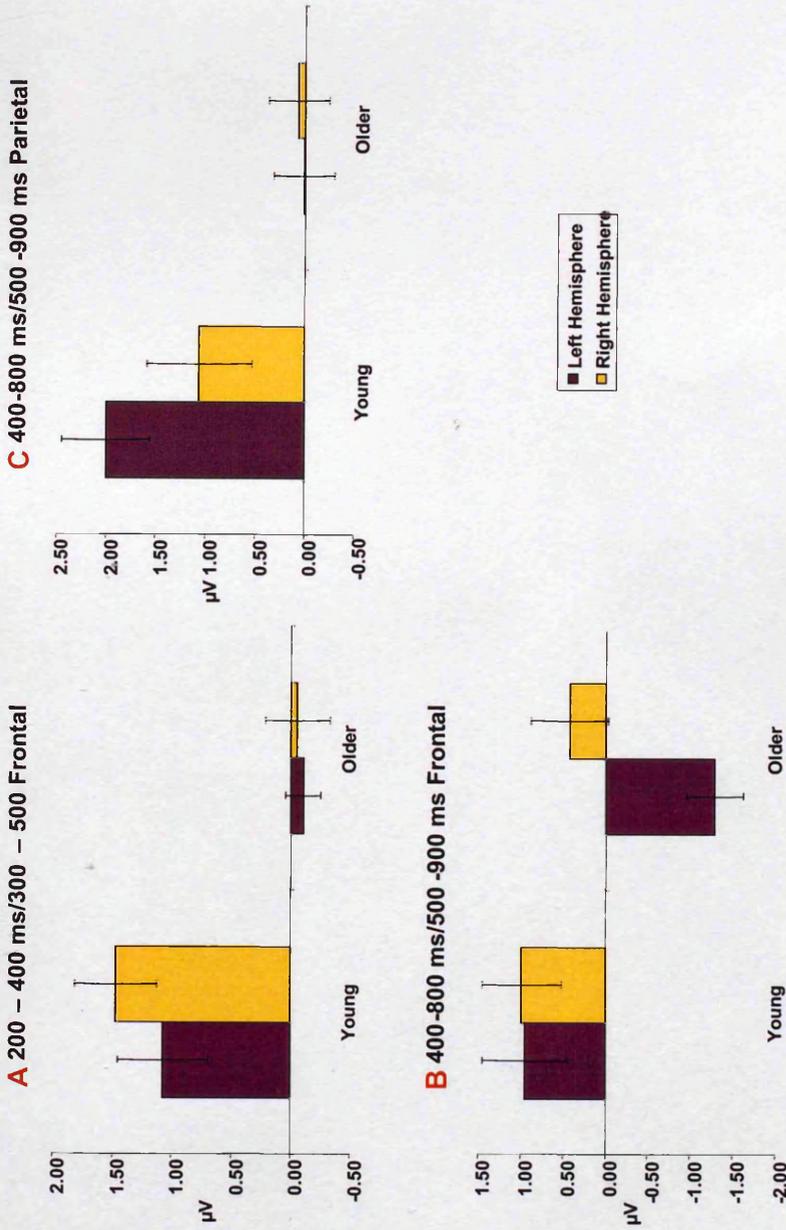


Figure 30. Mean amplitudes of selected item recognition ERP effects in the young and older groups in Experiment 3. The left hemisphere is collapsed across F1, F3 and F5 (frontal), P1, P3, and P5 (parietal); the right hemisphere is collapsed across F2, F4 and F6 (frontal), and P2, P4, and P6 (parietal).

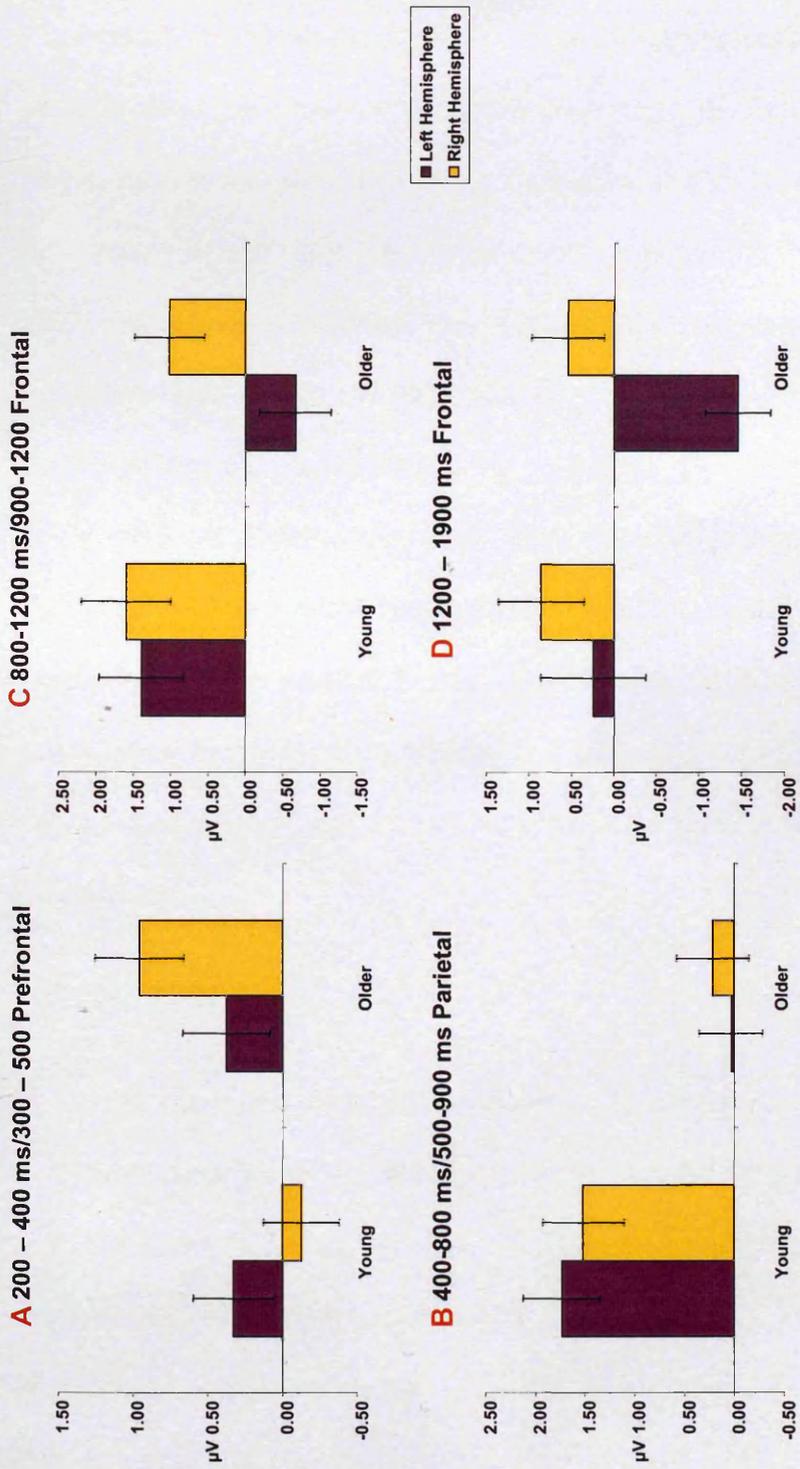


Figure 31. Mean amplitudes of selected associative recognition ERP effects in the young and older groups in Experiment 3. The left hemisphere is collapsed across F1, F3 and F5 (frontal), P1, P3, and P5 (parietal), and F7, AF7, and FP1 (prefrontal); the right hemisphere is collapsed across F2, F4 and F6 (frontal), P2, P4, and P6 (parietal), and F8, AF8, and FP2 (prefrontal).

Summary of ERP differences between young and older adults

The results of the current age comparison were highly similar to those in Experiment 2. In item recognition, the older participants failed to produce a left parietal effect, and instead demonstrated a negative modulation over left frontal and central electrodes. Moreover, as before, there were no robust ageing differences in late right-sided activations. In associative recognition, despite their improved performance, the older adults once again failed to demonstrate the left parietal or late central/posterior positive-going modulations that characterized the waveforms of the young adults. Instead, the elderly produced a late left fronto/central negativity. One important disparity in the ageing effects demonstrated by the current experiment and the randomized version was the appearance of an early right frontal component in older adults during associative recognition. Furthermore, unlike previously, there was no significant age-related reduction in the late right frontal activation elicited by associative recognition.

Discussion

As expected, the principle ageing differences in the ERP correlates of item and associative recognition reported in Experiment 2 remained when the retrieval tasks were blocked and the performance of the older adults increased. Specifically, the left parietal effect elicited by item recognition in young adults was absent from older adults, who instead showed an extended (500-1200 ms) left fronto-central negativity. In associative recognition, the left parietal and late central/posterior activity present in the young was again absent in the elderly, who exhibited a left fronto-central negativity (which this time onset later than in

Experiment 2). These age-related changes do not therefore appear to simply reflect an increase in subjective difficulty on the part of the older adults (Rugg & Morcom, 2004). However, the elderly participants in Experiment 3 also produced an additional component: an early right frontal positive-going same/rearranged difference that onset at about 300 ms post-stimulus over prefrontal sites.

Behavioural findings

As predicted, accuracy overall was increased when the retrieval tasks were blocked instead of randomly intermixed. However, as the performance enhancement was similar in both groups, behaviourally, the task-switch costs to older adults in the randomized version do not seem to have been disproportionate. Although this finding was not entirely in line with our expectation that the task-switch cost in Experiment 2 would be higher in the older group, previously task-switch costs in the elderly have been shown to reduce to the level of those in young adults with practice (Kramer et al., 1999, Experiment 1). The extensive pre-experimental training session undertaken by the older participants (see "General Methods" chapter), which gave them more opportunity to practice the task than the young adults, may explain this result.

In most respects, the pattern of behavioural ageing differences in the current experiment was very similar to that observed in Experiment 2. One noteworthy disparity was that the young adults appeared more confident than the older adults over associative correct rejections. According to dual process theory, this finding suggests that the elderly adults were more reliant on familiarity in associative recognition than young adults (c.f. Light et al., 2002).

However, as argued in Experiment 2, the lack of any age disparity in the confidence of item recognition judgements does not preclude the increased use of familiarity by older participants in this task.

The electrophysiological impact of reducing task-switching

Moving from a randomized to a blocked retrieval phase produced several changes in the ERPs elicited by item and associative recognition in both age groups. For the young adults, the electrophysiological findings from the current experiment were more consistent with the results of Experiment 1, than with those of Experiment 2. Specifically, the early mid-frontal and late right frontal effects were robust in item recognition, but not in associative recognition, and the late left prefrontal negativity in associative recognition was not significant. One notable difference between the experiments was the discrepancy in the timings of the latency periods required to analyse the young group's ERP data; with those selected in Experiments 1 and 3 generally earlier than those selected in Experiment 2. As the chosen latency periods appeared to best capture the evolution of ERP effects in each individual experiment, it seems unlikely that such timing issues underlie the electrophysiological differences between Experiments 2 and 3. For example, with regard to the early mid-frontal effect, there is no evidence of any old/new differences onsetting before 300 ms in item recognition in Experiment 2, and the time windows selected to analyse the late right frontal effect were identical in Experiments 2 and 3.

The current findings rule out one possible functional interpretation of the early mid-frontal effect in associative recognition. The absence of the modulation in the young group in Experiment 3 clearly indicates that the

component reported in Experiment 2 did not simply reflect the introduction of a two-stage judgement. The current result is more consistent with the interpretation of the early mid-frontal activity in associative recognition in the young adults in Experiment 2 as reflecting the high task-switch requirement (c.f. Donaldson & Rugg, 1999). Support for this argument comes from the appearance of an early (from 250 ms), but non-robust, mid-frontal activation in associative recognition in Experiment 1, where the task-switching requirement was identical to Experiment 2 (Figure 12, A and B, p168).

The current findings also elucidate a second effect in young adults. Specifically, the reduction of the late left prefrontal negativity in associative recognition suggests that this modulation does not index retrieval of context, as proposed in the previous chapter. Instead, the attenuation of the modulation when retrieval effort (as indexed by discriminability) was reduced is consistent with neuroimaging studies demonstrating that left prefrontal activation in young adults may be linked to retrieval effort (Buckner et al., 1998; Lundstrom et al., 2003).

ERP age-related differences

In older adults, meanwhile, blocking the retrieval tasks had a minimal effect on the ERP correlates of item recognition. Specifically, whilst Experiment 2 elicited a robust lateralised right frontal effect, the more central focus in the current experiment closely resembles the findings of a recent ERP ageing investigation of item recognition (Morcom & Rugg, 2004). In associative recognition, the main difference between the randomized and blocked versions was the appearance of an early right frontal positivity that became more

posterior as the epoch progressed. Therefore, although the task-switching requirement did not disproportionately affect the elderly adults' performance, it did, as predicted, appear to attenuate their early ERP effects.

Critically, the high degree of similarity between the elderly participants in Experiment 3 and those in Experiment 2 confirms that the ERP ageing effects reported in Experiment 2 did not simply reflect the performance decrement of the older adults. The continued age-related reduction of the left parietal effect when item and associative recognition were blocked suggests that older adults' recollective remembering remains impaired even when their performance is enhanced. The attenuation of the late central/posterior positivity likewise appears to reflect ageing changes in mnemonic operations, although the precise nature of these processes remains unclear. Finally, the persistence of left fronto-central negativities in both item and associative recognition in the high-performing older group does not preclude their interpretation as an ERP index of compensatory operations. Neuroimaging studies have reported an age-related increase in left prefrontal activation when elderly adults' accuracy levels were similar to those of young adults (Cabeza et al., 2000; and for reviews, see Grady, 2000; Grady & Craik, 2000). Furthermore, the reduced magnitude of the current associative recognition left fronto-central negativity, compared with Experiment 2, indicates that the engagement of the modulation's underlying processes was reduced when performance improved.

Another interesting difference between the left-sided negativities elicited in older adults in Experiments 2 and 3 was that not only did the item recognition modulation last longer (500-1200 ms vs. 500-900 ms) in the blocked version, but qualitative differences between the second and third time windows indicate

that it may represent two separate components: an early (500-900 ms) left frontal negativity and a later (900-1200 ms) central/posterior negativity. This second effect appears highly similar to the central negativities reported in previous ERP ageing studies (Trott et al., 1999; Wegesin et al., 2002; Li et al., 2004).

Early and late right frontal effects

Although the left-sided negativities elicited by item and associative recognition in older adults were not identical in Experiments 2 and 3, the most obvious difference between the experiments, as noted above, was the appearance of an early right frontal positivity in associative recognition. The early onset of the modulation, which was similar to that of the mid-frontal effect in young adults, suggests that it may represent familiarity processes in older adults. This interpretation of the early frontal positivity in older adults is further supported by the confidence data suggesting that the elderly participants were more reliant on familiarity in associative recognition than the young.

The familiarity account appears less consistent with the absence of the modulation from the older group's item recognition ERPs. As young adults produced an early mid-frontal effect in item recognition, and the confidence ratings did not suggest that they were more reliant on familiarity than the elderly, the familiarity interpretation would predict that an early right frontal effect should also be elicited by item recognition in older adults. Alternatively, the timing of the modulation, in conjunction with the older adults' increased accuracy in associative recognition in Experiment 3, could be interpreted as indicating that the early frontal positivity indexes the pre-retrieval operations

recruited by the elderly to support associative recognition decision-making (c.f. Fletcher & Henson, 2001). This account is consistent with the observation that the effect onsets well before any mnemonic decision is reached, and is evident only when the task-switch load is decreased. According to the reduced processing resources theory of cognitive ageing (e.g. Craik & Byrd, 1982; Craik, 1983), the lightening of the task-switch load should release more of the elderly adults' limited frontal executive processing resources to operations that are more directly involved in retrieval.

Meanwhile, differences were also apparent in the late right frontal effects elicited by both tasks in older adults. In item recognition, whilst the component exhibited a lateralized distribution in Experiment 2, it was more centrally distributed in Experiment 3. This finding indicates that the lateralization of the late right frontal effect may not reflect age-related alterations in the position of its neural generators, as was previously suggested. Moreover, the presence of robust late right frontal activity in item recognition in the current blocked version appears consistent with the view (see Experiment 1) that the component reflects the emphasis on the association between the word pairs during encoding, but not with its interpretation as indexing the randomized presentation of retrieval tasks. In associative recognition, the lack of an age-related reduction in late right frontal activation contradicts the findings of Experiment 2. The reason for this disparity remains unclear, but the current finding may reflect the enhanced performance of the older participants when the retrieval tasks were blocked (however, see "General Discussion" chapter for alternative explanations that account for the discrepant late right frontal results in both item and associative recognition).

Summary

The persistence of age-related reductions in the left parietal effect in item and associative recognition when the presentation of the retrieval tasks was both randomized and blocked, and when the older group's accuracy was comparable to that of a previous young group, appears to support the dual process account of recollection-based remembering being impaired in older adults. Other ageing changes, namely increases in left fronto-central negativities in both tasks, and the absence of the late central/posterior positivity in associative recognition, also remained constant across the two age comparisons conducted to date.

In contrast, the situation with regard to the potential ERP correlate of familiarity in older adults is less clear. The absence of any early frontal activation in the waveforms elicited by item recognition in the elderly participants (particularly when an early mid-frontal modulation was present in the young participants) is problematic for the familiarity account. However, it is possible that this finding may reflect the residual task-switching requirement in the current experiment (participants still had to change tasks halfway through each test phase). This explanation gains some support from the observation that the ERPs in young adults in the current experiment were highly similar to those reported in Experiment 1. Alternatively, the absence of the early right frontal modulation in item recognition in the elderly may be due to the increased complexity of the item recognition task caused by the associative encoding instructions. In an attempt to exclude the first of these possibilities, the following chapter presents an experiment from which the task-switching requirement was completely eliminated.

Chapter 9

Experiment 4

Introduction

Experiments 2 and 3 demonstrate that the ERP correlates elicited by item and associative recognition change markedly as people age. The left parietal index of recollection appears severely reduced or absent in older adults in both tasks, and a late right-sided central/posterior positive-going effect in associative recognition is present only in young adults. Meanwhile, older people produce left fronto-central negative-going modulations that onset early in item recognition and later in associative recognition. In addition, an early frontal positive-going effect was elicited by associative recognition in the older adults in Experiment 3. A familiarity interpretation of this component is consistent with evidence from the behavioural data suggesting that these participants were more reliant on familiarity than their young counterparts. However, since dual process theory predicts that the contribution of familiarity should be greater to

item recognition than to associative recognition, the familiarity account corresponds less well to the absence of the effect from the older adults' item recognition waveforms.

The current experiment aims to exclude the possibility that the residual task-switching requirement in Experiment 3 caused an attenuation of the early right frontal component in item recognition in the older group. Consequently, item and associative recognition will be blocked over the course of the entire experiment, with participants performing a single task during the first half of the experiment before proceeding to the other task for the remainder. As the modification to the task-switching requirement is minimal in this experiment, it is predicted that performance levels should be comparable to those in Experiment 3, and that, with the possible exception of the appearance of an early right frontal effect in older adults in item recognition, the ERP results from Experiment 3 will be closely replicated.

Methods

Participants

18 young (8 male; mean age 19.6 years, range 18-26) and 20 older (10 male; mean age 70.6 years, range 65-80) participants took part in the experiment. The data from one older participant was discarded because of technical difficulties, and another older participant was excluded because their blink correction was unsuccessful. 18 participants remained in the older group [8 male, mean age 70.3 years, range 65-77].

Neuropsychological tests

Table 21. Characteristics of the participants in Experiment 4 (mean \pm SD)

	Young	Older	p-value
Age (years)	19.6 \pm 2.2	70.3 \pm 3.8	<0.001
Gender	8/18 male	10/18 male	
Education (years)	14.4 \pm 2.0	14.3 \pm 3.4	n.s.
BDI	4.2 \pm 4.6	5.6 \pm 4.4	n.s.
Health	4.2 \pm 0.6	4.0 \pm 0.7	n.s.
IQ (WASI)	113 \pm 9	126 \pm 9	<0.001
WMS-R			
<i>Logical memory I</i>	49.2 \pm 8.4	40.2 \pm 8.2	<0.01
<i>Logical memory II</i>	30.8 \pm 8.3	23.1 \pm 6.7	<0.01.
<i>Paired associates I</i>	29.1 \pm 2.8	20.4 \pm 5.6	<0.001
<i>Paired associates II</i>	7.9 \pm 0.2	6.7 \pm 1.5	<0.01
<i>Letter number sequencing</i>	12.8 \pm 2.8	12.3 \pm 2.7	n.s.
MMS		29.1 \pm 1.1	

The neuropsychological tests (Table 21) demonstrated that the groups were matched on years of education, health ratings and BDI scores. However, the older participants were more intelligent and, similar to Experiment 3, the young group performed better on all the WMS-R subscales apart from letter number sequencing.

Stimulus materials, procedure and ERP recording

The current procedure differed from that employed in the previous experiment in several respects. There were 10 study/test blocks instead of 8: an additional 174 words were drawn from the pool presented in Appendix A, paired as described in the “General Methods” chapter, and added to the previous study lists to form two lists of 240 pairs. Participants learned 24 study pairings during each study block as before, but in each test block either 12 old and 12 new single words, or 12 same and 12 rearranged pairs, were randomly

interleaved. Five item recognition blocks were presented consecutively, as were five associative recognition blocks. The order of the retrieval tasks and the assignment of the study lists to each task was counterbalanced across participants.

Results

Behavioural

The performance data are summarised in Table 22 (below). The hits and correct rejections data produced a main effect of age [$F(1,34) = 13.39, p = 0.001$] reflecting greater accuracy from the young group. However, the analysis also revealed various interactions including a task, response category and age interaction [$F(1,34) = 11.74, p < 0.01$]. In item recognition, the young group were more accurate overall than the older group, whereas in associative recognition, although the hit rate was equivalent, the young adults produced more correct rejections than the older adults [$t(34) = 4.27, p < 0.001$].

The discriminability (Pr) analysis produced a main effect of age [$F(1,34) = 13.39, p = 0.001$] demonstrating that the elderly performed less well than the young on both tasks. The bias (Br) ANOVA gave rise to a main effects of age [$F(1,34) = 8.46, p < 0.01$] and task [$F(1,34) = 10.19, p < 0.01$], and an age by task interaction [$F(1,34) 6.77, p < 0.05$], indicating that (similar to Experiment 2) older adults adopted a more liberal criterion than young adults in associative recognition [$t(34) = 3.79, p = 0.001$].

The confidence data was divided into high and low confidence responses as previously. Analyses of high confidence responses once again produced main effects of task [$F(1,34) = 9.07, p < 0.01$] and response category

[$F(1,34) = 57.72, p < 0.001$] that were modulated by various interactions including a task, response category and age interaction [$F(1,34) = 9.06, p < 0.01$]. As before, participants were more confident about associative recognition than about item recognition, but, although both groups were generally more confident about hits than about correct rejections, in item recognition, similar to Experiment 2, the older adults were equally confident for both response-types. Moreover, post hoc t-tests failed to demonstrate any robust ageing differences for hits or correct rejections on either task (all p values > 0.06).

Table 22. Mean performance data (\pm S.D.) for Experiment 4.

