Episodic Memory for Emotional Information: Event-Related Potential and Functional Magnetic Resonance Imaging Studies

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Abstract

The neural correlates of emotional episodic memory are investigated in a series of neuroimaging experiments (ERP, fMRI) through the comparison of memory effects elicited during retrieval of emotional relative to neutral information. In the first two ERP studies, it is revealed that emotionally-valenced words influence recognition memory primarily by virtue of their high levels of 'semantic-cohesiveness'. Furthermore, the findings reveal that the arrangement of emotional and neutral retrieval cues at test (blocked versus intermixed) influences processing carried out upon retrieved emotional episodic information. The findings across the third and fourth ERP studies indicate that incidental retrieval of emotional context (encoding environment) gives rise to greater activity in neural systems supporting episodic retrieval than does retrieval of non-emotional context. When context retrieval is intentional, by contrast, emotional and non-emotional episodic memory are associated with equivalent levels of engagement. The findings of the fourth ERP study are consistent with the existence of additional neural circuitry that is activated selectively by emotionally toned episodic information. In a final event-related fMRI study it is revealed that the retrieval of emotionally negative relative to emotionally neutral context elicits enhanced activity in brain regions including prefrontal cortex, amygdala, hippocampus and retrosplenial cortex. Recognition of words from positive relative to neutral contexts is associated with increased activity in prefrontal and orbitofrontal cortex, and in the left anterior temporal lobe. The fMRI findings provide further support for the proposal that the incidental retrieval of emotional information enhances activity in networks supporting episodic retrieval of neutral information. In addition, the fMRI findings suggest that regions known to be activated when emotional information is encountered in the environment are also active when emotional information is retrieved from memory. Whilst the findings are noteworthy in their own right, they also have implications for future studies of emotional memory. It is proposed that the employment of paradigms which involve the retrieval of emotional context through presentation of non-emotional retrieval cues may offer advantages over paradigms wherein the retrieval cues themselves are emotional.

Declaration for the Degree of Ph.D.

(i) I Elizabeth Jayne Maratos hereby certify that this thesis, which is approximately 70, 000 words in length, has been written by me, that it is a record of work carried out by me, and that it has not been submitted in any previous application for a higher degree.

date signature of candidate

(ii) I was admitted as a research student in October 1997 and as a candidate for the degree of Doctor of Philosophy in October 1997; the higher study for which this is a record was carried out in the University of St. Andrews between 1997 and 1998, and the University College London between 1998 and 2000.

date signature of candidate

(iii) I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University College London and that the candidate is qualified to submit this thesis in application for that degree.

date signature of supervisor

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To my family and Daniel, the biggest thanks of all.

Foreword

And when thy slumbering conscience, fretting
By recollection's torturing flame,
Thou didst reveal the hideous setting
Of they life's current ere I came:
When suddenly I saw thee sicken,
And weeping, hide thine anguished face,
Revolted, Maddened, horror-stricken,
At memories of foul disgrace.

NEKRASSOV (from Dostoyevsky, 1864 pp 29).

The manner in which emotional memories may pervade our consciousness is frequently underscored in many pieces of brilliant literature. Indeed, the above prose was selected simply by allowing a Dostoyevsky novel to fall open onto a page. The frequency of descriptions of emotional memories in classic novels highlights well our fascination (and often unease) with the phenomena. The work presented in this thesis makes a small step toward delineating the neural mechanisms and cognitive processing subserving the retrieval of emotional events. One issue addressed is that emotional memory might take a number of forms which have properties corresponding to the separate sub-systems of memory, i.e. explicit, implicit, episodic etc. A second topic of investigation concerns the neural circuitry mediating the retrieval of emotional episodic memory and whether it differs from that mediating memory for non-emotional episodic information. A final topic addressed is the functional roles that dissociable brain regions play in emotional episodic memory.

The thesis is organised into three main sections. The first section consists of review chapters, each providing an overview of some aspect of the theoretical and methodological background to the experiments conducted. The thesis opens with an overview of the memory literature discussed from a cognitive neuroscience perspective. This is followed by a chapter which outlines Event-related Potential

(ERP) methodology - the principal neuroimaging method employed to investigate emotional memory in this thesis. Highlighted in this second chapter are assumptions underlying the use of psychophysiological measures to map between brain function and brain structure. Chapter 3 reviews neuroimaging (ERP and fMRI) studies of explicit memory retrieval. Influential concepts and studies which relate specifically to emotional memory within the field of affective neuroscience are discussed in the fourth (and final) review chapter. In addition, the final review chapter culminates in a brief synopsis of how and where questions regarding neural mediation of emotional explicit memory are addressed by the experiments in this thesis.

The second section of the thesis is concerned with the experimental work. This work can be sub-divided into two kinds of investigation. Chapters 1 and 2 compare the ERP correlates of recognition memory for emotional and neutral words. By contrast, chapters 3 to 5 investigate the neural mechanism underlying the retrieval of emotional context. The experiment chapters are each introduced with a selective review of the literature that relates specifically to the question addressed therein, thus providing a focused account of the reasons for the experiment. Whilst Experiments 1 to 4 (chapters 5 to 8) employed ERP methodology to investigate emotional memory, the final experiment provides a comparative (event-related) fMRI study (chapter 10). Chapter 10 is thus preceeded by a chapter devoted to fMRI methodology. Finally, interim summaries are provided where necessary in order to encapsulate conclusions that are made by way of comparisons across experiments.