	Item Recognition		Associative Recognition	
	Young	Older	Young	Older
<u>Accuracy</u>				
Hits	0.81 \pm 0.10	0.74 \pm 0.11	0.84 \pm 0.09	0.82 \pm 0.10
Correct Rejections (CR)	0.90 \pm 0.06	0.84 \pm 0.10	0.89 \pm 0.10	0.70 \pm 0.17
Confident Hits (rating = 5)	0.65 \pm 0.15	0.65 \pm 0.17	0.79 \pm 0.14	0.70 \pm 0.22
Confident CR (rating = 5)	0.39 \pm 0.22	0.51 \pm 0.33	0.55 \pm 0.20	0.39 \pm 0.30
Pr	0.71 \pm 0.12	0.58 \pm 0.13	0.73 \pm 0.15	0.51 \pm 0.22
Br	0.34 \pm 0.18	0.37 \pm 0.19	0.36 \pm 0.22	0.61 \pm 0.18
<u>RT(ms)</u>				
Hits	1210 \pm 272	1544 \pm 276	1552 \pm 357	1943 \pm 312
CR	1330 \pm 264	1644 \pm 351	1862 \pm 409	2363 \pm 322
<u>Study RT(ms)</u>	Young 4504 \pm 1758		Older 4964 \pm 2130	

The test RT ANOVA produced main effects of task [$F(1,34) = 176.68, p < 0.001$], response category [$F(1,34) = 46.58, p < 0.001$], and age [$F(1,34) = 17.27, p < 0.001$]. These results indicated that, as previously, associative recognition responses were slower than item recognition responses, that

correct rejections were slower than hits, and that the older group was slower than the young group.

Finally, although both groups produced similar RTs on the sentence generation study task [$t(34) = 0.71$, n.s.], Mann Whitney tests on the post-experimental questionnaire data (see "Appendix C") suggested that age-related encoding differences persisted. The elderly group found the task more difficult [$U = 102.5$, $z = 2.03$, $p < 0.05$], failed to make up sentences more often [$U = 98.5$, $z = 2.30$, $p < 0.05$], and tended to generate more simple sentences [$U = 109$, $z = 2.06$, $p < 0.05$] than the young group.

Summary of behavioural data

The behavioural pattern in the current experiment was comparable to those observed previously; the elderly were less accurate than the young participants in both item and associative recognition, and adopted a more liberal response criterion in associative recognition. The principle difference between this experiment and the previous age comparisons was the age-related equivalence in study RT.

Event-related potentials

Young group

Item Recognition

Figure 32 (p290) shows the grand average OLD and NEW waveforms for item recognition from 30 EEG electrode sites. The mean number of trials (\pm S.D.) contributing to the ERPs was 37 (8) OLD and 44 (7) NEW. The

waveforms appear to diverge from approximately 250 ms post-stimulus onset, with the ERPs for OLD words becoming globally more positive than those for NEW words. The modulation terminates at around 500 ms over frontal sites, but over parietal sites it exhibits a left-sided asymmetry and persists until approximately 750 ms. From 700 ms, OLD waveforms become more negative-going than NEW words over central sites. This negativity subsequently extends to parietal sites and persists until 1600 ms. A right frontal positivity is apparent from 1200 ms post-stimulus onset.

Associative Recognition

Figure 33 (p291) shows the grand average SAME and REARRANGED waveforms for associative recognition, again from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 40 (8) SAME and 42 (10) REARRANGED. The waveforms appear to diverge from around 300 ms post-stimulus onset, with the ERPs for SAME pairs becoming more positive than those for REARRANGED pairs over prefrontal sites. From around 500 ms, the focus shifts to parietal sites, where the modulation appears to exhibit a left-sided asymmetry and persists until 1600 ms. Over frontal electrodes, meanwhile, a bilateral positive component, which onsets at around 600 ms, develops a right-sided asymmetry from 1200 ms. This modulation becomes maximal over central and parietal electrodes towards the end of the recording epoch.

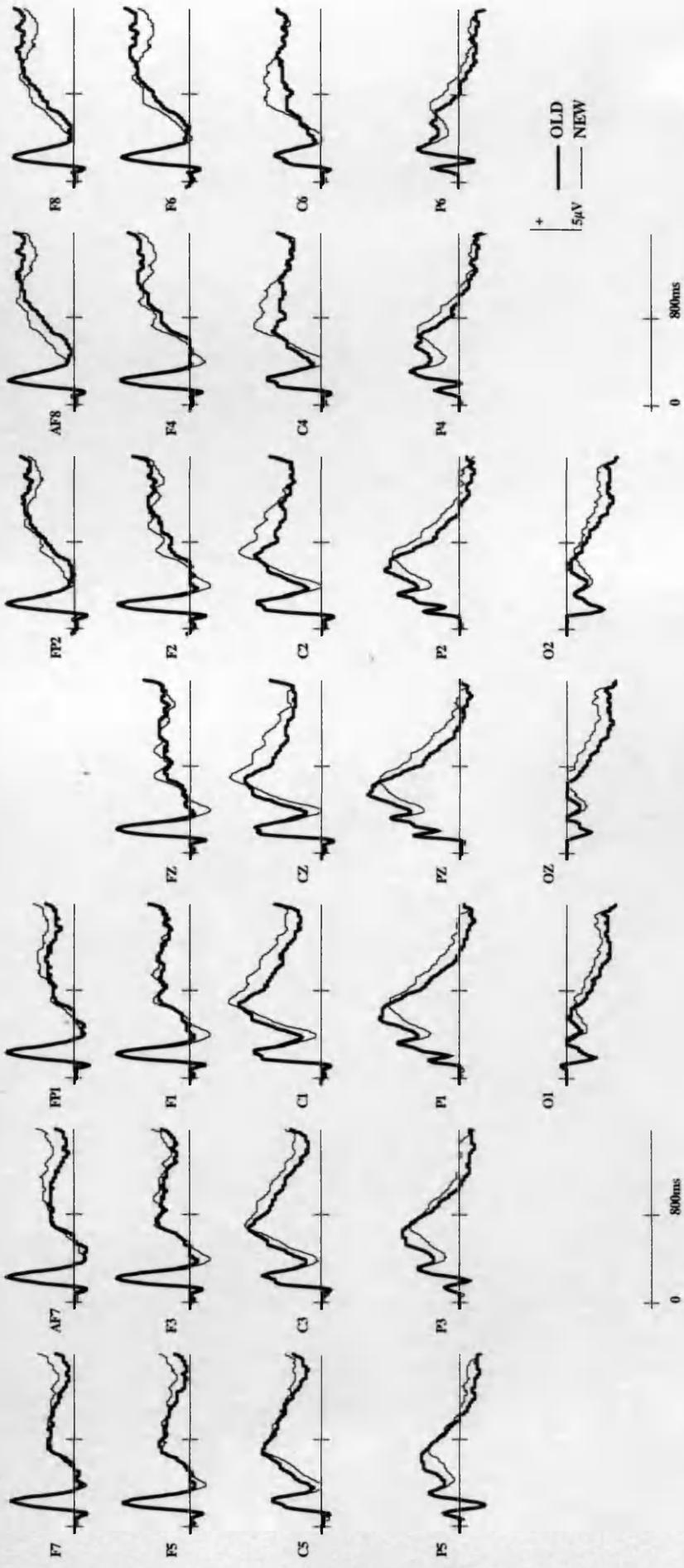


Figure 32. Grand average ERPs for the recognised (OLD) and NEW response categories for item recognition. Electrodes are shown as in Figure 10.

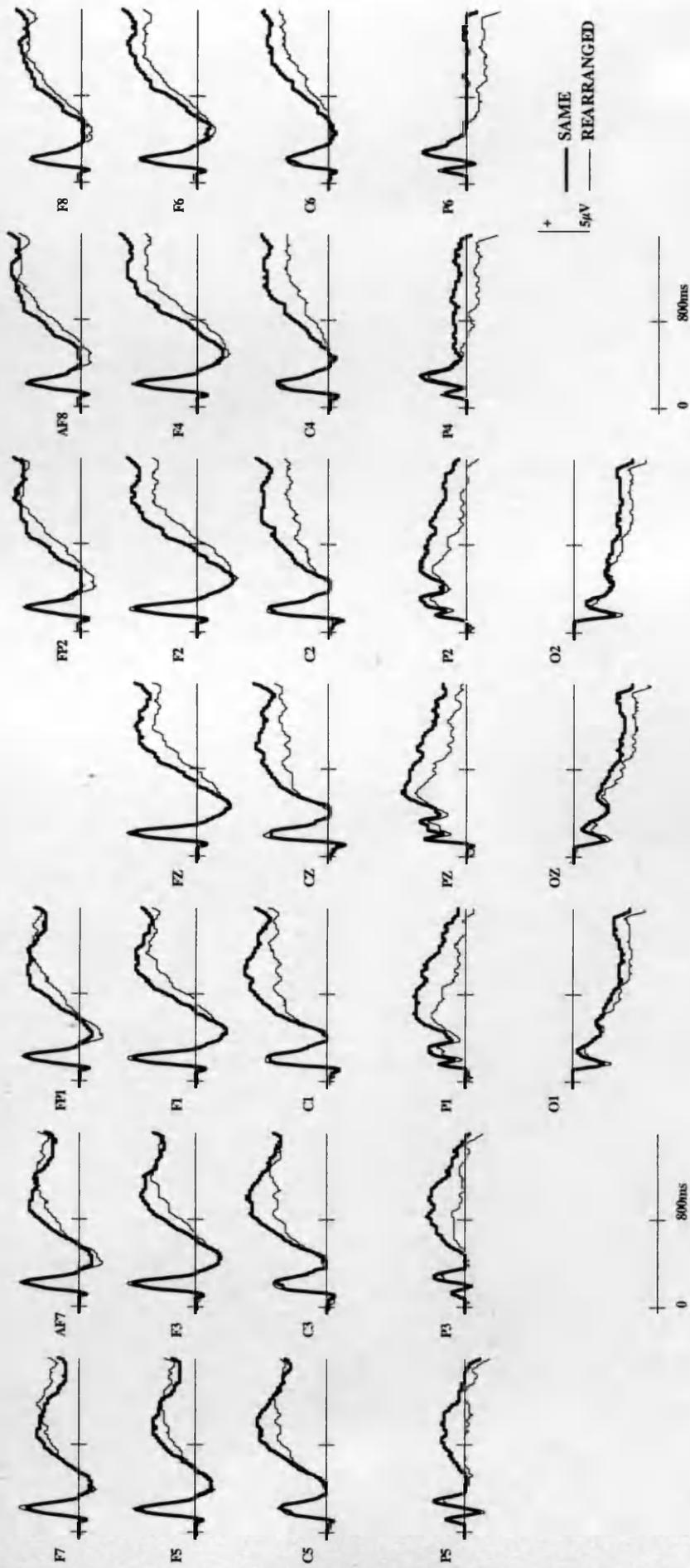


Figure 33. Grand average ERPs for the recognised (SAME) and REARRANGED response categories for associative recognition. Electrodes are shown as in Figure 10.

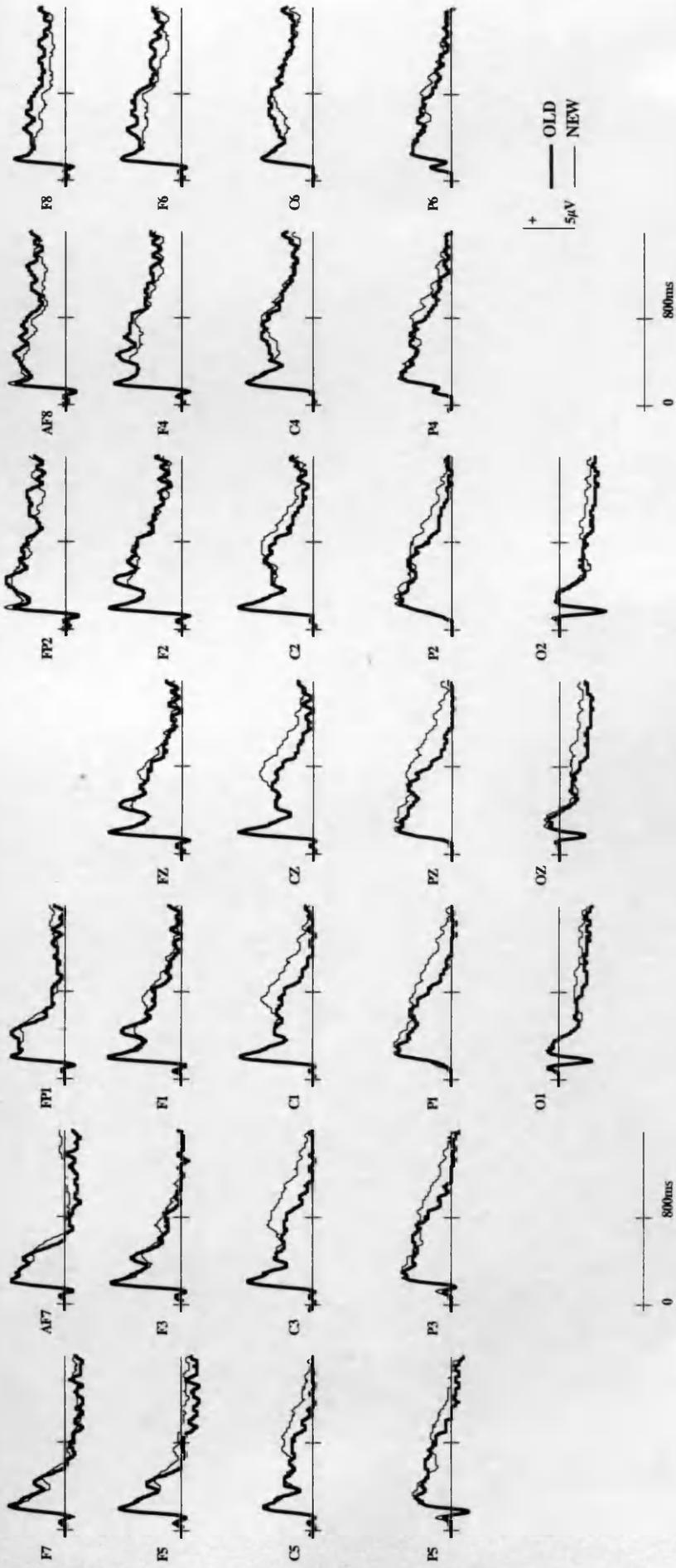


Figure 34. Grand average ERPs for the recognised (OLD) and NEW response categories for item recognition. Electrodes are shown as in Figure 10.

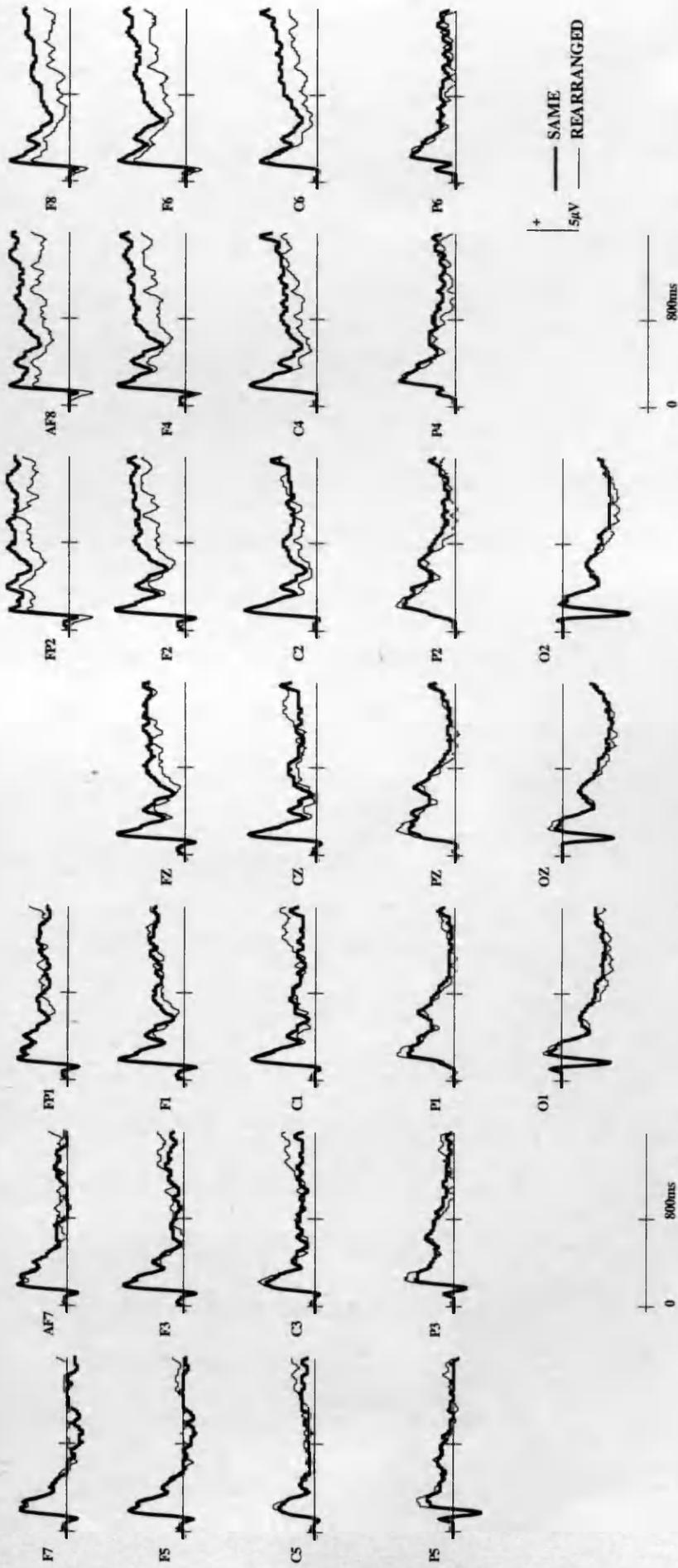


Figure 35. Grand average ERPs for the recognised (SAME) and REARRANGED response categories for associative recognition. Electrodes are shown as in Figure 10.

Older group

Item Recognition

Figure 34 (p292) shows the grand average OLD and NEW waveforms for item recognition from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 38 (10) OLD and 42 (7) NEW. The waveforms diverge from about 400 ms post-stimulus onset, with the ERPs for OLD words becoming more positive than those for NEW words over right frontal electrodes. This component lasts until around 800 ms. Between 500 and 700 ms, meanwhile, a small positivity is apparent over parietal electrodes. A negative-going modulation, which appears maximal the left central hemisphere, becomes evident from 650 ms. This effect later extends to left parietal sites and persists until approximately 1600 ms.

Associative Recognition

Figure 35 (p293) shows the grand average SAME and REARRANGED waveforms for associative recognition, again from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 38 (10) SAME and 33 (11) REARRANGED. The earliest SAME/REARRANGED difference is apparent at around 200 ms post-stimulus onset, with SAME waveforms becoming more positive than REARRANGED waveforms over right prefrontal, right frontal and right central sites. Following a decline in magnitude at approximately 500 ms, the frontal activation increases in magnitude again at around 600 ms and thereafter persists until around 1800 ms. Over left central sites, meanwhile, SAME waveforms appear to become more negative-going than REARRANGED waveforms from around 1200 ms onwards.

Rationale for the ERP analyses

As the rationale underlying the ERP analysis was similar to that described in the previous experiment, it is not repeated here. Preliminary analyses led to four latency periods (200-400 ms, 400-800 ms, 800-1200 ms and 1200-1900 ms) being selected for the young group, and four slightly different latency periods (200-500 ms, 500-900 ms, 900-1200 ms and 1200-1900 ms) being chosen for the older group. In this instance, due to the appearance of ERP effects over prefrontal electrodes in both groups, additional ANOVAs employing these sites were conducted. The results of the between-task analyses in the young group were highly similar to those in previous experiments, and are therefore not reported.

Young Group

Item Recognition

The earliest robust old/new differences were observed at 272 ms over frontal (F3, F1 and Fz) electrodes. A marginal main effect of response category in the Midline 200-400 ms ANOVA (Table 23, p296) appeared to indicate an early anterior positive-going effect that likely represents a non-robust early mid frontal effect (Figure 36, A, p298). Although subsidiary analyses investigating the two- and three-way interactions in the Main 400-800 ms ANOVA failed to reveal any robust old/new differences, as the ERP components appeared maximal over the left hemisphere (Figure 36, B), targeted t-tests of left frontal and parietal hemispheres were conducted. These analyses confirmed that the left parietal effect was robust [$t(17) = 2.58, p < 0.05$].

Table 23. Results of the magnitude analyses in the young group for the critical ERP comparisons for item and associative recognition.

Latency Region	TASK	
	Item Recognition (OLD vs. NEW)	Associative Recognition (SAME vs. REARRANGED)
200-400ms <i>Additional analyses</i> <i>RC(m)</i>	$F(1,17)=4.25,p=0.055$	No significant results
400-800ms RC RCxH RCxS RCxHxS <i>Additional analyses</i> <i>RCxH(c)</i> <i>RC(pf)</i>	$F(1,17)=13.70,p<0.01$ $F(1.5,26.2)=4.30,p<0.05$ $F(1,17)=9.35,p<0.01$	$F(1,17)=4.86,p<0.05$ $F(1.5,25.3)=4.73,p<0.05$ $F(1,17)=5.17,p<0.05$
800-1200ms RC RCxHxL RCxS <i>Additional analyses</i> <i>RC(c)</i> <i>RCxS(c)</i> <i>RCxHxS(c)</i> <i>RC(m)</i> <i>RC(pf)</i>	$F(1.2,19.7)=4.40,p<0.05$	$F(1,17)=21.06,p<0.001$ $F(1,17)=4.11,p=0.059$ $F(1.2,20.4)=6.13,p<0.05$ $F(1,17)=10.63,p<0.01$ $F(1.2,19.7)=4.80,p<0.05$ $F(1,17)=10.99,p<0.01$ $F(1,17)=7.98,p<0.05$
1200-1900ms RC RCxH RCxHxL RCxS RCxHxS RCxHxLxS <i>Additional analyses</i> <i>RCxS(c)</i> <i>RC(m)</i> <i>RCxH(pf)</i>	$F(1,17)=6.85,p<0.05$ $F(1,17)=5.08,p<0.05$ $F(1.4,23.1)=4.25,p<0.05$ $F(1.6,27.4)=7.13,p<0.01$ $F(1,17)=12.62,p<0.01$	$F(1,17)=7.11,p<0.05$ $F(1,17)=16.06,p=0.001$ $F(1.2,20.5)=5.10,p<0.05$ $F(1.6,27.7)=5.39,p<0.05$ $F(1.2,21.2)=6.18,p<0.05$ $F(1,17)=6.08,p<0.05$ $F(1,17)=7.04,p<0.05$

Between 800 and 1200 ms, the topographic map (Figure 36, C) suggested the existence of a negative-going modulation over central sites; however, the analyses conducted to investigate the three-way interaction in the Central ANOVA failed to produce any significant results. Finally, the presence

of a robust late right frontal effect (Figure 36, D) was confirmed by the subsidiary analyses of right frontal sites carried out to investigate the four-way interaction in the 1200-1900 ms Main ANOVA [main effect of response category – $F(1,17) = 4.52, p < 0.05$].

Associative Recognition

The earliest robust same/rearranged differences were observed at 544 ms over the left parietal electrode P1. Targeted t-tests of left and right parietal hemispheres following the main effect of response category in the Main 400 and 800 ms ANOVA (Table 23) demonstrated the presence of an onsetting left parietal component [$t(17) = 2.52, p = 0.088$] that was robust from 600 ms (as confirmed by post hoc analyses of the 100 ms bins). Meanwhile, the main effect of response category in the Prefrontal ANOVA reflected a prefrontal positivity that appeared slightly right-sided [right prefrontal – $t(17) = 2.59, p < 0.05$] (Figure 36, B).

Main effects in all four initial 800-1200ms ANOVAs confirmed that same/rearranged differences were reliable over prefrontal, frontal, central and parietal electrodes (Figure 36, C). Moreover, subsidiary analyses investigating the marginal three-way interaction in the Main ANOVA demonstrated the presence of robust modulations over frontal sites [main effect of response category, $F(1,17) = 12.64, p < 0.01$], and over both left [$t(17) = 4.45, p < 0.001$] and right [$t(17) = 4.67, p < 0.01$] parietal hemispheres.

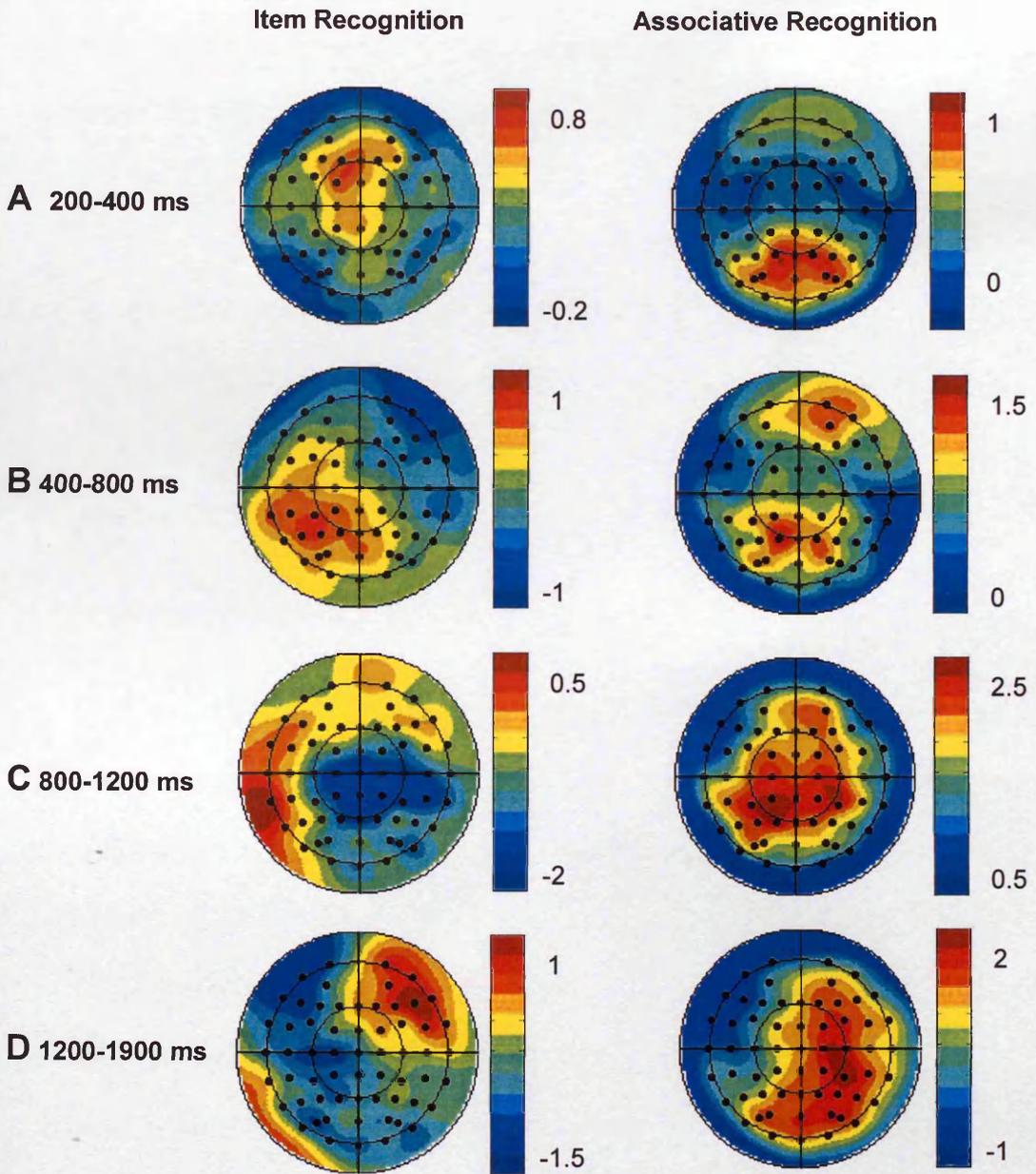


Figure 36. Topographic maps illustrating the scalp distribution of ERP effects for the young group in Experiment 4. Panel A illustrates the 200-400 ms latency region; B – 400-800 ms; C – 800-1200 ms; and D – 1200-1900 ms. The maps are shown as in Figure 12.

By 1200-1900 ms, the general right-sided asymmetry (Figure 36, D) was demonstrated by a main effect of response category [$F(1,17) = 15.89, p = 0.001$] in the subsidiary analysis of the right hemisphere conducted to investigate the three-way interaction in the Main ANOVA. Furthermore, targeted

t-tests confirmed that same/rearranged differences were robust over both right frontal [$t(17) = 3.16, p < 0.05$] and right parietal [$t(17) = 3.55, p < 0.01$] sites.

Topographic analyses

As robust ERP effects were absent from the first latency period in both item and associative recognition, only two sets of topographic comparisons were performed for each task (400-800 ms vs. 800-1200 ms and 800-1200 ms vs. 1200-1900 ms).

Item recognition

The 400-800 ms vs. 800-1200 ms ANOVAs revealed interactions involving epoch and location [Main ANOVA – $F(1,17) = 10.05, p < 0.01$; Midline – $F(1.9,32.3) = 6.07, p < 0.01$], epoch and site [Main – $F(1.1,18.3) = 8.81, p < 0.01$; Central – $F(1.1,18.1) = 6.21, p < 0.05$], and epoch, location and site [Main – $F(1.4,23.1) = 3.82, p = 0.051$]. In essence, these results confirm that the left parietal effect did not persist in the 800-1200 ms time window. The second comparison produced various interactions, including an epoch, hemisphere, location and site interaction in the Main ANOVA [$F(1.9,31.9) = 6.52, p < 0.01$], and epoch by hemisphere by site interactions in the Prefrontal [$F(1.3,22.4) = 4.52, p < 0.05$] and Central [$F(1.4,23.8) = 5.59, p < 0.05$] ANOVAs. These findings reflect the evolution of the right frontal effect in the final time window.

Associative recognition

The Main 400-800 ms vs. 800-1200 ms comparison revealed an interaction involving epoch, location and site [$F(1.5,25.9) = 14.91, p < 0.001$] that appeared to reflect the evolution from a left parietal effect to a widespread

bilateral positivity over frontal and parietal electrodes. In the 800-1200 ms vs. 1200-1900 ms analyses, interactions involving epoch, hemisphere and location in the Main ANOVA [$F(1.7,29.0) = 12.18, p < 0.001$], epoch, hemisphere and site in the Central ANOVA [$F(1.2,19.9) = 4.29, p < 0.05$], epoch and hemisphere [$F(1,17) = 7.50, p < 0.05$] in the Prefrontal ANOVA, and epoch and location in the Midline ANOVA [$F(2.1,35.3) = 5.03, p < 0.05$] reflected the progression to a widespread right-sided, positive-going modulation in the final time window.

Summary of the ERP effects elicited by item and associative recognition in young adults

In item recognition, the presence of a late right frontal effect, in addition to the left parietal effect, closely replicated the ERP findings from Experiment 3. In the current experiment, however, the early mid-frontal effect was not statistically reliable. In associative recognition, left parietal activity was robust by 800 ms, but became more widespread, and then right-sided, as the epoch progressed. Likewise, a widespread positivity, present over anterior and central sites from 800 ms, developed a right-sided asymmetry in the 1200-1900 ms latency period. As in Experiments 1 and 2, the late right frontal effect in associative recognition was significant; however, in contrast to all previous experiments, a robust prefrontal component, which appeared slightly right-sided, was evident between 400 and 800 ms.

Older Group

Item Recognition

Although the earliest robust old/new differences were observed at 440 ms over right frontal (F6 and FC6) electrodes, subsidiary analyses investigating interactions in the 200-500 ms and 500-900 ms ANOVAs (Table 24, below) failed to produce any significant results. Moreover, although the grand average waveforms (Figure 34, p292) suggested the presence of a short-lived parietal effect, additional 500-700 ms analyses failed to indicate any robust activity over the left parietal hemisphere.

During the 900-1200 ms latency period, subsidiary analyses investigating the marginal response category, hemisphere and site interaction in the Main ANOVA demonstrated a robust negative-going modulation over the left hemisphere [main effect of response category – $F(1,34) = 4.75, p < 0.05$]. However, targeted t-tests indicated that the effect was only robust over left central [$t(17) = 2.59, p < 0.05$] and left parietal [$t(17) = 2.40, p = 0.056$] sites (Figure 37, C, p305). Finally, the lack of significant findings in the 1200-1900 ms analyses demonstrated that, on this occasion, the late right frontal effect in item recognition (Figure 37, D) was not reliable.

Table 24. Results of the magnitude analyses in the older group for the critical ERP comparisons for item and associative recognition.

Latency Region	TASK	
	Item Recognition (OLD vs. NEW)	Associative Recognition (SAME vs. REARRANGED)
200-500ms RCxH RCxL RCxLxS <i>Additional analyses</i> RCxH(c) RCxHxS(c) RCxL(m) RC(pf) RCxH(pf)	F(1,17)=6.07,p<0.05 F(1.3,21.7)=4.65,p<0.05 F(1.6,27.3)=7.49,p<0.01	F(1,17)=6.49,p<0.05 F(1,17)=8.25,p<0.05 F(1,17)=6.33,p<0.05 F(1.3,22.7)=5.05,p<0.05 F(2.7,45.7)=5.80,p<0.01 F(1,17)=6.68,p<0.05 F(1,17)=6.11,p<0.05
500-900ms RC RCxH RCxHxL RCxS RCxHxLxS <i>Additional analyses</i> RC(c) RCxH(c) RCxS(c) RCxHxS(c) RC(m) RC(pf) RCxH(pf)	F(1,17)=11.84,p<0.01 F(1.2,21.2)=3.96,p=0.052 F(1.6,27.7)=4.91,p<0.05 F(1.1,19.6)=6.33,p<0.05	F(1,17)=7.16,p<0.05 F(1,17)=17.03,p=0.001 F(1,17)=10.19,p<0.01 F(1.3,22.2)=4.14,p<0.05 F(1.5,26.0)=4.77,p<0.05 F(1,17)=4.50,p<0.05 F(1,17)=19.20,p<0.001 F(1.7,28.4)=7.43,p<0.01 F(1,17)=5.32,p<0.05 F(1,17)=5.37,p<0.05 F(1,17)=34.15,p<0.001
900-1200ms RC RCxH RCxHxL RCxHxS RCxHxLxS <i>Additional analyses</i> RC(c) RCxH(c) RCxHxS(c) RC(m) RCxH(pf)	F(1.4,24.5)=3.53,p=0.058 F(1,17)= 3.56,p=0.076 F(1,17)=5.81,p<0.05	F(1,17)=4.52,p<0.05 F(1,17)=26.60,p<0.001 F(1,17)=12.15,p=0.059 F(1.9,31.9)=7.29,p<0.01 F(1,17)=8.89,p<0.01 F(1.4,23.8)=8.82,p<0.01 F(1,17)=27.53,p<0.001
1200-1900ms RCxH RCxHxL <i>Additional analyses</i> RCxH(c) RCxS(c) RCxHxS(c) RCxH(pf)	No significant results	F(1,17)=14.50,p=0.001 F(1,17)=5.81,p<0.05 F(1,17)=5.44,p<0.05 F(1.1,18.0)=5.26,p<0.05 F(1.3,22.4)=3.91,p=0.05 F(1,17)=12.24,p<0.01

Associative Recognition

The earliest robust same/rearranged differences in the older group were observed at around 190 ms over right prefrontal (AF8 and FP2) electrodes. Accordingly, subsidiary analyses investigating interactions in the Main, Prefrontal and Central 200-500 ms ANOVAs (Table 24) confirmed the existence of a widespread early right frontal effect [right prefrontal – $t(17) = 4.24$, $p < 0.01$; right frontal – $t(17) = 2.71$, $p < 0.05$; main effect of response category – right central, $F(1,17) = 7.17$, $p < 0.05$] (Figure 37, A).

The persistence of the early right frontal effect into the 500-900 ms latency period (Figure 37, B) was confirmed by subsidiary analyses investigating the two-, three- and four-way interactions in the Main, Prefrontal and Central ANOVAs [main effect of response category – right frontal, $F(1,17) = 21.58$, $p < 0.001$; right prefrontal – $t(17) = 4.32$, $p < 0.001$; right central – $t(17) = 3.30$, $p < 0.01$]. Between 900 and 1200 ms, robust same/rearranged differences persisted over right anterior and central sites: the subsidiary analyses following the two-, three- and four-way interactions in the Main, Prefrontal and Central ANOVAs produced a similar pattern of results as in the previous latency period [main effects of response category – right frontal, $F(1,17) = 18.64$, $p < 0.001$; right prefrontal, $F(1,17) = 17.36$, $p = 0.001$; right central, $F(1,17) = 8.60$, $p < 0.01$]. Here, however, the modulation also extended to the parietal location [main effect of response category – $F(1,17) = 4.63$, $p < 0.05$] (Figure 37, C).

By 1200-1900 ms, subsidiary analyses investigating two- and three-way interactions in the Prefrontal and Main ANOVAs indicated that the right-sided positive-going activity was once more focused over anterior sites [right

prefrontal – $t(17) = 2.89, p < 0.05$; right frontal – $t(17) = 2.41, p = 0.056$].

Importantly, investigations of the three-way interaction in the Central ANOVA showed that the late left-sided negative-going effect, which appeared maximal over the central location (Figure 37, D), was marginally significant [main effect of response category – $F(1,17) = 3.93, p = 0.064$].

Topographic analyses

For item recognition, as robust ERP effects were only found in the 900-1200 latency region, no within-task topographic analyses were conducted. In associative recognition, robust ERP effects were found in all four latency regions, therefore three within-task topographic comparisons were performed (200-500 ms vs. 500-900 ms, 500-900 ms vs. 900-1200 ms, and 900-1200 ms vs. 1200-1900 ms).

Associative recognition

The 200-500 ms vs. 500-900 ms comparison produced various interactions in the Main ANOVA, including a four-way epoch, hemisphere, location and site interaction [$F(1.6,26.7) = 5.74, p < 0.05$] that appeared to reflect the spread of the right prefrontal modulation to right frontal electrodes in the second time window. The following (500-900 ms vs. 900-1200 ms) comparison produced epoch by site interactions in the Central [$F(1.2,20.1) = 13.59, p = 0.001$] and Prefrontal [$F(1.2,20.2) = 5.95, p < 0.05$] ANOVAs, and an epoch by location interaction in the Midline [$F(1.4,23.8) = 5.31, p < 0.05$] ANOVA. These results confirmed the more posterior distribution of the right-sided positivity in the 900-1200 ms latency period. There were no significant interactions in the 900-1200 ms vs. 1200-1900 ms ANOVAs.

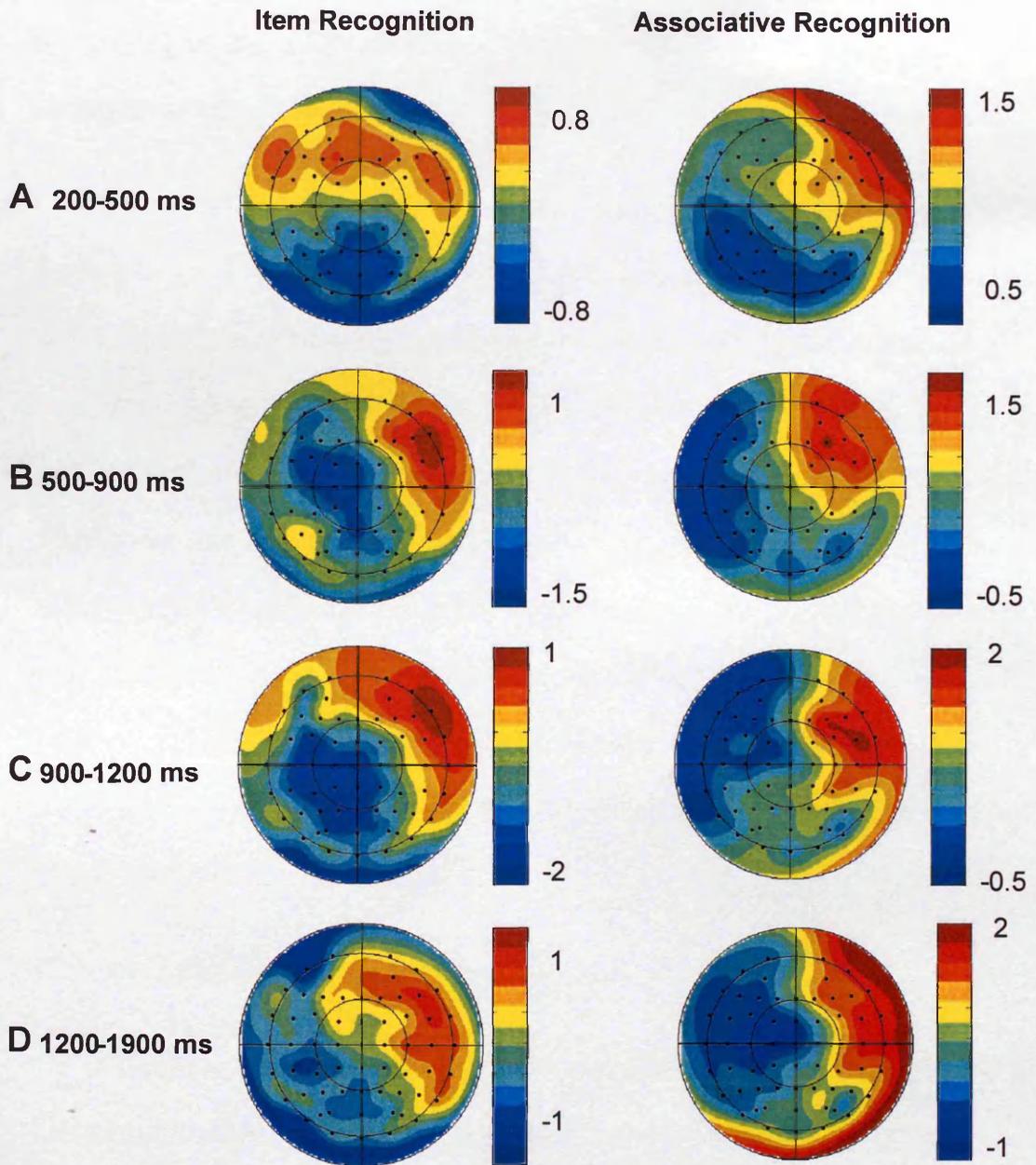


Figure 37. Topographic maps illustrating the scalp distribution of ERP effects for the older group in Experiment 4. Panel A illustrates the 200-500 ms latency region; B – 500-900 ms; C – 900-1200 ms; and D – 1200-1900 ms. The maps are shown as in Figure 12.

Summary of the ERP effects elicited by item and associative recognition in older adults

The sole robust effect in item recognition was a left-sided negativity that onset later (at 900 ms compared to 500 ms) than in the previous experiments, and appeared to have a more posterior distribution. Moreover, although Experiments 2 and 3 reported robust late right-sided positive-going effects for item recognition in older adults, the late right frontal effect in the current experiment was not reliable. The associative recognition waveforms were dominated by a right-sided positivity from 200 ms onwards. This component initially appeared similar to the early right frontal effect in Experiment 3; however, in later epochs, its distribution became more posterior than previously. Finally, the late left fronto-central negativity was maximal over the central location.

Item vs. associative recognition in older adults

Between-task magnitude comparisons were conducted over all four time windows. However, as item recognition only elicited robust ERP effects between 900 and 1200 ms, a single set of between-task topographic analyses was performed.

Subsidiary analyses following the 200-500 ms Main magnitude ANOVA indicated that the three way interaction (Table 25, below) reflected between-task differences in non-robust parietal modulations [task by site interaction – $F(1.3,22.5) = 5.70, p < 0.05$]. Importantly, there was no significant disparity in the magnitude of the right frontal activation elicited by item and associative recognition, despite the fact that the early right frontal effect was only robust in

the associative task. Similarly, although the main effect of task in the 500-900 ms Midline ANOVA demonstrated the presence of more positive-going effects in associative recognition, targeted t-tests confirmed that there were no robust between-task differences over right frontal or right prefrontal sites (both p values > 0.1).

Table 25. Results of the between-task magnitude and topographic comparisons of difference waveforms in the older group.

Latency Region	Magnitude	Topographic
200-500ms TxLxS	$F(1.3,22.4)=4.65,p<0.05$	Not performed
500-900ms TxS <i>Additional analyses</i> TxS(c) T(m)	$F(1.2,20.4)=7.96,p<0.01$ $F(1.2,20.4)=6.39,p<0.05$ $F(1,17)=5.02,p<0.05$	Not performed
900-1200ms T TxS <i>Additional analyses</i> T(c) T(m)	$F(1,17)=6.48,p<0.05$ $F(1.2,21.1)=4.27,p<0.05$ $F(1,17)=6.79,p<0.05$ $F(1,17)=7.63,p<0.05$	$F(1.2,21.1)=4.28,p<0.05$
1200-1900ms	Not significant	Not performed

The results of the 900-1200 ms magnitude and topographic ANOVAs reflected the contrast between an extensive right-sided positivity in associative recognition and a left centro-parietal negativity in item recognition. Targeted t-tests confirmed that the between-task magnitude differences were robust over left [$t(17) = 3.10, p < 0.05$] and right [$t(17) = 2.74, p = 0.056$] parietal hemispheres, as well as over the central location. The lack of significant findings in the 1200-1900 ms ANOVAs indicated that, on this occasion, the late

onsetting ERP correlates of item and associative recognition in older adults were highly similar.

Summary of ERP differences between item and associative recognition in older adults

In the current experiment, the principle between-task differences appeared in the 900-1200 ms latency period, when the left-sided negativity in item recognition juxtaposed a right-sided positivity in associative recognition. Associative recognition once again produced an early right frontal effect, however, unlike Experiment 2, this component did not differ significantly from non-robust early activity in item recognition. Finally, despite the presence of a reliable late right frontal effect and a marginally significant left fronto-central negativity only in associative recognition, no significant between task differences were demonstrated in the 1200-1900 ms latency period.

Comparing young and older groups

In item recognition, since neither group produced robust ERP effects during the first time window, only three magnitude comparisons [400-800 ms (young) vs. 500-900 ms (older); 800-1200 ms (young) vs. 900-1200 ms (older); 1200-1900 (young vs. older)] were performed. Moreover, as the older group only demonstrated significant effects in the 900-1200 ms latency period, a single [800-1200 ms (young) vs. 900-1200 ms (older)] topographic comparison was conducted for the item task. In associative recognition, the earliest time window was excluded from the topographic analyses as the young group only produced robust modulations from 400 ms onwards.

Item recognition

Subsidiary analyses investigating the three-way interaction in the Prefrontal 400-800/500-900 ms ANOVA (Table 26, below) indicated that despite the absence of any robust prefrontal effects in either participant group, the magnitude of right prefrontal activation was significantly greater in older adults [main effect of age – $F(1,34) = 5.03, p < 0.05$]. Moreover, age by site interactions [right frontal/parietal – $F(1.4,47.5) = 10.50, p = 0.001$; right central – $F(1.3,44.8) = 5.52, p < 0.05$] were revealed by the investigations of age, hemisphere and site interactions in the Main and Central ANOVAs. Although these findings reflected more positive-going activity over right inferior sites in the older group, the ageing differences were not robust. Finally, targeted t-tests following the age, hemisphere and location interaction in the Main ANOVA demonstrated a marginally significant age reduction in the magnitude of the left parietal effect [$t(34) = 2.15, p = 0.078$] (Figure 38).

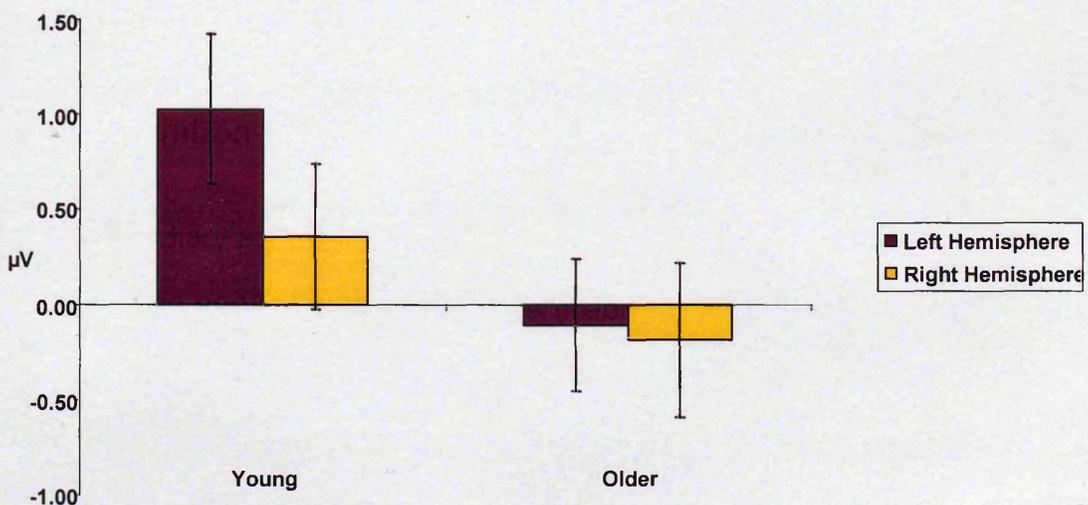


Figure 38. Mean amplitude of the parietal activity elicited by item recognition during the second latency region (400-800 ms – young; 500-900 ms – older). The left hemisphere is collapsed across P1, P3 and P5; the right hemisphere is collapsed across P2, P4, and P6.

Table 26. Results of the magnitude age comparison for both item and associative recognition.

Latency Region	TASK	
	Item Recognition	Associative Recognition
200-400/200-500ms AxL AxS <i>Additional analyses</i> <i>A(m)</i> <i>AxL(m)</i>	Not performed	$F(1,34)=6.11, p<0.05$ $F(2.1, 70.8)=5.03, p<0.01$
400-800/500-900ms AxH AxHxL AxS AxHxS <i>Additional analyses</i> <i>AxH(c)</i> <i>AxS(c)</i> <i>AxHxS(c)</i> <i>AxH(pf)</i> <i>AxHxS(pf)</i>	$F(1,34)=11.11, p<0.01$ $F(1,34)=6.72, p<0.05$ $F(1.3, 42.8)=4.37, p<0.05$ $F(1.8, 60.9)=7.00, p<0.01$ $F(1, 34)=10.39, p<0.01$ $F(1.4, 48.0)=4.32, p<0.05$ $F(1, 34)=5.49, p<0.05$ $F(1.5, 50.1)=3.85, p<0.05$	$F(1,34)=6.48, p<0.05$ $F(1, 34)=7.35, p=0.01$ $F(1.4, 48.1)=3.86, p<0.05$ $F(1.9, 65.5)=5.47, p<0.01$ $F(1, 34)=4.98, p<0.05$
800-1200/900-1200ms A AxH AxHxS <i>Additional analyses</i> <i>AxH(c)</i> <i>AxS(c)</i> <i>AxHxS(c)</i> <i>A(m)</i> <i>AxH(pf)</i>	$F(1.6, 52.8)=3.87, p<0.05$ $F(1.4, 48.4)=4.76, p<0.05$	$F(1,34)=4.68, p<0.05$ $F(1,34)=12.88, p=0.01$ $F(1, 34)=4.57, p<0.05$ $F(1.2, 40.0)=7.39, p<0.01$ $F(1.7, 59.0)=4.47, p<0.05$ $F(1, 34)=3.85, p=0.058$ $F(1, 34)=11.92, p<0.01$
1200-1900ms <i>Additional analyses</i> <i>AxS(c)</i> <i>A(m)</i>	No significant results	$F(1.2, 39.0)=11.41, p=0.001$ $F(1, 34)=4.08, p=0.051$

Interactions involving age, hemisphere and site in the Main and Central 800-1200/900-1200 ms magnitude ANOVAs reflected the presence of the left central/posterior negativity in older adults compared to a more right-sided, non-robust, central negative modulation in young adults. Although subsidiary analyses failed to find any significant age-related magnitude differences, three-

way interactions in the Main and Central topographic ANOVAs (Table 27) suggested that these components were qualitatively distinct.

Associative recognition

Subsidiary analyses investigating age by location interactions in the Main and Midline magnitude 200-400/200-500 ms ANOVAs (Table 26) did not reveal any significant age-related differences in early right frontal and prefrontal activity (Figure 36, A vs. Figure 37, A). Likewise, the subsidiary analyses that followed the interactions in the Main, Central and Prefrontal 400-800/500-900 ms magnitude ANOVAs also failed to show any robust ageing changes over right anterior, right central or left parietal electrodes.

Table 27. Results of the topographic age comparison for both item and associative recognition.

Latency Region	TASK	
	Item Recognition	Associative Recognition
400-800/500-900ms <i>Additional analyses</i> <i>AxH(c)</i>	Not performed	$F(1,34)=4.19,p<0.05$
800-1200/900-1200ms <i>AxH</i> <i>AxHxS</i> <i>Additional analyses</i> <i>AxS(c)</i> <i>AxHxS(c)</i> <i>AxH(pf)</i>	$F(1.5,52.5)=3.55,p<0.05$ $F(1.4,47.7)=4.98,p<0.05$	$F(1,34)=9.17,p<0.01$ $F(1.2,39.7)=7.18,p<0.01$ $F(1.8,60.5)=3.25,p=0.051$ $F(1,34)=8.12,p<0.01$
1200-1900ms <i>Additional analyses</i> <i>AxS(c)</i>	Not performed	$F(1.1,38.5)=11.24,p=0.001$

In contrast, the presence of a left parietal effect (and more anterior positive activity) only in young adults was confirmed by subsidiary and targeted analyses investigating two- and three-way interactions in the Main and Central

800-1200/900-1200 ms ANOVAs [left parietal – $t(34) = 2.84, p < 0.05$; left central – main effect of age, $F(1,34) = 10.23, p = 0.001$; left frontal – $t(34) = 2.35, p = 0.05$] (Figure 36, C). Moreover, similar interactions in the Main and Central topographic ANOVAs (Table 27) confirmed that the ERPs elicited by young and older adults were qualitatively different.

The marginal Main effect of age in the 1200-1900 ms Midline magnitude ANOVA principally reflected the more positive-going activation along the midline in the young group. However, despite age by site interactions in the Central magnitude and topographic ANOVAs confirming that same/rearranged differences were more lateralized in older adults over the central location (Figure 36, D vs. Figure 37, D), targeted t-tests indicated that there were no age-related magnitude differences in right central/posterior, left fronto-central, or right frontal activity.

Summary of ERP differences between young and older adults

Although the ERP findings in Experiment 4 on occasion appeared to lack statistical reliability, the overall pattern appears reasonably consistent with that observed in Experiments 2 and 3. In item recognition, as previously, the left parietal effect in young adults was reduced in older adults, who instead produced a left central negative-going effect that was qualitatively different from a more right-sided negative modulation in young adults. The age-equivalence in the late right frontal effect was also replicated here; however, the magnitude of early right frontal activity was increased in the older adults.

In associative recognition, once again the left parietal effect was severely reduced in the older adults. However, on this occasion, there were no

significant age differences in either late left fronto-central negativity or early right prefrontal activity. Furthermore, the magnitude of the late right-sided central/posterior modulation appeared equivalent in both age groups, but in older adults the component was more lateralised.

Discussion

Despite some unexpected disparity (particularly in the older group) between the ERP results of this experiment and those reported in Experiment 3, left parietal activity was still reduced in the elderly participants in both item and associative recognition. Moreover, although the left-sided negativity elicited by item recognition in older adults was later onsetting, and more posterior, than that observed previously, this modulation appeared to be qualitatively different from the more right-sided, negative-going effect observed in young adults.

Importantly, however, item recognition failed to produce an early right frontal effect in older adults, even when the task-switch requirement was eliminated. In contrast, an early right frontal component was once again produced by associative recognition in the elderly; but, on this occasion, no age-related magnitude or distributional differences were observed. Moreover, the late left fronto-central effect in associative recognition was reduced compared to previously, and did not appear to differ from a non-robust, left-sided negative activation in young adults. Finally, in contrast to both previous ageing experiments, the late right-sided positivity elicited by associative recognition in the older group extended to parietal electrodes. The magnitude of this modulation was equivalent to the late central/posterior effect in young adults, but it was more lateralized.

Behavioural findings

The main behavioural difference between Experiment 4 and previous experiments was the age-equivalence in the time taken over the sentence generation encoding task. This result principally reflected a reduction in the older adults' study RTs (mean = 4964 ms in Experiment 4 vs. 5922 ms in Experiment 3 vs. 6670 ms in Experiment 2). The reduced time at encoding did not, however, impair the elderly group's recognition accuracy: independent t-tests comparing the discriminability of the older group in Experiment 3 with the current older cohort were non-significant for both item and associative recognition (p values > 0.13). Likewise, as predicted, the performance of the current young adults was similar to that in Experiment 3 on both tasks (p values > 0.07). In associative recognition, as before, older adults were poorer at identifying rearranged pairs than young adults. However, in item recognition, the elderly were impaired at identifying new, as well as old, words. Finally, as in Experiment 2, both groups were equally confident for all response-types, including associative correct rejections, and the more liberal response bias in the older adults in associative recognition, but not in item recognition, suggested an underlying difference in the way the two age groups performed the associative task.

A novel ERP finding in young adults?

Contrary to our predictions, the ERP results of the current experiment did not entirely replicate those observed in Experiment 3. The main discrepancy in young adults was the presence of an early (400-800 ms) right prefrontal activation in associative recognition. One possible interpretation of

this component is that it is equivalent to the early mid-frontal effect elicited by associative recognition in the young group in Experiment 2, with the right-sided asymmetry on this occasion merely reflecting differences in the timings of the latency periods. Figure 39, A confirms that the present component was more bilaterally distributed between 300 and 500 ms post-stimulus, but also demonstrates its high similarity to an early (100-300 ms) frontopolar effect (Figure 39, B) that has been variously linked to familiarity (Duarte et al., 2004), to repetition priming, and to the "emergence of information about prior occurrence that contributes to recognition judgements" (Tsvivilis et al., 2001, p502; and see "General Discussion" chapter for further consideration of this point).

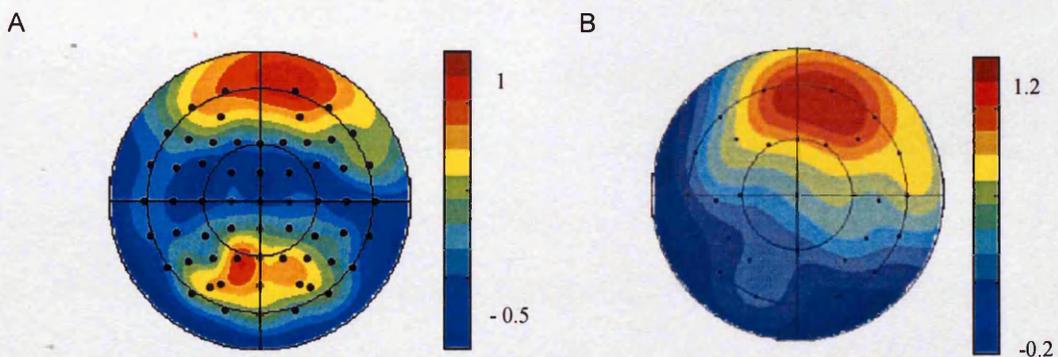


Figure 39. Topographic maps: Panel A illustrates the ERP effects elicited by associative recognition between 300 and 500 ms in young adults in Experiment 4. Panel B depicts the early (100-300 ms) frontopolar effect, adapted from Tsvivilis et al. (2001). The maps are shown as in Figure 12.

The fractionation of the left-sided negativity in item recognition?

In older adults, the principle difference between the current and previous experiments was the later onset and more posterior distribution of the left-sided negativity in item recognition. This modulation appears highly similar to

Wegesin and colleagues' (2002) negative-going component, which was maximal over the Cz electrode between 1000 ms and 1100 ms, and to the late (800 ms onwards) left central/posterior negativity reported by Li and colleagues' (2004). Interestingly, in Li and colleagues' data, a more anterior left-sided negative-going modulation was apparent during an earlier (500-800 ms) time window, where it closely resembled the negativity elicited by item recognition between 500 and 900 ms in Experiments 2 and 3. This observation supports the suggestion that the left-sided negative activation produced by item recognition in older adults in the current research may represent two components: an early anterior effect and a later central/posterior effect.

As central/posterior negativities have only previously been reported in source memory studies, it has been suggested that the effect reflects additional processes recruited by older adults in the search for, or retrieval of, source information (Wegesin et al., 2002). The presence of the central/posterior negativity in item recognition may therefore reflect the retrieval of some task-irrelevant contextual information; and since the encoding instructions required participants to associate two words together, it is conceivable that the old words' study partners were also being retrieved involuntarily. This interpretation is consistent with the inhibition deficit hypothesis assertion that elderly adults are less able than young adults to inhibit goal-irrelevant mental clutter (Hasher & Zacks, 1988; Zacks & Hasher, 1994; Hasher et al., 1999).

The ERP ageing comparison

As anticipated, many of the electrophysiological ageing findings demonstrated in the preceding chapters were replicated in the current

experiment. Notably, the left parietal effect was reduced in older adults in both item and associative recognition, and despite the lack of robust late right-sided activity in item recognition in the current older group, once again there was no age-related difference in the magnitude of the late right frontal effects elicited by either task. However, in some other respects, the current results were not entirely in agreement with those reported to date.

Left-sided negative modulations

Age-related differences in left-sided, negative-going effects appeared to be less pronounced than previously. In item recognition, although the magnitude of late central, negative-going activity was equivalent in both age groups, qualitative differences between a left-sided component in older adults and a slightly right-sided modulation in young adults suggested that the two effects were distinct. One important caveat to this interpretation is that such qualitative ageing effects may not necessarily reflect the engagement of different cognitive operations in young and older adults, but may simply index ageing changes in brain morphology (Rugg & Morcom, 2004). Nevertheless, previous distinctions between late central negative-going effects in older adults and more posterior components in young adults have been informed by similar topographical differences (Wegelesin et al., 2002; Li et al., 2004).

The absence of an ageing difference in the late left fronto-central activation elicited by associative recognition primarily reflects the decreased magnitude of the older group's modulation, which, as Figure 40 (below) shows, appears to reduce across the experiments as the task-switch load decreases. It is therefore possible that the modulation might reflect the additional processing

that elderly people require to switch from one task to the next. Furthermore, this compensatory processes interpretation of left fronto-central activity gains direct support from the demonstration of significant negative correlations between the left fronto-central voltage amplitude in the older participants in Experiments 2, 3 and 4 and their associative hit [$r = -0.325, p < 0.05$] and associative correct rejection [$r = -0.373, p < 0.01$] RTs. These findings suggest that as the task becomes more difficult (as indexed by lengthening RTs) the left fronto-central negativity increases.

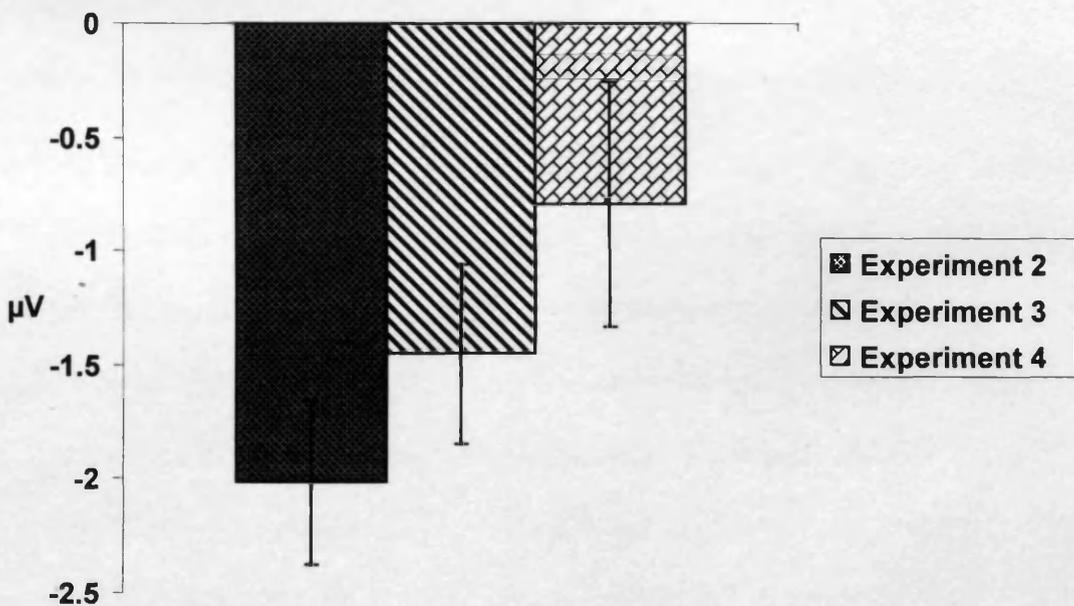


Figure 40. Mean amplitude of the late (1200-1900 ms) left fronto-central effect (collapsed over F1, F3, F5, C1, C3, C5, FP1, AF7 and F7 electrodes) elicited by associative recognition in the older participants in Experiments 2, 3, and 4.

Right-sided positivities in associative recognition

The age-equivalence of early right frontal activation in associative recognition appears to reflect the presence of an early frontopolar effect in the current young group. However, whilst topographically similar early right frontal

effects were found in older adults on the two occasions where the retrieval tasks were blocked, the early frontal components elicited by associative recognition in young adults seem to lack any consistent form or logic. The early frontal effect in the current young group appears more anterior than the mid-frontal component produced by associative recognition in Experiment 2. Yet importantly, both fronto-polar and mid-frontal effects in young adults have been linked to familiarity (fronto-polar effect – Duarte et al., 2004; mid-frontal effect – e.g. Rugg et al., 1998a; Curran, 2000; Curran & Cleary, 2003; Nessler & Mecklinger, 2003; Groh-Bordin et al., 2005) or to processes that likely occur upstream of familiarity (fronto-polar effect – Tsivilis et al., 2001).

Previously, a familiarity interpretation of the early right prefrontal effect in older adults appeared inconsistent with the absence of any similar modulation in item recognition. However, in the current experiment, although the elimination of the task-switch requirement failed to produce a reliable early frontal effect in the older group in item recognition, the preliminary analyses revealed that the earliest old/new differences were located over right frontal (F6 and FC6) electrodes. Moreover, the magnitude of this activation was significantly greater than that elicited by item recognition in the young group.

Finally, in contrast to the findings of Experiments 2 and 3, there was no age-related magnitude difference in the late central/posterior positivity elicited by associative recognition, although the older adults' component did appear more lateralised. Importantly, despite the absence of any reliable left-sided negative-going effects in the elderly, robust positive-going activity was apparent over right, but not left, parietal sites between 900 and 1200 ms. This observation suggests that a previous argument that an age-related reduction in

the left parietal effect reflected the modulation being "swamped" by a dominant left-sided negative-going component (Li et al., 2004) cannot account for the current findings.

Summary

The reduction of the magnitude of the late left fronto-central negativity elicited by associative recognition across the experiments, and its relation to task difficulty, are consistent with the modulation's interpretation as an index of compensatory processes in older adults. However, in item recognition, topographical differences between an early left fronto-central effect and a more posterior negative component suggest that the modulations are functionally distinct. Finally, although eliminating the task-switch requirement failed to produce a robust early right frontal effect in item recognition, old/new differences were apparent over lateral right frontal electrodes from 440 ms post-stimulus. The final experimental chapter in this thesis presents a simplified item recognition paradigm that aims to test the hypothesis that the absence of the early right frontal putative correlate of familiarity from older adults in item recognition may reflect an increase in task complexity following the associative encoding instructions. Experiment 5 will also provide an evaluation of the proposal that the left central/posterior negativity in item recognition indexes processes involved in the retrieval of task-irrelevant contextual information in older adults.

Chapter 10

Experiment 5

Introduction

The evidence from the previous experiments appears coherent with regard to the effect of ageing on the left parietal effect. The severe attenuation of this modulation, even when the use of recollection is promoted in associative recognition, is consistent with the dual process assertion that recollective processes are disproportionately impaired in older people. The story is less clear, however, with regard to both an early frontal effect that may represent the ERP correlate of familiarity in older adults and the left-sided negative-going components that have been variously elicited in the older groups in item and associative recognition.

The absence of robust early right frontal activity from item recognition is particularly problematic for the familiarity interpretation of the effect as dual process theory predicts that the contribution of familiarity should be greater to

item recognition than to associative recognition (for a review, see Yonelinas, 2002). However, the presence of an early right-sided component in older adults during a simple item recognition task (Morcom & Rugg, 2004) suggests that the complexity of the experimental design in the current research may underlie the severe attenuation of the early right frontal effect in item recognition.

The negative-going activations elicited by item recognition seem to represent more than one ERP effect: an early (500-900 ms) frontal modulation was evident in Experiments 2 and 3, but absent from Experiment 4; here, a later (900-1200 ms) negative-going component had a more posterior distribution. This late negativity closely resembles a central/posterior negative-going modulation that has previously been associated with the retrieval of source information in older adults (Trott et al., 1997; Wegesin et al., 2002; Li et al., 2004), but which was not reported in a recent item recognition ERP ageing study (Morcom & Rugg, 2004). However, as the experiments in this thesis have all required participants to encode words associatively, rather than individually, it has been argued that the central/posterior effect in item recognition in Experiments 3 and 4 may reflect some task-irrelevant retrieval of study context in older adults.

The final experiment aims to address the question of the functional significance of the early right frontal and central/posterior effects in older adults by simplifying the experimental design and reducing any potential confound of context. Specifically, study words will be presented and encoded individually. Moreover, a study/test lag manipulation will be included to provide a contrast between an easy and a more difficult condition, thereby allowing an investigation of the ERP correlates of retrieval effort (as indexed by

performance) in older adults. It is anticipated that the simplification of the encoding task will improve performance by reducing 'mental clutter' (Hasher & Zacks, 1988; Zacks & Hasher, 1994; Hasher et al., 1999), and that accuracy will further be increased in the short lag (easy) condition.

Electrophysiologically, the appearance of early right frontal old/new effects in both short lag (easy) and long lag (difficult) conditions would support its interpretation as the ERP correlate of familiarity in older adults. Secondly, the reduction of the left central/posterior negativity when words are encoded individually would be consistent with the retrieval of context account of the modulation. Finally, if compensatory processes in older adults are indexed by left fronto-central negative-going modulations, then the short/long lag retrieval effort comparison should reveal ERP differences over left anterior sites.

Methods

Participants

20 participants (11 male, mean age 69.0 years, range 66-77) took part in the experiment; all had been involved in one of the earlier experiments between 3 and 14 (mean 8.5) months previously. On this occasion, payment was not offered, but any expenses were reimbursed. During a single visit to the laboratory, the participants were trained on the experimental task, before being capped for the EEG recording of the main experiment; they also completed a self-rated health assessment form and the Beck's Depression Inventory (Beck et al., 1961). The data from one female had to be discarded due to technical difficulties and one male was excluded on behavioural grounds. 18 participants (10 male, mean age 69.2, range 66-77) remained, all of whom were free from

depression [mean BDI score (\pm S.D.) 5.44 (3.3)] and rated themselves to be in fair to excellent health at the time of testing.

Stimulus materials, procedure and ERP recording

The “General Methods” chapter provides details about the stimulus materials, and the ERP recording and analysis. However, the current procedure differs from that given previously, and is therefore described in detail here.

The main experiment comprised 5 study/test blocks. In order to maximise performance, and to keep the length of the study phase consistent with previous experiments, 24 single words were presented during each study phase. The study task, generating a sentence using each word, also mirrored the previous experiments. The words in the first half of each study phase contributed to the long lag (difficult) condition, those in the second half contributed to the short lag (easy) condition. The presentation of the words was randomized within each lag manipulation.

At test, the words from the short lag study condition (short old) were presented first, randomly intermixed with an equal number of unseen new words. The long lag study words (long old), again randomly intermixed with an equivalent number of new words, were presented after a 5 minute interval during which participants performed a filler task (counting backwards from 5000 in steps of 8) to prevent any rehearsal. Participants were required to make an old/new decision to each test word followed by a confidence judgment. The timing during the study and test phases was identical to that in Experiments 2, 3 and 4. The allocation of words to the old, new, short lag and long lag conditions,

the response hand in the study phase, and the hand-response mapping in the test phase, were counterbalanced across participants.

The 480 single words used in this experiment were drawn from the two study word lists used in Experiment 4. 240 words were taken from each list, but were kept separate to ensure that no participant would see any word that they had viewed on their previous visit. A short learning block (3 long and 3 short lag words at study) and a full length practice block, administered prior to capping, were compiled using words that had been seen in previous experiments.

Results

Behavioural

Table 28. Mean performance data (\pm S.D.) for Experiment 5.

	Short Lag	Long Lag
<u>Accuracy</u>		
Hits	0.94 \pm 0.05	0.90 \pm 0.06
Correct Rejections (CR)	0.94 \pm 0.07	0.92 \pm 0.09
Confident Hits (rating = 5)	0.87 \pm 0.14	0.83 \pm 0.18
Confident CR (rating = 5)	0.67 \pm 0.27	0.61 \pm 0.32
Pr	0.88 \pm 0.10	0.82 \pm 0.11
Br	0.40 \pm 0.38	0.37 \pm 0.29
<u>RT(ms)</u>		
Hits	1224 \pm 201	1336 \pm 266
CR	1388 \pm 270	1462 \pm 291
<u>Study RT(ms)</u>	2614 \pm 1230	

The performance data are summarised in Table 28. The hits and correct rejections ANOVA produced a main effect of lag [$F(1,17) = 15.52, p = 0.001$] reflecting greater accuracy in the short lag condition. This result was supported

by a paired t-test of the discriminability index (Pr) [$t(17) = 3.94$, $p = 0.001$]. The t-test of the bias index (Br) was not significant.

The confidence data was divided into high and low confidence ratings and analysed as previously. Main effects of response category [$F(1,17) = 25.74$, $p < 0.001$] and lag [$F(1,17) = 14.01$, $p < 0.01$] indicated that participants were more confident about hit responses and in the short lag condition. The RT ANOVA, likewise, produced main effects of response category [$F(1,17) = 10.27$, $p < 0.01$] and lag [$F(1,17) = 18.61$, $p < 0.001$] demonstrating that responses were quicker for hits and in the short lag condition.

Summary of behavioural data

The behavioural results demonstrate that, as expected, performance was superior in the short lag (easy) condition compared to the long lag (difficult) condition. Participants were also more confident about short lag responses than about long lag responses; hits were produced faster, and with greater confidence, than correct rejections, but bias was equivalent in the two conditions. Moreover, performance in both conditions was superior to that of the older adults in Experiments 2, 3 and 4.

Event-related potentials

Short lag (easy)

Figure 41 (p328) shows the grand average OLD and NEW waveforms for the short lag condition from 30 EEG electrode sites. The mean number of trials (\pm S.D.) contributing to the ERPs was 47 (9) OLD, and 47 (8) NEW. The waveforms diverge from approximately 350 ms post-stimulus onset, with the ERPs for OLD words becoming more positive than those for NEW words, chiefly over the right hemisphere. Between 500 and 700 ms, the posterior positivity is maximal over left parietal electrodes. Meanwhile, a short-lived negative-going component is apparent over left central and left frontal sites from 600 to 800 ms. Finally, at around 1100 ms, right frontal and right central modulations increase in amplitude and persist until the end of the recording epoch.

Long lag (difficult)

Figure 42 (p329) shows the grand average OLD and NEW waveforms for the long lag condition from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 42 (10) OLD and 44 (8) NEW. Positive old/new differences onset at about 350 ms post-stimulus and appear maximal over right prefrontal and right frontal electrodes. A small negative-going old/new difference is also present over left and right parietal sites, and over left central electrodes between 500 and 1100 ms. The right frontal positivity persists until the end of the recording epoch, but extends to right central sites from around 900 ms.

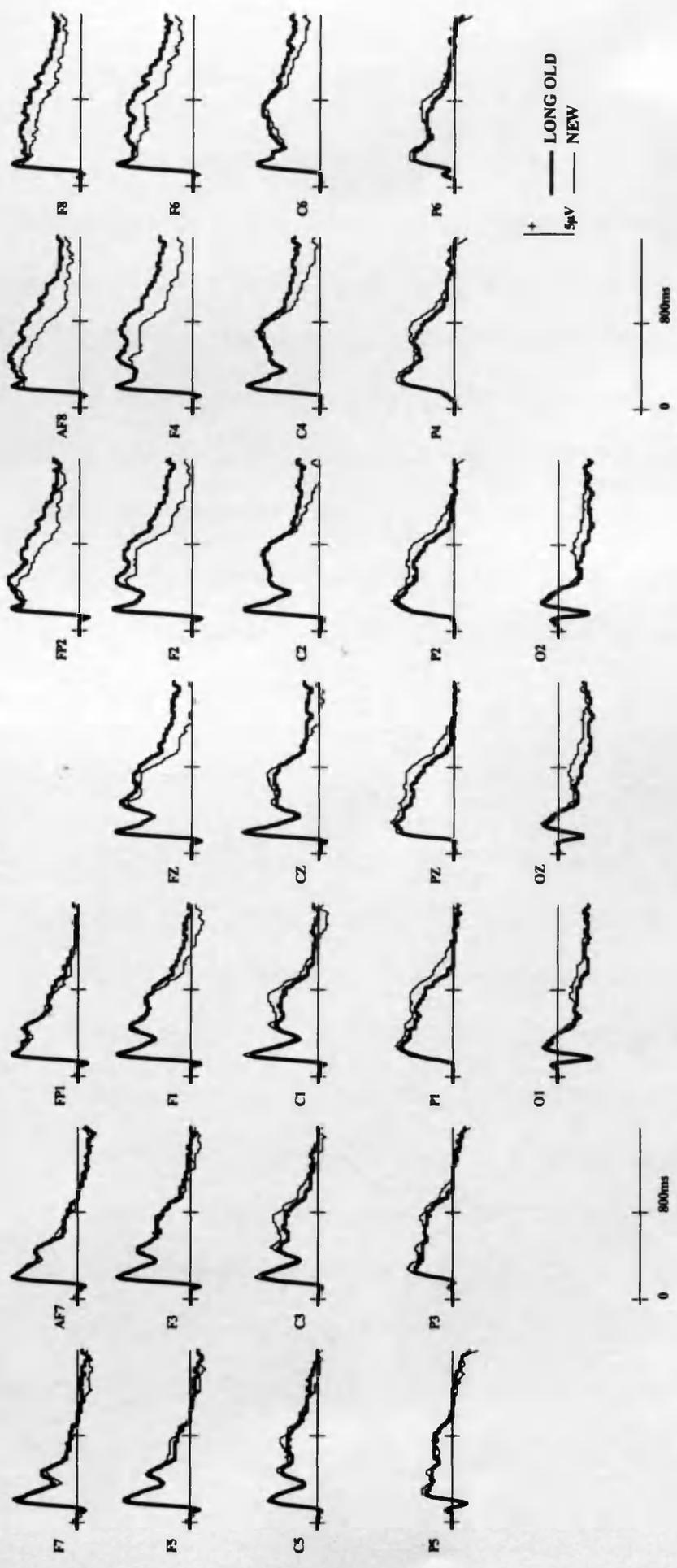


Figure 42. Grand average ERPs for the recognised (LONG OLD) and NEW response categories for the long lag condition. Electrodes are shown as in Figure 10.

Rationale for the ERP analyses

This experiment aimed to investigate the ERP effects elicited by a simple item recognition task in older adults under easy and more difficult test conditions. The critical comparisons were therefore between OLD and NEW words from the short (easy) and long (difficult) study/test lag manipulations. Preliminary analyses suggested the following four latency periods best reflected the development of ERP effects over the course of the epoch: 300-500 ms, 500-900 ms, 900-1200 ms and 1200-1900 ms. The design of the ANOVAs is similar to those described in the "General Methods" chapter and Experiment 2, however, in the between-condition ANOVAs the factor of task was replaced by lag 'LG' (short vs. long).

Short lag (easy)

The earliest significant old/new differences in the short lag condition were observed at 376 ms over the right parietal electrode P6. However, subsidiary analyses indicated that the response category, hemisphere and location interaction in the Main 300-500 ms ANOVA (Table 29, below) principally reflected a marginally significant early right frontal component [$t(17) = 2.18, p = 0.088$]. By 500-900 ms, this early right frontal effect was robust and had spread to right prefrontal sites, as shown by the subsidiary analyses investigating the interactions in the Prefrontal and Main ANOVAs [right prefrontal – $t(17) = 2.60, p < 0.05$; main effect of response category – right frontal, $F(1,17) = 12.92, p < 0.01$] (Figure 43, B). Importantly, the left fronto-central old/new difference was not significant.

Table 29. Results of the amplitude analysis for the critical ERP comparisons for short and long lag conditions.

Latency Region	Lag	
	Short	Long
300-500ms RCxL RCxHxL <i>Additional analyses</i> RCxS(c) RCxL(m) RC(pf)	F(1,17)=9.16,p<0.01	F(1,17)=12.43,p<0.01 F(1,17)=4.49,p<0.05 F(1.9,32.7)=7.67,p<0.05 F(1.8,30.1)=5.51,p<0.05 F(1,17)=4.38,p=0.052
500-900ms RCxH RCxL RCxHxL RCxHxS RCxHxLxS <i>Additional analyses</i> RCxL(m) RC(pf) RCxH(pf)	F(1,17)=8.55,p<0.01 F(1,17)=97.27,p<0.001 F(1.9,32.7)=15.61,p<0.001 F(1,17)=10.16,p<0.01	F(1,17)=5.79,p<0.05 F(1,17)=11.54,p<0.01 F(1,17)=17.38,p=0.001 F(1.6,26.4)=15.76,p<0.001 F(2.2,37.1)=9.77,p<0.001 F(1,17)=7.54,p<0.05 F(1,17)=13.47,p<0.01
900-1200ms RCxL RCxHxL RCxLxS RCxHxLxS <i>Additional analyses</i> RCxL(m) RC(pf) RCxH(pf)	F(1,17)=16.12,p=0.001 F(1.1,18.6)=6.05,p<0.05 F(1.9,31.7)=4.60,p<0.05	F(1,17)=13.74,p<0.01 F(1,17)=9.07,p=0.091 F(1.3,22.6)=18.22,p<0.001 F(1.8,30.5)=6.00,p<0.01 F(1.7,29.2)=11.95,p<0.001 F(1,17)=7.03,p<0.05 F(1,17)=6.88,p<0.05
1200-1900ms RC RCxH RCxHxL RCxS RCxLxS RCxHxLxS <i>Additional analyses</i> RC(c) RCxS(c) RC(m) RCxL(m) RCxH(pf)	F(1,17)=5.91,p<0.05 F(1,17)=7.00,p<0.05 F(1,17)=4.37,p=0.052 F(1.3,22.5)=5.22,p<0.05 F(1,17)=5.83,p<0.05 F(1.1,19.4)=4.92,p<0.05 F(1,17)=6.82,p<0.05 F(1,17)=6.32,p<0.05	F(1,17)=7.61,p<0.05 F(1.7,29.7)=10.78,p<0.001 F(1.9,32.4)=3.59,p<0.05 F(1,17)=7.74,p<0.05 F(1,17)=4.95,p<0.05 F(1.7,28.7)=8.63,p<0.01

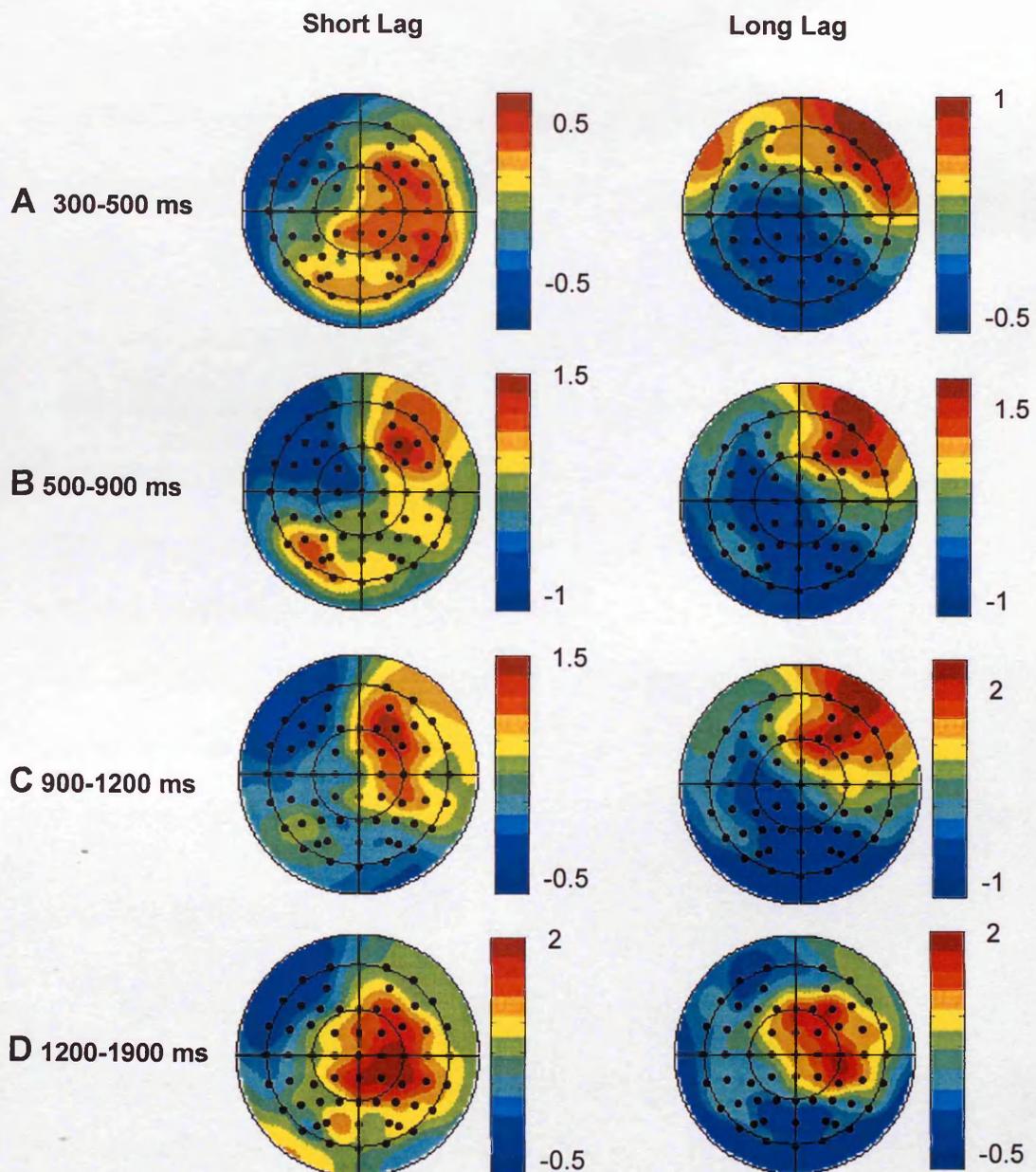


Figure 43. Topographic maps illustrating the scalp distribution of ERP effects for the short and long lag conditions in Experiment 5. Panel A illustrates the 300-500 ms latency region; B – 500-900 ms; C – 900-1200 ms; and D – 1200-1900 ms. The maps are shown as in Figure 12.

The offset of right frontal activity during the 900-1200 ms latency period, was confirmed by a post hoc t-test of right frontal sites investigating the four-way interaction in the Main ANOVA [$t(17) = 2.10$, n.s.]. Finally, although main effects of response category in the Main, Central and Midline 1200-1900 ms ANOVAs suggested that OLD waveforms were globally more positive than

NEW waveforms, targeted t-tests investigating the three-way interaction in the Main ANOVA demonstrated that the modulation was right-sided and had a central/posterior focus [right parietal – $t(17) = 3.52$, $p < 0.01$; right frontal – $t(17) = 2.35$, $p = 0.06$] (Figure 43, D).

Importantly, Figure 41 and Figure 43, B indicate that a short-lived left parietal effect may be present in the short lag condition. Therefore, an ANOVA of frontal and parietal locations of the 500-700 ms latency period was conducted. This analysis revealed various interactions including a four-way response category, hemisphere, location and site interaction [$F(1.8,30.7) = 14.14$, $p < 0.001$]. Subsidiary analyses confirmed the presence of significant parietal old/new differences over both left [$t(17) = 2.75$, $p < 0.05$] and right [$t(17) = 3.05$, $p < 0.05$] hemispheres.

Long lag (difficult)

The earliest old/new differences in the long lag condition were observed at 376 ms over the right prefrontal electrode AF8. Accordingly, although the Prefrontal 300-500 ms ANOVA produced a marginal main effect of response category (Table 29), targeted t-tests indicated that old/new differences were only robust over the right prefrontal hemisphere [$t(17) = 2.76$, $p < 0.05$] (Figure 43, A). Subsidiary analyses investigating the three-way interaction in the Main ANOVA did not reveal any significant results. Between 500 and 900 ms, investigations of the interactions in the Prefrontal and Main ANOVAs again principally reflected the presence of a reliable early right frontal ERP effect [right prefrontal – $t(17) = 4.60$, $p < 0.001$; main effect of response category –

right frontal, $F(1,17) = 19.38, p < 0.001$]. Importantly, there was no indication of any left parietal voltage differences.

Subsidiary analyses investigating interactions in the Prefrontal and Main 900-1200 ms ANOVAs demonstrated the continuing presence of right anterior old/new differences [right prefrontal – $t(17) = 3.30, p < 0.01$; main effect of response category – right frontal, $F(1,17) = 8.78, p < 0.01$] (Figure 43, C). Finally, the 1200-1900 ms epoch was characterised by a seemingly right-sided fronto/central positivity (Figure 43, D). However, a main effect of response category [$F(1,17) = 8.60, p < 0.01$] in the subsidiary analysis of the frontal location, which followed the four-way interaction in the Main ANOVA, was modulated by a response category by site interaction [$F(1.7,29.3) = 8.94, p = 0.001$]. This pattern of results suggested that the modulation was more bilateral over frontal sites.

Topographic analyses

In view of the presence of robust (or marginally significant) ERP effects in all four latency regions, three sets of topographic comparisons were performed (300-500 ms vs. 500-900 ms, 500-900 ms vs. 900-1200 ms and 900-1200 ms vs. 1200-1900 ms) for each condition.

Short lag (easy)

An epoch, hemisphere, location and site interaction [$F(2.0,33.4) = 4.36, p < 0.05$] in the Main 300-500 ms vs. 500-900 ms ANOVA confirmed the more left-sided posterior distribution in the second time window. The second comparison failed to reveal any significant interactions, suggesting that the

distributions in the 500-900 ms and 900-1200 ms time windows were similar. The 900-1200 ms vs. 1200-1900 ms comparison produced interactions involving epoch, hemisphere and location [$F(1,17) = 8.74, p < 0.01$], and epoch, location and site [$F(1.2,21.2) = 6.12, p < 0.05$] in the Main ANOVA, and a marginal epoch by site interaction [$F(1.5,24.8) = 3.62, p = 0.054$] in the Central ANOVA. These results primarily indicate the increase in right central/posterior activity in the 1200-1900 ms time period.

Long lag (difficult)

The only noteworthy topographical differences appeared in the 900-1200 ms vs. 1200-1900 ms comparisons. Here, a marginal epoch by site interaction [$F(1.2,19.8) = 3.86, p = 0.058$] in the Main ANOVA, and an epoch by location interaction [$F(2.1,35.0) = 4.13, p < 0.05$] in the Midline ANOVA, confirmed the more bilateral and posterior distribution in the final time window.

Summary of the ERP effects by item recognition in the short and long lag conditions

The short lag (easy) condition produced a robust early right frontal positivity that seemed to be onsetting in the 300-500 ms latency period, but was maximal between 500 and 900 ms. A short-lived left parietal effect was present between 500 and 700 ms, and was accompanied by a right-sided parietal old/new difference that appeared to reflect the onset of a later right central/posterior positivity (Figure 43, B and C). The earliest old/new differences in the long lag (difficult) condition were present over right prefrontal sites between 300 and 500 ms. This modulation spread to right frontal sites in the following time window and appeared to persist until 1200 ms. The final latency

period was characterised by a bilateral fronto-central positive effect.

Importantly, there were no robust left-sided negative-going components in either condition.

Old/new effects – short lag vs. long lag

As both conditions produced robust (or marginally significant) ERP effects in all four time windows, four sets of between-condition magnitude and topographic comparisons were conducted. A Main magnitude ANOVA was also conducted over the reduced 500-700 ms latency region to assess differences in left parietal activity between the short and long lag conditions.

Table 30. Results of the between-condition magnitude and topographic comparisons.

Latency Region	Magnitude	Topographic
300-500ms LGxL	$F(1,17)=6.51, p<0.05$	$F(1,17)=5.45, p<0.05$
500-900ms LGxL <i>Additional analyses</i> LGxL(m) LG(pf)	$F(1,17)=17.16, p=0.01$ $F(2.0,34.3)=12.10, p<0.001$ $F(1,17)=5.04, p<0.05$	$F(1,17)=15.63, p=0.001$ $F(2.0,34.5)=10.68, p<0.001$
900-1200ms LGxL <i>Additional analyses</i> LGxL(m) LG(pf)	$F(1,17)=13.22, p<0.01$ $F(2.1,35.3)=8.35, p=0.001$ $F(1,17)=4.68, p<0.05$	$F(1,17)=4.50, p<0.05$
1200-1900ms <i>Additional analyses</i> LGxL(m)	$F(1.7,29.6)=5.31, p<0.05$	$F(1,17)=8.16, p<0.01$

The disparity between the ERP effects elicited by the short lag and long lag conditions was minimal in the 300-500 ms latency period. Lag by location interactions in the Main magnitude and topographic ANOVAs (Table 30)

principally reflected differences over the parietal location, where a non-robust positivity in the short lag condition contrasted with a non-robust negativity in the long lag condition. Importantly, no reliable main effects or interactions were observed over right frontal or right prefrontal sites.

The Main 500-900 ms magnitude and topographic analyses produced lag by location interactions, which, as revealed by subsidiary magnitude analyses, reflected between-condition differences over the parietal location [$t(17) = 2.79, p < 0.05$]. Accordingly, a targeted t-test following a lag by location interaction in the Main 500-700 ms magnitude ANOVA [$F(1, 17) = 19.53, p < 0.001$] demonstrated that the left parietal effect was only present in the short lag condition [$t(17) = 3.20, p = 0.01$]. Meanwhile, although the main effect of lag in the 500-900 ms Prefrontal magnitude ANOVA suggested that prefrontal activity was more positive-going in the long lag condition, a targeted t-test of right prefrontal sites was not significant [$t(18) = 1.90, p > 0.15$].

This pattern of between-task differences continued during the 900-1200 ms latency period; however, targeted t-tests revealed that the parietal differences principally reflected the increased right central/posterior positivity in the long lag condition [right parietal – $t(17) = 2.77, p < 0.05$] (Figure 43, C). Finally, between 1200 and 1900 ms, although widespread centrally-focused right-sided positivities were evident in both conditions, lag by location interactions in the Midline magnitude and topographic analyses suggested that this modulation was more posterior in the short lag condition (Figure 43, D).

Summary of ERP differences between the short and long lag conditions

The principle differences between the short lag (easy) and long lag (difficult) conditions appeared over the posterior location and included the presence of a short-lived (500-700 ms) left parietal effect only in the short lag condition. Despite the seemingly earlier onset of right anterior old/new effects in the long lag condition, there were no robust between-condition differences over right frontal or right prefrontal sites. However, a widespread late right-sided modulation appeared to have a more posterior distribution in the short lag condition.

The ERP indices of retrieval effort

As predicted, following the removal of the associative encoding instructions, left-sided central/posterior negativities were absent from both lag conditions. This finding supports the interpretation of this modulation as reflecting task-irrelevant retrieval of context in Experiments 3 and 4. However, the question of the functional significance of the more anterior left fronto-central negativity observed in item recognition in Experiments 2 and 3 has not yet been addressed. If, as has previously been suggested, this modulation reflects compensatory retrieval operations in older adults, it would be predicted that the extent to which these processes are engaged should increase as a task becomes more difficult. The following section presents an ERP comparison aimed at testing the compensatory processes account of left fronto-central activity in item recognition. Contrasting the correct rejection (NEW) waveforms of the long lag (difficult) and short lag (easy) conditions provides a measure of

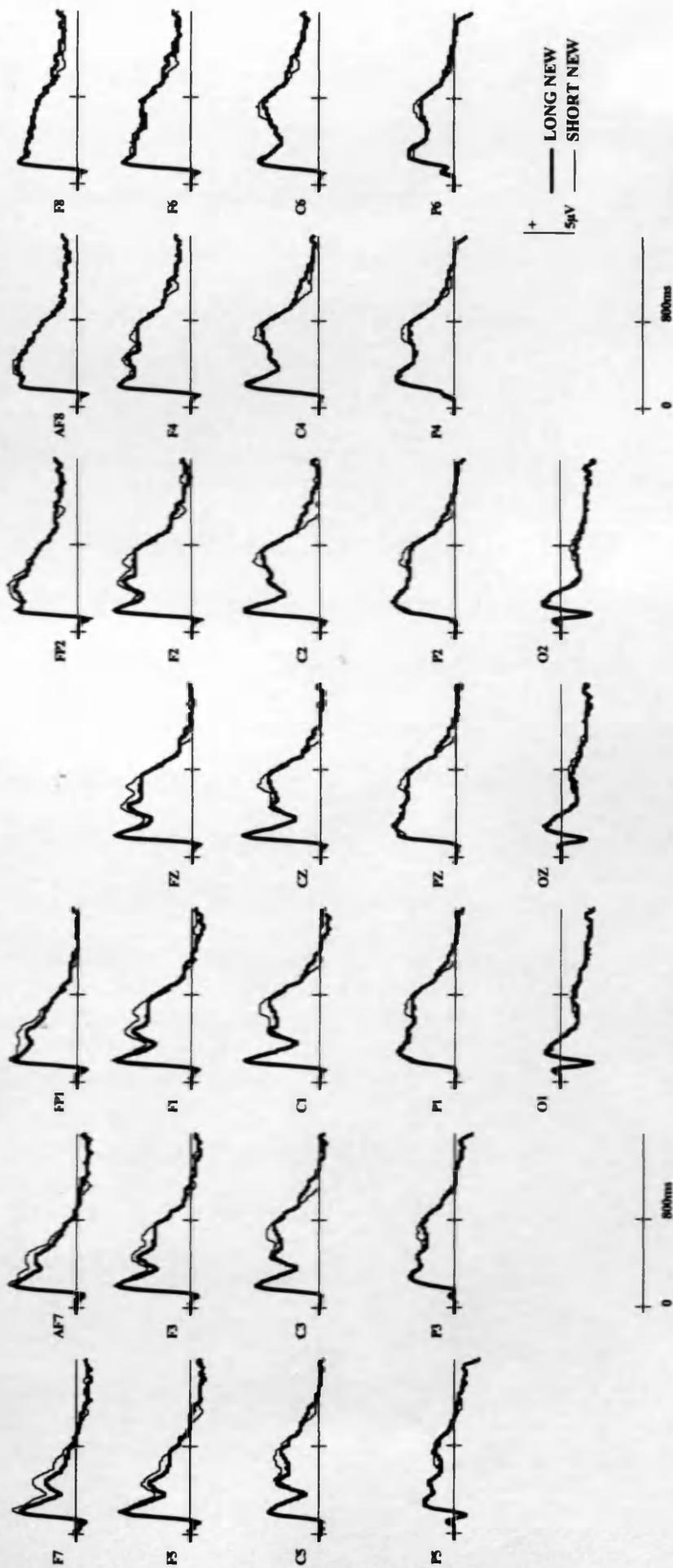


Figure 44. Grand average ERPs for the correct rejections from the long lag (LONG NEW) and short lag (SHORT NEW) conditions. Electrodes are shown as in Figure 10.

the ERP indices of retrieval effort independent of any confound of retrieval success or orientation (Rugg & Wilding, 2000). If left fronto-central negative modulations are related to compensatory operations, it would be predicted that the correct rejection waveforms elicited by the long lag condition should be more negative-going over left anterior sites than those elicited by the short lag condition.

Correct rejections – short lag vs. long lag

Figure 44 (above) shows the grand average NEW waveforms for the short lag and long lag conditions from 30 EEG electrode sites. The mean number of trials contributing to the ERPs was 47 (8) SHORT and 44 (8) LONG. The waveforms diverge from approximately 270 ms post-stimulus onset, with the LONG NEW waveforms becoming more negative-going than the SHORT NEW waveforms chiefly over left frontal and prefrontal sites. This modulation lasts until about 720 ms, but appears to extend towards left central sites from about 400 ms. Furthermore, between 1000 and 1200 ms, LONG NEW waveforms appear to be more positive-going than SHORT NEW waveforms, chiefly over central sites.

Consequently, the preliminary analyses suggested that the detailed analysis of two latency periods (300-700 ms and 1000-1200 ms) was sufficient to portray the principle ERP differences between the short lag and long lag conditions. The design of the magnitude and topographic ANOVAs was highly similar to those used in the within-condition magnitude comparison; the only difference being that the factor of lag 'LG' (short vs. long) now replaced that of response category.

Lag by location interactions in the Main and Midline 300-700 ms ANOVAs (Table 31, below) reflected the presence of a negative-going modulation over frontal sites. However, the lag by hemisphere interaction in the Prefrontal ANOVA demonstrated that voltage differences were only robust over the left prefrontal hemisphere [$t(17) = 3.27, p < 0.01$], and targeted t-tests of the frontal location also supported the left-sided asymmetry of the modulation [left frontal – $t(17) = 3.11, p < 0.05$; right frontal – $t(17) = 1.67, n.s.$] (Figure 45, A, p342). Between 1000 and 1200 ms, the main effect of lag in the Central ANOVA and the lag by location interaction in the Midline ANOVA demonstrated an increased positivity of LONG NEW waveforms that appeared slightly right-sided over the central location (Figure 45, B). The subsidiary analyses investigating the three-way interaction in the Main ANOVA failed to reveal any significant results.

Table 31. Results of the between-condition magnitude comparisons for the correct rejection waveforms.

Latency Region	Magnitude
300-700ms	
LGxL	$F(1,17)=7.30,p<0.05$
<i>Additional analyses</i>	
<i>LGxL(m)</i>	$F(1.78,30.2)=4.88,p<0.05$
<i>LG(pf)</i>	$F(1,17)=6.22,p<0.05$
<i>LGxH(pf)</i>	$F(1,17)=5.93,p<0.05$
1000-1200ms	
LGxLxS	$F(1.4,24.4)=4.26,p<0.05$
<i>Additional analyses</i>	
<i>LG(c)</i>	$F(1,17)=8.6,p<0.01$
<i>LGxL(m)</i>	$F(1,17)=3.60,p<0.05$

The topographic (300-700 ms vs. 1000-1200 ms) comparison revealed epoch by location interactions in the Main [$F(1,17) = 10.30, p < 0.01$] and Midline [$F(2.3,38.6) = 19.77, p < 0.001$] ANOVAs, an epoch by site interaction

in the Central ANOVA [$F(1.4,23.3) = 5.35, p < 0.05$], and an epoch by hemisphere by site interaction in the Prefrontal ANOVA [$F(2.0,33.7) = 7.47, p < 0.01$]. These results confirm the progression from the left anterior negative-going modulation in the first time window to the bilateral central component in the second time window.

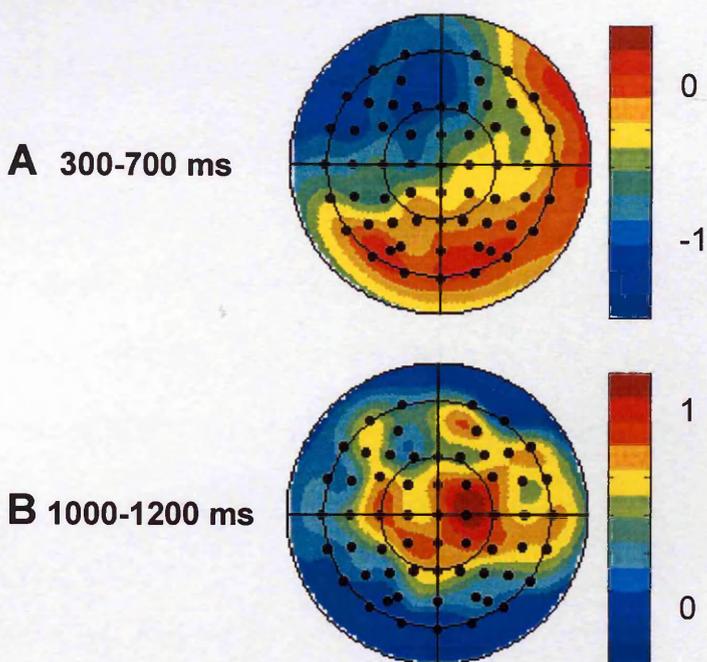


Figure 45. Topographic maps illustrating the scalp distribution of ERP differences between long lag and short lag CRs in Experiment 5. Panel A illustrates the 300-700 ms latency region; B – 1000-1200 ms. The maps are shown as in Figure 12.

Summary

As predicted by the compensatory processes account, correct rejection waveforms in the long lag (difficult) condition were more negative-going than those in the short lag (easy) condition over left frontal and prefrontal sites. This modulation was reliable between 300 and 700 ms, and was followed by a short-lived (1000-1200 ms) slightly right-sided central positivity.

Discussion

The results of Experiment 5 were in line with our predictions: First, the presence of early frontal effects in both lag conditions, confirms that their absence in Experiments 2, 3 and 4 most likely reflected the complexity of the experimental design. The results support the interpretation of the early frontal effect as the ERP correlate of familiarity in older adults. Second, the absence of any left central/posterior negativity following the removal of the associative encoding instructions is consistent with its interpretation as previously indexing task-irrelevant retrieval of study context in item recognition. Finally, the increased left fronto-central negativity to correct rejections in the long lag (difficult) condition supports the argument that the left fronto-central old/new effect represents compensatory processes in older people.

Behavioural findings

The observed improvement in accuracy when the encoding task was simplified, and the superior performance in the short lag condition, compared to the long lag condition, were both consistent with our predictions. Moreover, participants were more confident about their responses in the short lag condition. Although prior studies of young adults have indicated that familiarity decays more rapidly than recollection over short delays (Hockley, 1991), mindful of the caveat that increased confidence can reflect greater high confidence familiarity rather than greater recollection (Yonelinas, 2001a; 2001b; 2002), the current confidence data suggest that in older adults, recollection declines to a greater extent than familiarity over intermediate delays.

Left parietal effect present in short lag condition

The proposal that recollection suffers a disproportionate decline over intermediate delays is also consistent with the presence of a short-lived (500-700 ms) left parietal index of recollection in the short, but not the long, lag condition. The reason for the appearance of a left parietal effect here, but not in a short delay condition in a previous item recognition ERP ageing study (Morcom & Rugg, 2004), is unclear. The discrepancy could reflect the high accuracy in the current experiment (mean $Pr = 0.88 \pm 0.10$) compared to the Morcom and Rugg study (mean $Pr = 0.77 \pm 0.13$). At first sight this explanation may seem unlikely given the presence of robust left parietal activation in an item recognition condition where the older groups' performance was greatly reduced (Experiment 2). However, the left parietal activation in Experiment 2 (Figure 20, B, p210) appears to originate from a posterior bilateral component, whereas the modulation in Experiment 5 has clear left-sided focus (Figure 43, B, p332).

Does the early frontal effect reflect familiarity?

The presence of an early frontal effect in both lag conditions confirms that this modulation is elicited during simple item recognition tasks, which, according to behavioural research, should be heavily reliant on familiarity (Hintzman & Curran, 1994; Hintzman & Caulton, 1997; Hintzman et al., 1998). Although the modulation did not appear to be robust in the short lag condition until the second time window, post hoc Main and Prefrontal analyses of the 300-400 ms and 400-500 ms time periods confirmed that the effect became robust between 400 and 500 ms in both conditions [short lag – right frontal,

$t(17) = 2.57, p < 0.05$; long lag – right frontal, $t(17) = 2.62, p < 0.05$, right prefrontal, $t(17) = 3.08, p < 0.05$].

In the short lag condition, the early right frontal modulation offset at about 900 ms, whereas in the long lag condition, the lack of qualitative differences until the final latency period suggests that the effect persisted until 1200 ms. This extended duration may seem problematic for the familiarity interpretation, as in young adults the mid-frontal component tends to be short-lived (e.g. Rugg et al., 1998a). However, Morcom and Rugg (2004) did not find any topographic differences in their older group's ERPs, and Wegesin and colleagues' (2002) early right frontal modulation appears to persist until 1000 ms post-stimulus. It is therefore possible that the extended duration of the effect may reflect the participants' reliance on familiarity as their primary basis for retrieval in the long lag condition. Alternatively, the current results may simply reflect the shortcomings of the normalisation procedure carried out prior to the topographic comparisons (c.f. Haig et al., 1997).

The functional significance of the left-sided negative-going modulations

Although some negative-going activation was evident in both conditions, it was not reliable in either case; critically, as predicted, there were no robust left-sided central/posterior negative modulations. Although this result supports the contextual retrieval account of the central/posterior negativity, the increased performance in Experiment 5 could be taken to suggest that the concomitant disappearance of the central/posterior component might equally reflect

decreased retrieval effort. This account appears unlikely, however, as the modulation was not observed in Experiment 2 where task difficulty was highest.

Instead, the demonstration that retrieval effort was indexed by a left frontal component is consistent with the compensatory processes account of the early left fronto-central old/new negativities reported in Experiments 2 and 3. In further support of this interpretation, a significant negative correlation was found between the magnitude of the early left fronto-central modulations in Experiments 2 and 3 and item recognition Pr [$r = -0.374$, $p < 0.05$]. Moreover, a comparable effect was evident in older adults in a contrast between the correct rejection waveforms elicited by words that had been studied as pictures and those elicited by words that had been studied as words (Morcom & Rugg, 2004). Although this component was considered to reflect retrieval cue processing effects, the important point with regard to the current argument was that performance was reduced in the word-picture condition compared to the word-word condition (but see Robb & Rugg, 2002, for evidence suggesting that ERP effort effects are confined to the first 300 ms post-stimulus).

Late right frontal effects

The late right-sided effects in the final time window had a central rather than a frontal focus in both conditions. Nevertheless, these modulations were highly similar to a late right-sided component elicited by item recognition in the older group in Experiment 3 that was statistically indistinguishable from the late right frontal effect in young adults (see also Morcom & Rugg, 2004).

Interestingly, however, in the current experiment, distributional differences were observed between the components produced by the long and short lag

conditions. Recent event-related fMRI studies have demonstrated that distinct right prefrontal (PFC) regions play different roles in episodic retrieval in young adults. Specifically, whilst right anterior PFC is associated with the quantity of episodic information retrieved, right dorsolateral PFC is associated with retrieval-monitoring processes or effort (Henson et al., 2000; for a review, see Fletcher & Henson, 2001). The current findings suggest that a similar functional dissociation may exist within the right prefrontal cortex of older adults.

Finally, a short-lived (1000-1200 ms) right central positivity to correct rejections in the long lag condition appeared highly similar to a component that was interpreted as reflecting semantic processing in young adults following a contrast between a shallow encoding condition and a deep encoding condition (Rugg et al., 2000). However, the equivalence in the semantic demands of both lag conditions in the current experiment appears inconsistent with the semantic processing account. Instead, the timing of the modulation (it occurs 200-400 ms before the mean correct rejection RT), and the reduced performance in both long lag and Rugg and colleagues' (2000) shallow encoding conditions, suggest that, like the earlier left fronto-central component, it may index processes relating to the difficulty of the retrieval decision. The precise nature of these operations is unclear; however, the temporal and topographic dissociations between the fronto-central negativity and the central positivity confirm that these two modulations are distinct.

Summary

Experiment 5 provides a degree of insight into the functional significance of the ERP effects elicited by recognition memory in older adults. The presence

of an early right frontal effect in both lag conditions supports its interpretation as the ERP index of familiarity in older adults. Moreover, the evidence of a left frontal ERP correlate of retrieval effort is consistent with the account of the left fronto-central negative-going component in item recognition in Experiments 2, 3 and 4 as an index of compensatory processes. The final chapter in this thesis will present an overview of these and the other experimental findings reported in the last five chapters, and will attempt to integrate them into the current framework of knowledge regarding episodic retrieval and ageing.

Chapter 11

General Discussion

The research reported in this thesis had two principle aims: Firstly, to identify differences in the ERP correlates of item and associative recognition in young adults. Secondly, to examine the effect of ageing on these correlates, particularly with reference to the dual process prediction that recollection would be compromised in older adults whilst familiarity remained relatively intact. As the behavioural results have already been discussed within the context of each relevant experiment chapter, the current chapter will focus on the electrophysiological data. Accordingly, the ERP findings will be summarized, discussed (with reference to the behavioural results where appropriate), and sited within the framework of current knowledge regarding the neural correlates of episodic memory and the impact of ageing on these correlates.

The ERP correlates of recognition in young adults

Components common to item and associative recognition

The first four experiments allowed the ERP indices of item and associative recognition in young adults to be directly compared, free from any confound of different encoding tasks and separate participant groups. The most consistent finding was, as predicted by dual process theory, the presence of left parietal indices of recollection of similar magnitude in both item and associative recognition. Somewhat unexpectedly, however, the late right frontal index of post-retrieval processing was also equivalent in both tasks. Although previous ERP studies had suggested that the late right frontal effect should be increased in more demanding tasks, such as those requiring source or context memory (Wilding & Rugg, 1996; 1997a; 1997b), the component was consistently elicited by item recognition, regardless of whether the test phase was randomised, blocked, or involved one or two-stage decisions. This constancy across the various retrieval manipulations suggests that the presence of the late right frontal effect in item recognition likely reflects some aspect of the encoding task. Accordingly, focusing on the association between the words during encoding may have increased the complexity of the item recognition task, leading to the recruitment of additional post-retrieval monitoring operations (for other examples of late right frontal effects in complex item recognition tasks, see Düzel et al., 1997; Rugg et al., 1998b).

The foregoing conclusion remains tentative and needs to be tested through a direct comparison of the waveforms elicited by item recognition following the encoding of either item or associative information. Nevertheless,

this example highlights the utility of ERPs as a research tool, insofar as behavioural experiments have suggested that instructions to focus on associative information at encoding have no impact on item recognition (Hockley & Cristi, 1996).

Strategic recollection in associative recognition?

The presence of robust late right frontal effects in associative recognition demonstrates that the deployment of post-retrieval monitoring/evaluation processes was increased for same pairs compared to rearranged pairs. This evidence, in conjunction with the reliable left parietal same/rearranged differences, and the longer RTs to rearranged pairs (compared to same pairs), suggests that associative correct rejections were being produced by default following the failure to recollect a study pair. A second possible interpretation of the test RT data, the recall-to-reject account (Rotello & Heit, 2000; Rotello et al., 2000; and see "Experiment 1"), is not supported by the electrophysiological data. The recall-to-reject account, which suggests that associative correct rejections follow the recollection of both the study pairs that contribute to a rearranged pair, would predict that left parietal activity should be greater for rearranged pairs than for same pairs.

Interestingly, however, the electrophysiological signature of a rearranged pair may be dependent on its target status. A previous ERP comparison involving rearranged and new (two unseen words) pairs demonstrated a left parietal effect to rearranged pairs when they were classed as targets (Donaldson & Rugg, 1998, Experiment 1). In contrast, a second study, where (similar to the current research) rearranged pairs were classed as

non-targets, reported no left parietal rearranged/new differences (Cheng & Rugg, 2004). Taken together, these results suggest that the current young participants may have adopted a selective retrieval strategy for associative recognition.

This selective retrieval interpretation echoes findings from exclusion studies that have demonstrated selective target-specific recollection when targets and non-targets were highly distinct (Herron & Rugg, 2003a; 2003b; Herron & Wilding, 2005; Dzulkifli & Wilding, 2005). In associative recognition, however, selective recollection appears to occur in the absence of high target/non-target distinctiveness. Moreover, although the target (same pairs) hit rate was generally high (0.83 – 0.91) in the current experiments, Cheng and Rugg (2004) failed to find any left parietal rearranged/new differences when target accuracy was much lower (0.67). This latter finding is consistent with the recent contention that target accuracy is not a critical determinant of selective recollection (Herron & Wilding, 2005). As the common factor in the current research and the Cheng and Rugg study was the emphasis on the association at encoding, it seems likely that the encoding task may be an important determinant of whether selective recollection is adopted in associative recognition.

The late central/posterior positivity in associative recognition

The principle dissociation between the ERPs elicited by item and associative recognition was the presence of a late central/posterior positive-going effect in associative recognition. This modulation became more right-sided as the epoch progressed (likely reflecting the offsetting left parietal

effect). Previous ERP studies of associative recognition, which have also included a new pairs condition, indicate that the late central/posterior component may reflect a negative-going modulation of rearranged waveforms, in conjunction with a positive-going modulation of same waveforms (Donaldson & Rugg, 1998; Van Petten et al., 2002). It has therefore been suggested that, similar to the late posterior negative slow wave (LPN) observed in source recognition studies (Cycowicz et al., 2001; Johansson et al., 2002), the associative recognition central/posterior positivity may index the maintenance of word-word associations whilst a same/rearranged judgement is made.

This maintenance of associations interpretation is consistent with the observation that the magnitude of the central/posterior component varied accordingly to the degree of uniqueness among the learned associations (Van Petten et al., 2002). The account also gains support from two recent event-related fMRI studies: First, Bunge and colleagues (2002) demonstrated the involvement of parietal cortex in maintaining a representation of competing stimulus-response associations during decision-making. Second, Achim and Lepage (2005) reported that activation in bilateral superior parietal cortex was increased in associative recognition compared to item recognition.

The early mid-frontal effect and familiarity

According to dual process theory, familiarity should contribute to item recognition, whereas associative recognition should depend heavily on recollection. However, the prediction that the early mid-frontal ERP correlate of familiarity should only be present in item recognition was not entirely upheld. Although, as expected, the modulation was present in item recognition in

Experiments 1 (randomized) and 3 (blocked), it was not reliable in Experiments 2 (randomized) and 4 (blocked). Here, robust early anterior activity was instead elicited by associative recognition. If the familiarity account of the early mid-frontal effect is veridical, despite lacking a consistent pattern, the results demonstrate that familiarity can contribute to associative recognition under certain conditions.

The foregoing conclusion evidently contradicts versions of dual process theory that preclude familiarity from being involved in associative recognition (Atkinson & Juola, 1974; Mandler, 1980). Other dual process authors, however, assert that familiarity can contribute to associative recognition under some circumstances (e.g. Jacoby & Dallas, 1981; Yonelinas et al., 1999). Moreover, although the increased rate of know responses to item hits in the remember/know phase of Experiment 1 was cited as evidence of a greater contribution of familiarity to item recognition than to associative recognition, the mutual exclusivity assumption underlying the original remember/know methodology (Tulving, 1985b) is not universally accepted. An alternative independence remember/know procedure (Yonelinas & Jacoby, 1995) estimates familiarity (F) as the probability of a know (K) response to an old item, given that the item was not remembered (R) [i.e. $F = K/(1-R)$]. Application of this equation to the remember/know data in Experiment 1 suggests that the contribution of familiarity to item and associative recognition was highly similar [mean proportion of familiarity-based responding – item recognition = 0.68 ± 0.25 , associative recognition = 0.76 ± 0.26 ; $t(22) = 1.21$, n.s].

The proposal that familiarity contributed to associative recognition in Experiment 4 relies not only on the assumption that the early mid-frontal effect

reflects familiarity, but also on the suggestion that it is functionally related to an early (from 400 ms) fronto-polar component that was elicited by the associative task in the fully blocked paradigm. A recent study examining the effect of changes in study/test modality on the early onset ERPs elicited by verbal stimuli appears to offer some insight into the relationship between early mid-frontal and fronto-polar effects. Curran and Dien (2003) found two early fronto-polar modulations, the first of which had a similar onset (176 ms) to the fronto-polar components observed in several studies using pictorial stimuli (Tsvilis et al., 2001; Duarte et al., 2004; Düzel et al., 2004). More importantly, a second fronto-polar component, which was maximal at 400 ms post-stimulus, contributed to the early mid-frontal effect and was only revealed when the mid-frontal modulation was decomposed using principal component analysis (see "Event-Related Potentials" chapter). Furthermore, whereas the sensitivity of the first fronto-polar effect to changes between study and test modality suggested that it indexed perceptual priming processes, the insensitivity of the second fronto-polar component to the modality manipulation indicated that it most likely reflected an amodal familiarity process.

In item recognition, although the mid-frontal effect was only intermittently reliable (in Experiments 1 and 3), there was evidence of early non-robust bilateral frontal activation elsewhere (Experiments 2 and 4). It is therefore likely that familiarity did contribute to item recognition in all four experiments, but the emphasis on the association during encoding may have disproportionately promoted the use of recollection during retrieval. Evidently, the lack of a consistent pattern in either task means that the foregoing interpretations are tentative. This caveat notwithstanding, the results appear inconsistent with the

trial structure interpretation of the early mid-frontal effect proposed in Experiment 3 (see also Donaldson & Rugg, 1999). The component was present in both item and associative recognition, not only when the retrieval tasks were randomized, but also when they were blocked.

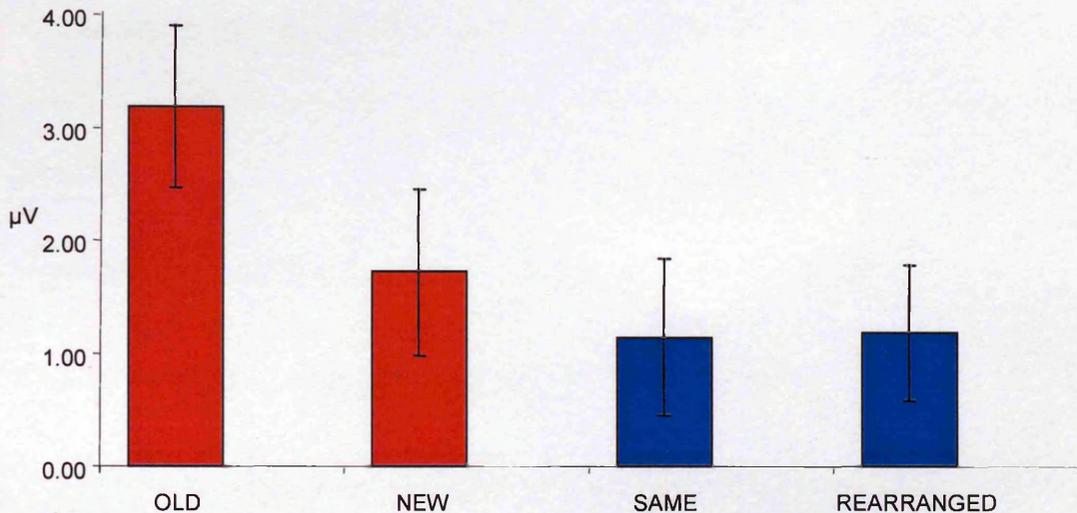


Figure 46. Mean mid-frontal amplitudes for each of the four critical retrieval conditions between 250 and 450 ms in Experiment 1. The voltages are averaged over 5 electrodes sites (F3, F1, Fz, F2, and F4). Item recognition (OLD and NEW) is shown in red, and associative recognition (SAME and REARRANGED) is shown in blue.

Finally, the current findings also run counter to the view of the early mid-frontal component as a negative-going index of novelty (Tsvilis et al., 2001; Schloerscheidt & Rugg, 2004). Whereas the novelty account predicts that NEW words should produce the least positive-going waveforms, Figure 46 clearly demonstrates that the amplitude of new waveforms was not significantly different from that of same or rearranged waveforms, both of which contained no novel stimuli. Re-examination of Tsvilis and colleagues' (2001) study suggests that their results are not completely at variance with the familiarity

interpretation of the mid-frontal effect. Despite being instructed to ignore the background scene, there is no evidence that their participants did so successfully. Indeed, in a subsequent behavioural remember/know procedure, more same stimuli than rearranged or old/new stimuli were 'remembered', suggesting that the background scene was being taken into account when recognition judgements were made. The background scenes were all shown seven times in the experiment, making them particularly salient and therefore familiar.

Age effects on the ERP correlates of recognition

The left parietal effect is reduced in older adults

The left parietal index of recollection was severely reduced or absent in older adults in both tasks. In item recognition, this finding agrees not only with our predictions, but also with a previous ERP ageing investigation of item recognition (Morcom & Rugg, 2004), and with the dual process expectation that recollection should be compromised in older adults. In contrast, the complete absence of a left parietal component in associative recognition was unexpected, because, like the source memory paradigms that reported statistically similar left parietal effects in young and older adults (Mark & Rugg, 1998; Trott et al., 1999; Wegesin et al., 2002), this task was expected to promote recollection.

Previously, the absence of a left parietal effect in older adults in one source memory experiment was attributed to its attenuation by an extensive negative-going modulation that dominated the left hemisphere (Li et al., 2004). This conclusion followed the observation that there was no age-related

reduction in the magnitude of right parietal activity. However, two observations preclude this interpretation of the current associative recognition data: First, the left parietal component in young adults and the left fronto-central negativity in older adults were temporally distinct. Second, in Experiments 2 and 3, where the left fronto-central negativities were maximal, there was no evidence of any right parietal same/rearranged difference in older adults.

Indeed, the demonstration by a series of exclusion studies (Dywan et al., 1998; 2001; 2002) that parietal activation distinguished between target and non-target stimuli in young adults, but not in older adults, may be more relevant to the current findings. Accordingly, whilst the young adults may have adopted a target-specific recollection strategy in associative recognition (see "Strategic recollection in associative recognition?", above), the elderly participants' inability to inhibit the goal-irrelevant retrieval of non-target (rearranged) stimuli would account for the absence of left parietal activation. In further support of this interpretation, the more liberal criterion adopted by the older groups in associative recognition [$t(106) = 4.74, p < 0.001$], suggests that the young and older groups were using different retrieval strategies.

The ERP correlate of familiarity in older adults?

Age-related delays in the onset of ERP effects are commonly reported (e.g. Mark & Rugg, 1998; Wegesin et al., 2002; Li et al., 2004). In contrast, in two out of the three age comparisons reported in this thesis, the associative recognition components in older adults onset at about the same time (or earlier) as those in young adults. (The exception to this pattern in Experiment 2 likely reflected the high task-switch load in that paradigm.) Although these early right-

sided frontal positivities were absent from item recognition in older adults when the encoding task focused on the association between the word pairs, this finding may have been an artifact of component overlap. Specifically, the early frontal positive-going effects seem to have been attenuated by early left fronto-central negativities; when the encoding task was simplified and the left-sided negativities reduced (Experiment 5), early right frontal components were observed in item recognition in both long and short lag conditions.

The appearance of early frontal effects in item recognition following the removal of the associative element of the encoding task is inconsistent with the proposal (see Experiment 3) that early right frontal activation in older adults indexes their recruitment of pre-retrieval operations to enhance associative recognition performance (c.f. Fletcher & Henson, 2001). In contrast, the early onset of the right frontal component, its general age equivalence, and its presence in both item and associative recognition, are consistent with a familiarity interpretation of the effect. In view of the dual process tenet that familiarity should be preserved in the elderly, it is surprising that few ERP ageing studies to date have made any mention of a potential ERP correlate of familiarity in older adults. Nevertheless, early right frontal effects similar to those observed in the current older group have been reported in one source memory study (Wegesin et al., 2002) and one item recognition study (Morcom & Rugg, 2004). Furthermore, two other ERP ageing investigations of episodic retrieval have also shown evidence of similar non-robust activations in their older participants (Li et al., 2004; Dywan et al., 2002).

The apparent distributional difference between the early frontal effects in young and older adults raises the issue of whether these components index

separate neural correlates. Such an interpretation would be problematic for dual process theory, which does not predict that either recollection or familiarity should be operationally different in young and older people. However, the lack of a consistent pattern to the appearance of the early mid-frontal effect in the young adults' ERPs means that a direct topographical ageing comparison of early frontal activations could only be conducted for associative recognition in Experiment 4. Importantly, these limited analyses failed to reveal any significant qualitative ageing differences. Furthermore, it remains unclear whether minor alterations in ERP morphology and scalp distribution between young and older adults are functionally interesting, or merely reflect age-correlated changes in the underlying cerebral architecture (Rugg & Morcom, 2004).

Finally, the intermittent appearance of early frontal activity in associative recognition in young adults may, in part, reflect their adoption of a target-specific recollection strategy; the early mid-frontal effect did not appear to differentiate between targets and non-targets when individuals were using strategic recollection (Herron & Wilding, 2005). In contrast, older adults' reduced capacity for recollection, and their inability to inhibit non-target information, means that they will be forced to rely on familiarity as their primary basis for same/rearranged distinctions. The behavioural data are consistent with this interpretation; while familiarity may serve well to identify same pairs, it lacks the precision required to detect rearranged pairs, leading to the increased associative recognition false alarm rate in the older groups (c.f. Light et al., 2002).

Late right frontal age-invariance

The late right frontal effect elicited by item recognition was equivalent in young and older adults. This result replicates that of previous ERP ageing studies (Mark & Rugg, 1998; Li et al., 2004; Morcom & Rugg, 2004) and is consistent with fMRI evidence that right PFC activation in episodic retrieval is often age-equivalent, or increased in older adults (Madden et al., 1999; Daselaar et al., 2003; for reviews, see Grady, 2000; Grady & Craik, 2000; Cabeza, 2002; Park & Gutchess, 2004). Older adults therefore appear able to recruit the same post-retrieval monitoring/evaluation operations as young adults. Nevertheless, the efficiency of these operations may be reduced, and the more diffuse distribution of the late right frontal effect in the current older participants may reflect the engagement of additional processes. In support of this argument, a PET study of cued-recall revealed a more posterior pattern of frontal activation for older adults, than for young adults (Schacter et al., 1996). Moreover, topographic differences between the right frontal effects elicited by the long lag (difficult) and short lag (easy) conditions in the older adults in Experiment 5 may reflect the greater activation of regions of right frontal cortex involved in effortful retrieval in the long lag condition (for a review of functional dissociations in prefrontal cortex, see Fletcher & Henson, 2001).

In associative recognition, while Experiments 3 and 4 replicated the foregoing age-invariance, in Experiment 2, the elderly adults' late right frontal activation was reduced compared to that of the young. This finding mirrors two ERP source memory studies that also reported an age-related reduction in the late right frontal effect (Trott et al., 1999; Wegesin et al., 2002). One factor that the three experiments have in common is the presence of sizeable late

negative-going modulations. In Experiment 2, the magnitude of the left fronto-central negativity was greater than in Experiments 3 and 4, and in the source memory studies, the central negativity was more bilateral than that observed elsewhere. The age-related right frontal reduction in associative recognition in Experiment 2, and in the previous source memory studies, may therefore simply reflect component overlap; specifically, the attenuation of the modulation by the concurrent negative-going effects.

Functional accounts of the left-sided negativities in older adults

Topographic differences between the left-sided negativities elicited by item recognition during the 500-900 ms and 900-1200 ms latency periods suggest that the left fronto-central activation may represent two separate underlying components. The timing and distribution of the later central/posterior modulation closely resembles the central negativities reported in older adults in previous source memory studies (Trott et al., 1999; Wegesin et al., 2002; Li et al., 2004). It has been suggested that this effect may reflect the search for, or retrieval of, source information (Wegesin et al., 2002), and while the retrieval of context was not an explicit requirement of the item recognition task in Experiments 2, 3 and 4, the associative encoding instructions may have promoted a degree of task-irrelevant retrieval of study context in the older adults. This interpretation, although speculative, is consistent with the proposal that elderly adults exert less control over retrieval than young adults, and is further supported by the disappearance of the central/posterior negativity when the encoding task was simplified.

An alternative account of the modulation as reflecting older adults' predisposition to retrieve visually-based information, instead of the more abstract, conceptually-based information retrieved by young adults (Li et al., 2004), is not supported by the current data. Whilst, the post-experimental questionnaire revealed that both age groups occasionally found images springing to mind instead of sentences during encoding, there was no age-related difference in the degree to which this happened. Indeed, young participants reported actively using visual representations to remember the study pairings more often than older adults.

The central/posterior negativity in item recognition was preceded by another left-sided negative-going modulation whose more anterior distribution appears to resemble that of the later-onsetting fronto-central component elicited by associative recognition. The comparable topography of these effects suggests that they may reflect the time-varying activity of common neural generators. The ERP data therefore demonstrate that, in certain situations, older adults produce both left and right frontal activation; a pattern that is consistent with PET reports of bilateral PFC activation in older adults during episodic retrieval (compared to the right-sided PFC activation typically observed in young adults, see Bäckman et al., 1997; Cabeza et al., 1997a; Madden et al., 1999; Cabeza et al., 2002). Importantly, Cabeza and colleagues (2002) grouped their elderly participants according to their performance on a battery of neuropsychological memory tests. During a source recognition task, high scorers on the memory battery produced bilateral PFC activation, whereas the low scorers' PFC activity was confined to the right hemisphere. This finding is consistent with the argument elaborated over the course of the experimental

chapters that left fronto-central negative-going ERP effects index compensatory processes in older adults. These compensatory operations appear to be recruited when tasks are more complex and/or require more effort, and may counteract inefficiencies in, or reductions of, the mnemonic processes normally recruited by young adults (e.g. the operations indexed by the left parietal effect).

Finally, the temporal delay of the left fronto-central effect in associative recognition, compared to item recognition, may account for the absence of the later central/posterior negativity from the associative task. If the retrieval of context account of the central/posterior effect is veridical, the component would be expected to be elicited by associative recognition; however, its onset latency may fall outwith the 2048 ms time period covered by the current epoch. Alternatively, the older groups' inability to implement a strategic recollection strategy in associative recognition may underlie the non-appearance of the central/posterior component in the associative task. According to this interpretation, operations involved in the search for, or retrieval of, contextual information should be engaged by older adults for both same and rearranged pairs.

Hypotheses of ageing and memory revisited

Processing speed

Whilst processing speed theories of ageing (Salthouse, 1996; Verhaeghen & Salthouse, 1997) undoubtedly underpin some of the cognitive decline observed in older adults, they do not fully account for the findings reported in this thesis. Behaviourally, whilst increased RTs were evident in

older adults, these were not universal, particularly in item recognition.

Moreover, electrophysiologically, although the onset of robust components was delayed in older adults when the task-switch requirement was high (Experiment 2), the early frontal associative recognition effects in the older participants in Experiment 4 (where the retrieval tasks were blocked across the experiment) preceded the appearance of any reliable same/rearranged differences in the young participants.

Reduced processing resources

Similarly, the reduced processing resources hypothesis of cognitive ageing (Craik & Byrd, 1982; Craik, 1983) appears inconsistent with the presence of additional left frontal activations in older adults in both item and associative recognition. Furthermore, the reduced processing prediction that the age-related performance decrement should be larger for associative recognition than for item recognition (because same/rearranged judgements should be more cognitively demanding than old/new judgements) was only partially upheld. Post hoc analyses revealed that although associative recognition was disproportionately compromised when the task-switch load was high (Experiment 2) [$F(1, 17) = 4.62, p < 0.001$], the age-related decrement in discriminability was similar in item and associative recognition when the retrieval tasks were blocked (Experiments 3 and 4).

Dual process theory, reduced inhibitory control and the frontal lobes

The current findings more clearly map onto dual process theories of age-related memory decline (Jennings & Jacoby, 1993). The severe reduction of the

left parietal effect is consistent with the dual process prediction that recollection is compromised as people age. Moreover, if the familiarity interpretation of the early right frontal effect in older adults is accepted, the ERP data confirms that this process can be preserved in ageing when recollection is impaired.

However, the absence of the left parietal effect from associative recognition in the older participants in Experiments 2, 3 and 4 suggests that dual process accounts may represent an oversimplification of age-related changes in episodic memory. The lack of any left parietal same/rearranged differences when the associative task was expected to promote recollection, indicates that the older adults' performance decrement in associative recognition may be due to their failure to adopt an appropriate retrieval strategy, rather than to a simple recollection deficit per se. The strategic retrieval account is highly consistent with the inhibition deficit hypothesis of ageing (Hasher & Zacks, 1988; Zacks & Hasher, 1994; Hasher et al., 1999), which proposes that the disruption of inhibitory attentional processes makes older people less able to suppress the activation of extraneous goal-irrelevant information, and therefore poorer at recalling details.

As it is generally accepted that executive operations are subserved by the prefrontal cortex (Moscovitch, 1994), the proposal that older adults have less control over retrieval processes than young adults provides tacit support for the frontal lobe hypothesis of cognitive ageing (Moscovitch & Winocur, 1995; West, 1996). Importantly, the age-equivalence of the late right frontal effect does not necessarily mean that the mnemonic processes subserved by right frontal cortex are identical in young and older adults. Evaluation and monitoring operations in the elderly may still be less efficient, slower and less accurate

than those in young adults (Cabeza et al., 1997a), and the presence of left fronto-central negative-going modulations, which may index compensatory processes in older adults, in both tasks, is also consistent with the view that ageing deficits are associated with changes in the neural operations subserved by the frontal lobes.

Finally, although the current data provide support for the frontal lobe hypothesis of cognitive ageing, frontal lobe theory may not account for the severe age-related reduction of the left parietal effect in item recognition. This finding, which has parallels in neuroimaging studies (e.g. Grady et al., 1995), suggests that operations of the medial temporal lobe and parietal cortex may also be compromised as people grow older. Indeed, the observed ERP ageing differences appear consistent with a proposal that different neural networks are engaged by young and older adults in episodic retrieval. Specifically, it has been argued that older adults demonstrate an increased reliance on executive-type frontal functions in their pursuit of memory traces (c.f. Schiavetto et al., 2002; Grady et al., 2003).

Conclusions and future directions

Item vs. associative recognition in young adults

Although the ERPs of young adults indicate that the contributions of recollection and post-retrieval monitoring processes to item and associative recognition are comparable, the presence of left parietal and right frontal same/rearranged differences may index the adoption of a selective recollection strategy in associative recognition. A late central/posterior positive modulation, present only in associative recognition, may reflect the maintenance of the

learned associations whilst a same/rearranged decision is made. Finally, the presence of early frontal activation in the associative task suggests that familiarity can contribute to associative recognition under certain circumstances.

In order to gain a better understanding of the functional significance of the neural correlates of associative recognition, further studies are required to assess the validity of the strategic recollection account. The use of new pairs at test, in addition to same and rearranged pairs, would allow a within-participant comparison between the ERPs elicited when rearranged pairs were targets (inclusion) and when they were non-targets (exclusion). The selective retrieval account would predict that left parietal and right frontal rearranged/new differences should be elicited only when rearranged pairs were given target status.

The functional significance of the central/posterior positivity should also be the focus of future research. For example, the degree of learned association within a word pair could be manipulated by comparing the retrieval ERPs elicited when each member of the pairing was encoded separately, with those elicited when the words were encoded associatively. If the central/posterior effect reflects the maintenance of learned associations, its magnitude should be reduced when words are encoded individually.

In addition, investigations should be conducted to determine the conditions under which familiarity contributes to associative recognition. These studies should include new-new pairs at test to provide a baseline containing no recently-seen stimuli against which the familiarity of same and rearranged pairs could be assessed. Assuming that the early mid-frontal effect in associative

recognition does reflect familiarity, it should be possible to produce a gradation of the waveforms at mid-frontal sites, with same pairs (which contain two familiar words and a familiar association) being most positive, and new pairs being least positive. Altering the exposure frequency at study and the response deadline at test are two possible methods by which familiarity could be manipulated (c.f. Light et al., 2002). Here, it would be predicted that the early mid-frontal effect should be maximal when the study exposure frequency is increased and the response deadline decreased. Finally, varying the extent to which studied pairings are encoded associatively could also be used to ascertain if 'unitization' at encoding is an important determinant of whether familiarity can contribute to associative recognition (Yonelinas et al., 1996; 1999).

The ERP ageing comparison

The current research produced several very interesting findings that provide a more coherent framework within which future ERP ageing research can be interpreted. First, the unexpected absence of the left parietal effect in associative recognition may reflect the inability of elderly adults to engage in strategic recollection. This result, which would account for the presence of the left parietal effect in older adults in source memory, but not exclusion, studies, is consistent with the inhibition deficit hypothesis prediction that elderly adults are less able to suppress goal-irrelevant information. Second, the early right frontal effect emerged as a clear candidate for the ERP correlate of familiarity in older adults. Accordingly, the appearance of this modulation in item and associative recognition, together with the absence of left parietal effects in both

tasks, is consistent with the dual process view that whilst recollection is compromised in older adults, familiarity is relatively preserved. Third, age-invariance in the late right frontal effect suggests that age-related memory deficits are not due to older people's under-recruitment of the post-retrieval evaluation/monitoring processes that support episodic retrieval in the young. However, the more diffuse distribution of the late right frontal modulation in older adults may reflect the engagement of additional operations.

Moreover, a left-sided negative-going effect elicited by item recognition in older adults when the encoding task focused on associative information, appeared to represent two components. The first of these, which was topographically similar to a later-onsetting, fronto-central modulation in associative recognition, may represent the compensatory processes engaged by older adults to maximise their performance under certain conditions. The functional significance of a second, more central, negative effect in item recognition is less apparent. However, the similarity of the component to the central negativities reported in previous ERP source memory studies, suggests that it may reflect the incidental retrieval of context in item recognition.

The majority of published ERP investigations of episodic retrieval and ageing have focused on electrophysiological differences between young and older adults. Whilst these age comparisons have provided valuable information with regard to the impact of ageing on the ERP components that have already been identified in young adults (e.g. the left parietal and right frontal effects), they have been less informative with regard to the functional significance of the novel components that have emerged in older adults. Accordingly, a primary

goal of any future research should be to test the functional interpretations presented in this thesis.

Priority should be given to the resolution of the functional significance of the left-sided negative-going modulations observed in older adults. Here, the high level of variation present in older adults' general cognitive capacity (Morse, 1993) may prove extremely useful. Specifically, segregating older adults in ERP studies according to their underlying cognitive capabilities (as assessed by neuropsychological tests) would reduce any inherent variability within each participant group and allow a clearer picture to emerge from the electrophysiological data. For example, haemodynamic imaging studies have suggested that the pattern of engagement of prefrontal operations in older adults may depend on underlying individual differences in memory (Cabeza et al., 2002). Therefore an ERP comparison in which older participants are subdivided into high and low mnemonic ability groups could be used to test the compensatory processes interpretation of the left fronto-central negative effect.

Likewise, older adults who score well on tests of frontal function appear to be able to exert more control over retrieval processes than their 'low frontal' counterparts (Glisky et al., 1995). Accordingly, 'high frontal' older adults may be capable of strategic recollection in associative recognition. Therefore, if the strategic recollection account of the age-related absence of the left parietal effect in associative recognition is correct, it would be anticipated that this component should be observed in 'high frontal', but not in 'low frontal', older adults.

Further research is also needed to elucidate the functional significance of the early right frontal effect in older adults. To this end, manipulations that

have been shown to differentially affect the early mid-frontal putative ERP correlate of familiarity in young people could be conducted using older participants to ascertain whether the early right frontal component responds in a similar fashion.

Another critical issue with regard to the early right frontal effect is whether, if it is confirmed as being functionally similar to the early mid-frontal effect in young adults, the two components represent the same, or different, underlying neural generators. Although ERPs currently lack the spatial resolution required for accurate source localization, recent progress in the use of structural MRI scans to constrain the localization of the neural sources of scalp-recorded EEG may greatly improve their spatial precision (c.f. Gonsalves et al., 2005). Moreover, the development of EEG amplifiers suitable for use in MRI scanners will allow the simultaneous acquisition of spatially-acute fMRI data and temporally-acute ERP data (Hopfinger et al., 2005). Such technological advances should help resolve the issue of whether age-related differences in scalp topography, such as those observed in the early frontal effects, represent the engagement of separate cognitive operations by young and older adults.

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Appendix A

Appendix A contains the word pool from which word lists used in the experimental chapters were generated. The words were selected from the MRC Psycholinguistic Database (Coltheart, 1981) according to the following criteria: all words were medium frequency (mean 17.1 per million, range 10 to 30) nouns and verbs of between 4 and 8 letters in length.

TRICK	TRANSIT	COMMIT	PITY
CONVEY	VEIN	REWARD	TOMB
MIDST	MEADOW	RUST	CLUE
MULTIPLY	SPORT	UNITE	EATEN
ODDS	VISITOR	RANCH	LOVER
TOLL	WALNUT	LUGGAGE	DOME
DIALECT	COUCH	MEAL	SAUCE
DECENCY	INPUT	OUTWARD	SLEEVE
CREST	FLAME	CONVERT	DRUG
COLLAR	RESTRICT	REFLECT	RATION
WAITER	TUNNEL	REBEL	BARBECUE
DOUGH	CRIMINAL	HARDWARE	STREAK
OPPOSE	POLE	CROWN	TICKET
HAIL	MINERAL	PICNIC	POLLEN
BATH	MEANTIME	SPECIMEN	CHIP
CIGAR	CONCERTO	LION	PERFORM
FOREHEAD	SUBMIT	LUXURY	IDEOLOGY
IODINE	MODE	RELY	FABRIC
PLEADING	PEPPER	FARMER	INSECT
LIGHTER	CHART	JUNGLE	SWEEP
VIOLIN	COMMUTER	ARCH	WORKER
ASSAULT	FORUM	DISTRESS	FEVER
EXPOSURE	CHEEK	WORN	LAUGH
CHAPEL	TURMOIL	RADAR	THUNDER
NUDE	BRONZE	DIALYSIS	CANDLE
FAME	SNAP	MODERATE	CRACK

Appendix A

BOSS	STALL	MIXTURE	WAIST
STABLE	REGIME	COMPACT	BREAST
BARE	DURATION	CAUTION	WITNESS
ESSAY	DAIRY	IDLE	COSTUME
DEVIL	PROTEIN	CAVALRY	THEATRE
MERCURY	SAIL	ARRIVAL	WHISKY
REMIND	BREED	MOTIVE	APPETITE
CLIMAX	CONTENTS	RABBIT	ALIEN
ENTITY	SHIRT	SLIM	MASON
CIVILIAN	CHILL	HANG	CAVITY
ENTRY	TACKLE	LISTENER	RUBBER
RESPOND	RELIEVE	CRITIC	IMPERIAL
EIGHTEEN	ORBIT	QUARREL	PARTISAN
NURSE	LOOP	CATHODE	STROKE
FRIGHTEN	INQUIRY	INTERIM	REVEREND
AMEN	SECURE	DRAIN	INVASION
COACH	BORDER	CRAFT	ANTIBODY
DISK	SPIT	HORROR	CHARM
AUTONOMY	NARRATOR	BLOOM	LIFT
SUSPECT	GRIN	SAVAGE	TUNE
DIAGRAM	REPAIR	FOLKLORE	COMMUTE
HIDE	RAID	HEATER	FLEW
PASSION	DECREASE	CRIED	DELIGHT
LIFETIME	REACT	MILEAGE	DEVOTION
CONTEST	SPARE	PURSUIT	PAUSE
HELIUM	CANVAS	BLESSING	CARD
SURPLUS	OCCUPY	CRYSTAL	RESCUE
CANYON	VESSEL	BULL	ANTIQUE
FERRY	PLEA	NORM	CARDINAL
REFUSAL	PRIVACY	BARN	STOLEN
CELLAR	SLUG	REEF	MUZZLE
PROPOSE	NONSENSE	ORDERLY	TRAY
VOLTAGE	RIBBON	GLOBE	GENIUS
BUILDER	MISERY	SERGEANT	CORRIDOR
RENDER	NEST	CITIZEN	PRODUCER
DETECT	LEVER	TOBACCO	CRISES
LEASE	APPENDIX	LAGOON	RESTRAIN
FOIL	CONCORD	BOLT	LEAN
CYCLE	CONSIST	INSURE	MOMENTUM
MADDEN	BURIAL	CLIMB	ORGANIZE

RESIST	REALM	FORTUNE	KNIGHT
SPLIT	PIANIST	POVERTY	JUICE
ADOPT	INSIGHT	DESERVE	PATROL
LIME	LONGING	GRAPH	PLANET
ABSENT	SPONSOR	ADJUST	INTERVAL
EMERGE	DESTINY	USAGE	STERN
REPORTER	SLOPE	EPIDEMIC	THREAD
LEISURE	DELAY	CYLINDER	RISEN
LANDLORD	GULF	ORAL	DRAG
MONUMENT	WEEKLY	NICK	FRICTION
NUCLEUS	ANACONDA	DRUM	POSE
BULK	OPPONENT	COMPRISE	SOAP
DISLIKE	RANG	DISPOSAL	VICTOR
HARNESS	BASS	KISS	DESIGNER
RECOVER	ATTIC	TREMBLE	ACID
PRINCESS	DEFICIT	BELT	WHIP
JEEP	TIDE	BOOST	SPUR
MASTERY	SUCCEED	PARADISE	GLORY
JERSEY	SLID	LEGEND	SLAVE
FLUNG	DISCOUNT	GLOOM	DENTIST
GLOW	OBSTACLE	IVORY	NEGLECT
ENABLE	CABINET	REPEAT	BOWL
RIDER	SHAKE	WIDOW	WIPE
LECTURE	EXCUSE	POSSESS	THUMB
SHEEP	MARRY	FRACTION	ELECTRON
BAKE	PASSIVE	ZONE	RABBI
PRAISE	INTEND	SPAN	SWEAT
AUNT	EPIC	TOURIST	RAZOR
BATTERY	BULLET	CONSULT	COOLER
PANIC	SEAL	NERVE	SLIDE
EARNINGS	TEXTILE	THESIS	MOSQUE
SCAR	MIRROR	OPTIMISM	LIKING
SKIRT	INTIMATE	SATISFY	DIET
RELAX	SMART	INSERT	GOSPEL
BUNDLE	COCKTAIL	DITCH	WRIST
STRIP	LADDER	PEAK	BARK
HUNGER	DOORWAY	SHORTAGE	SLATE
EXCEED	LANDING	SIGH	STRAW
TANK	CHORUS	HONESTY	HIDDEN
TIMBER	CLIMATE	MARE	PROCEED

Appendix A

PERCEIVE	FLUX	BACON	SCHOLAR
THRUST	ADVISE	TRIM	MESS
HORMONE	VECTOR	LOBBY	HAWK
DILEMMA	ELBOW	PISTOL	TENURE
ANCHOR	COMPOUND	EXERT	RECEIVER
REMEDY	SERVANT	ARGUE	MOUNT
DULL	FOUNTAIN	EMPEROR	WARD
DEPUTY	POULTRY	EXACT	RIDGE
MERGER	PROTEST	DEADLOCK	SIXTEEN
TOILET	SALOON	TACTICS	FLED
EMBRACE	NINETEEN	SINK	SEGMENT
COMPARE	VERSE	BRICK	COTTAGE
FOSTER	CONFIRM	DISH	FATIGUE
IMPLY	COPPER	PIONEER	BUNK
ESSENCE	TRAILER	GOSSIP	TILE
SERMON	MINING	RENT	MOISTURE
CUSTOM	PERFUME	FORD	ZERO
FORGE	THREATEN	NINETY	AIRPORT
GRAIN	ALCOHOL	MERIT	ASSIGN
SCRIPT	THEFT	CABIN	BELL
FOLLY	LEAP	PUPIL	REVEAL
PROSE	SUSTAIN	BUFFER	SILK
CHARCOAL	SANCTION	COMBAT	FLEET
BALLOON	TENT	IRONY	ELITE
LESSON	LENS	ROPE	MERCHANT
DEDUCT	LANTERN	ADVOCATE	BEAM
SUITE	REFER	BRACE	LABEL
DIFFER	ORANGE	UTOPIAN	APPROVE
INVITE	LAYER	FANCY	STRATEGY
KNOCK	CONSENT	PUMP	ROOT
POWDER	PINE	STRAY	DEALT
ARISE	SLIP	UPRIGHT	HOLDER
GAUGE	PENNY	LEMON	EPISODE
DAWN	BUTTER	RANK	SLEPT
FAKE	AMBITION	ZINC	SPARK
KINGDOM	RESOLVE	ANALOGY	WOOL
VETERAN	FAREWELL	BEND	STADIUM
COLONY	ADULT	DEBT	RADICAL
HORIZON	REGISTER	CHIN	MICE
BUTTON	ANALYSES	POSTURE	GEAR

Appendix A

BLANKET	PORTER	ELEVATOR	VICTIM
CHUCK	ARREST	WING	DEBUT
BUFFALO	FANTASY	MIST	HUNT
SILVER	STOLE	AUTUMN	TRIBUTE
ONION	BURN	SOLVE	TAIL
ELDER	MORALE	CLUSTER	SHAME
QUALIFY	CEMETRY	MONOPOLY	ENVELOPE
ANTENNA	STARE	GOWN	RUSH
PROSPECT	COWBOY	ATLAS	EXHIBIT
BEATEN	PIPE	PITCH	SCENERY
SERUM	STEEP	DOSE	SWEATER
EIGHTY	KICK	GAZETTE	PURITY
SUBURB	STRING	VENT	GATHER
TEAR	ACADEMY	SALESMAN	AMATEUR
TERROR	SPHERE	BOULDER	CREAM
SPRAY	COMPETE	SHALLOW	PRIEST
SCRUTINY	RITUAL	PERSUADE	DECK
ABANDON	HAVEN	INSPECT	STAKE
DESPAIR	PATRIOT	TOKEN	PINT
PRESTIGE	PATIENCE	CEREMONY	TENNIS
SHELF	EXPORT	VELOCITY	SWALLOW
WARN	PETITION	QUIT	SELECT
NOON	HAZARD	BUBBLE	OVERHEAD
SWORE	DISASTER	TROPICAL	DARLING
ROAR	LAMP	HARM	PACK
UTILIZE	FACILITY	SWIM	ARRAY
FORECAST	BULLETIN	RESIDENT	MOVABLE
ATTAIN	REPLACE	STATUE	SPELL
TRACE	OUTFIT	JUSTIFY	QUOTE
COMBINE	VETO	CEREAL	FORGIVE
CALCIUM	NICKNAME	BITE	OPIUM
EARN	NOVELIST	SEWER	RAKE
CURSE	PRAY	ACCESS	DRYING
PLASTER	MARBLE	LIVER	PLASMA
STAR	ROAST	ORGAN	PARENT
FAINT	EXPAND	DEER	ATTRACT
REGIMENT	FLASH	JAIL	ECHO
LUNG	MARGIN	HUMANITY	CHAMPION
TWIST	SHAFT	IMPORT	JOKE
TORN	CLARIFY	AWAKE	ENGAGE

Appendix A

EDUCATOR	MATE	STORM	CREATURE
GRIP	ALLIANCE	LEAF	WHISPER
DERIVE	SHEER	DUMB	DESERT
STRIDE	CROP	CONCEIVE	GRIEF
SODIUM	MEDICINE	HATRED	QUEST
STUCK	LINGUIST	SKETCH	OUTSET
PAINTER	OVERCOME	CURTAIN	TENSE
RENTAL	PHYSICS	BISHOP	SCREAM
PRIORITY	PACKAGE	PILE	FOUNDER
RHYTHM	OBSERVER	COIN	HONEY
MIDNIGHT	CRUELTY	TROOP	CEMENT
MEDIA	RETREAT	REJECT	PROFIT
WIDTH	PRINT	MISTER	STRETCH
FORK	FLUID	WORTHY	TANGENT
BRASS	ABUSE	RALLY	PORT
ACCUSE	BORE	REFUND	CLOTHING
SIXTY	ACQUIRE	EMPLOY	KNIT
GHOST	COPE	INFANT	BATON
SQUEEZE	ANGEL	GANG	BEHAVE
STEAK	SHERIFF	OVERALL	COINCIDE
LOCATE	STOCKADE	ACTOR	TOAST
HESITATE	DICE	MERCY	MANAGE
SOLE	WEALTH	PENALTY	GAZE
DEFINE	MOVIE	CATEGORY	SEMESTER
CREEK	VERDICT	FLAG	FRIEZE
MORTGAGE	BUNCH	FIRING	MAGNUM
ROMANCE	RECRUIT	HOLSTER	HOLIDAY
BALLOT	DIALOGUE	MORALITY	GRILL
VIRTUE	FESTIVAL	LOYALTY	POND
BOTHER	NEON	PITCHER	LODGE
SHADE	CEASE	DEFEND	ALARM
YARN	GHETTO	SHOE	PLUG
MINISTRY	POTTERY	BREEZE	GIANT
IDENTIFY	TOWER	LYRIC	SANK
MIRACLE	TEMPER	BEARING	MELODY
SHOOT	CONE	BIRTHDAY	CLOVER
MAKER	ASSERT	VALIDITY	SHOWER
SORE	WORKSHOP	RETAIN	TRAP
WOUND	PURSUE	BLAST	RULING
SOUP	TRIUMPH	ETHICS	MAINLAND

Appendix A

EMPIRE	REALISM	PENTAGON	BLADE
SAVING	CLERGY	EVALUATE	ERECT
CURB	PAVEMENT	OXEN	DENIAL
MARSHAL	RESUME	PENSION	FLUSH
VENTURE	PRAYER	EXPLORE	MISTAKEN
SURGEON	BOATING	SANG	DIVIDE
COMPASS	DIVE	CANE	SLICE
ELEGANCE	COUNSEL	BOOT	SUMMIT
PLATE	NOBLE	PREFER	CRAWL
ALTER	DIVORCE	MILL	SAINT
BOIL	HIRE	COLT	CLOCK
CULT	BASKET	BLEW	DRAFT
FLOOD	CENSUS	BEHALF	MOUSE
CLIFF	MILITIA	RAIL	OUTLINE
EXPERT	LEATHER	BUCK	LINK
NEEDLE	BARREL	PREMIUM	RESORT
PALM	TURNPIKE	PURPLE	DOLL
LAUNCH	REVOLVER	DASH	HERALD
DELIVER	SUICIDE	TIRE	URGENCY
FURNISH	SQUAD	LANE	DAYLIGHT
PASTE	VITALITY	DAMP	WAKE
SADDLE	ATTACH	CURE	FORGOT
REFRAIN	DEALER	RATING	MORTAR
CARPET	HALT	LUNCHEON	FLOWER
MEMORIAL	THERAPY	OKAY	HARVEST
CHANNEL	SOLITARY	PARTICLE	ASSIST
TAXATION	FLOCK	LEND	DRIFT
SUNSET	SINGULAR	SANDWICH	DECAY
CONFESS	SHED	CROSSING	PREACHER
POUND	CRASH	TOOTH	ABSORB
ADMIRE	PUZZLE	HUMBLE	VOID
HEAP	IMAGERY	PONY	DRANK
FROZEN	CIRCUIT	CONTEMPT	BOUNDARY
DESCENT	PICKING	NURSERY	HOLLOW
ROBBERY	PATCH	GRAB	GRASP
REFUSE	HUFF	JUMP	HERITAGE
FENCE	UPSET	RETAIL	JOURNEY
CHASE	GRADIENT	PURSE	CALF
CURRENCY	IMPULSE	FRINGE	PROMPT
BUZZ	CREATOR	HUNTER	RIVAL

Appendix A

SECTOR	REFORM	BRAND
GRADUATE	SHELL	INJURY
WARRANT	FURNACE	
MUSTARD	EMBASSY	
PULLEY	OBSCURE	
PARISH	FURY	
VIRUS	DISCUSS	
FRONTIER	ARRANGE	
RAILWAY	AFFIRM	
CLOUD	UTILITY	
CAKE	EXAMINER	
DOCUMENT	STEAM	
WEEP	DEPOT	
SCOPE	BRAVE	
REUNION	NITROGEN	
CLOSET	SPECTRUM	
FOLIAGE	ANNOUNCE	
TENDER	ARROW	
SUMMARY	BLOCKADE	
STEREO	PROFILE	
REVERSE	MUSICIAN	
MUDDY	BUSH	
WART	UTTER	
FIST	EQUALITY	
COMPUTER	LOCK	
CAPTURE	TERMINAL	
PRIZE	STOVE	
PRAIRIE	LIMP	
MORTAL	SUNRISE	
SPADE	SETTLE	
CARBON	TYRANNY	
IGNORE	OUTCOME	
COVERAGE	POISON	
COLLECT	LAWN	
CARRIAGE	TRACTOR	
INTEGRAL	RUIN	
MINORITY	CHAOS	
DODGE	PROCLAIM	
APPLAUSE	VACUUM	
MINIMIZE	TRIGGER	

Appendix B

Instructions for Remember/Know procedure used in Experiment 1.

Adapted from (Gardiner & Richardson-Klavehn, 2000).

The experiment you have just completed tested your recognition memory for the words and word pairs you had seen in the study phases. The next part of the experiment is going to ask you to describe exactly what type of memory you had for the words and word pairs you recognised.

Recognition memory is associated with two different kinds of awareness. Quite often recognition brings back to mind something you recollect about what it is you recognise. An example of this is when you recognise someone's face in the street, and REMEMBER talking to this person at a party at the weekend.

At other times recognition brings back nothing to mind about what it is you recognise. For example, you may be confident that you recognise someone, indeed you KNOW you recognise them, because you have strong feelings of familiarity about them. However, you have no conscious recollection of seeing this person before, and do not remember anything about them.

The same kinds of awareness are associated with recognising the words and word pairs you have just seen in the first part of the experiment. Sometimes when you recognised the words or word pairs, recognition will have brought back to mind something you remember thinking about when the word appeared in the study phase. In other words you will recollect something you consciously experienced at that time (perhaps you recollect the sentence you generated, or perhaps you recollect something else about the study word pair). But sometimes recognising the word or word pair will not have brought back to mind anything you remember about the study phase. Instead, the word or word pair will merely seem familiar so that you feel confident you saw it in the study

Appendix B

phase, even though you don't consciously recollect anything you experienced when you saw it then.

You are now going to see all the words you said you recognised in the first part of the experiment. If that recognition was accompanied by some recollective experience, please press the "1" key. If it was accompanied by strong feelings of familiarity without any recollective experience, please press the "5" key. There will also have been times when you simply made a GUESS. If this was the case, please press the "3" key.

Please try and make your responses as honest as possible

Appendix C

A Post Experimental Questionnaire

Study Phase

1) How often did you manage to make up sentences? *(Please circle one)*

1	2	3	4	5
Never	Sometimes	Often	Usually	Always

2) How easy did you find it to make up sentences? *(Please circle one)*

1	2	3	4	5
Very easy	Relatively easy	OK	Relatively Difficult	Very Difficult

3) Did you find yourself generating a detailed sentence? *(Please circle one)*

1	2	3	4	5
Never	Sometimes	Often	Usually	Always

4) Did you find yourself generating a simple sentence then carrying on quickly to the next word pair? *(Please circle one)*

1	2	3	4	5
Never	Sometimes	Often	Usually	Always

5) How often did you find images springing to mind instead of sentences?

(Please circle one)

1	2	3	4	5
Never	Sometimes	Often	Usually	Always

6) Did you use any other method to try to remember the word pairs?

(Please circle one)

Yes

No

If YES, what

Test Phase

1) How easy was it to discriminate between same and rearranged word pairs?

(Please circle one)

1	2	3	4	5
Very easy	Relatively easy	OK	Relatively Difficult	Very Difficult

2) How easy was it to discriminate between old and new single words?

(Please circle one)

1	2	3	4	5
Very easy	Relatively easy	OK	Relatively Difficult	Very Difficult

3) Which did you find easier? *(Please circle one)*

Pairs	Single Words	Both the same
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4) With the word pairs did you find yourself running out of time and guessing?

(Please circle one)

1	2	3	4	5
Never	Sometimes	Often	Usually	Always

5) With the single words did you find yourself running out of time and guessing? *(Please circle one)*

1	2	3	4	5
Never	Sometimes	Often	Usually	Always

6) Have you any other comments/observations you'd like to make?

If there was anything you were unsure about in this questionnaire, please ask.

Thank You Once Again For Your Participation

B Median responses to post-experimental questionnaires (range in brackets)

Experiment 2

	Young	Older
Study Phase		
Q1	4(2-5)	3.5(2-5)
Q2	3(2-4)	4(1-5)
Q3	2(1-4)	2(1-3)
Q4	3(2-5)	3(2-4)
Q5	3(2-5)	3(1-4)
Test Phase		
Q1	3(2-4)	4(2-5)
Q2	3(1-5)	3(1-4)
Q3	Pairs(55.6%)	Single words(77.8%)
Q4	2(1-2)	2(2-3)
Q5	2(1-3)	2(1-3)

Experiment 3

	Young	Older
Study Phase		
Q1	4(2-5)	4(2-5)
Q2	2(2-4)	3(2-4)
Q3	2(1-4)	2(1-5)
Q4	3(2-4)	2(1-4)
Q5	2.5(1-5)	2(1-4)
Test Phase		
Q1	2(1-4)	3.5(1-5)
Q2	3(1-4)	3(1-5)
Q3	Pairs(83.3%)	Single words(66.7%)
Q4	2(1-4)	2(1-3)
Q5	2(1-4)	2(1-3)

Experiment 4

	Young	Older
Study Phase		
Q1	4(2-5)	4(2-4)
Q2	3(1-4)	3(2-4)
Q3	2(1-4)	2(1-4)
Q4	3(2-4)	3.5(2-4)
Q5	3(1-5)	3(1-4)
Test Phase		
Q1	3(2-3)	3(2-4)
Q2	3(2-4)	3(2-4)
Q3	Pairs(77.8%)	Pairs(44.4%)
Q4	2(1-3)	2(1-3)
Q5	2(1-3)	2(1-3)