The third and final section of the thesis provides a broader discussion of the work presented in the thesis. Existing research and theories concerning emotional memory are revisited in light of the findings from the thesis, and implications with regard to the direction of future research in investigations of emotional memory are discussed. Finally, a number of future experiments are detailed.

Chapter 1

Episodic Memory

Introduction

Cognitive neuroscience is concerned with the identification of the cognitive operations and neural mechanisms underlying cognition and behaviour. The relevant literature is extensive, incorporating research from a variety of disciplines including cognitive psychology, neuroscience, experimental psychology and neuropsychology. This chapter reviews the principal theories relating to a part of this literature: conscious awareness for prior autobiographical episodes – that is, episodic memory. The chapter first provides an overview of models of memory before addressing more specifically episodic memory and illuminating issues relating to the design of memory tasks, theories of recognition memory and the anatomy of episodic memory. The main purpose of the chapter is to familiarise the reader with a number of concepts and definitions which have become pedestrian to research into the neural underpinnings of memory. Thus this chapter provides a general background to the following introductory and experimental chapters.

Models of Memory

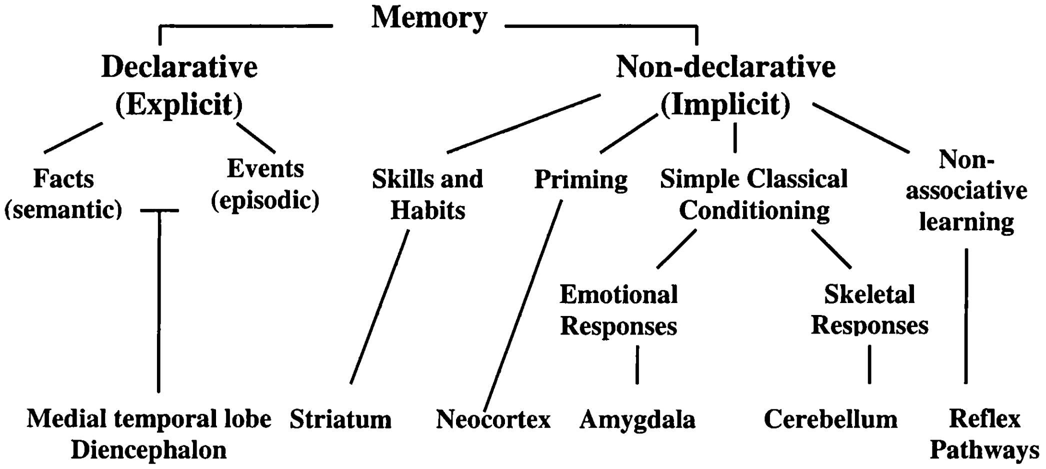
An influential concept to researchers is that memory is fractionated into separate sub-systems. Neuropsychological evidence for the existence of separate sub-systems in memory was pioneered by Scoville and Milners' (1957) description of H.M., a patient who developed severe anterograde amnesia (with relative sparing of other mental abilities such as intellect, language and short-term memory) following bilateral medial temporal lobe resection for intractable epilepsy (for reviews of this and similar cases see Scoville and Correll, 1973; Channon and Polkey, 1990). A contrasting pattern of memory impairment (specifically impaired short-term memory with relative sparing of long term memory) subsequently followed in reports of patients with left parietal lobe lesions (Shallice and Warrington, 1970; Butterworth, Cipolotti and Warrington, 1996; see Markowitsch, Kalbe et al., 1999 for review). Notwithstanding controversy over the role of the parietal lobe in the storage of short-term memories (see Kolb and Whishaw, 1980; pp 329-330), such double dissociations between brain lesions and impairments in memory provided convincing evidence that memory is not a unitary system, rather that it can be fractionated into short-term 'working' memory and, germane to this thesis, long-term memory.

Long-term memory can also be subdivided into separate systems. Long-term memory sub-systems were established from neuropsychological evidence that temporal lobe amnesics may be severely impaired in conscious memory for prior events, yet exhibit normal, or near normal, memory when influence by the past event is unconscious and expressed through effects such as facilitation on task time. For example, H.M. showed considerable retention of perceptual-motor skills such as mirror tracing (Milner, 1962). In addition it was subsequently revealed that amnesics exhibit normal priming effects – that is, their behaviour towards an item changes simply as a result of having previously encountered the item (Warrington and Weiskrantz, 1968; for review see Parkin, 1982).

On the basis of such evidence, Graf and Schacter, (1985) suggested that long-term memory can be broadly subdivided into two systems: explicit and implicit. A similar distinction between 'declarative' and 'non-declarative' long-term memory was subsequently made by Squire and Zola-Morgan (1991) roughly corresponding to Schacter and colleagues' explicit versus implicit distinction respectively. The two different classes of memory have been distinguished primarily through whether there is conscious awareness of the retrieved memory (explicit/declarative), or whether memory is manifest as an influence on behaviour without necessitating conscious awareness (implicit/non-declarative). It was further proposed that both implicit and explicit memory are subdivided by a number of specialised memory stores characterised in terms of their specific functions or attributes (Figure 1.1). For example, explicit memory is subdivided by the type of information characterising the memory - memory for facts/knowledge versus memory for prior events (for reviews see Schacter and Tulving, 1994; Squire and Zola, 1996).

A third model of memory systems was proposed by Tulving and colleagues (Tulving, 1983; Tulving, 1985a; Tulving, 1993a). In this model, memory is fractionated into a larger number of categories including episodic memory (memory for events); semantic memory (memory for facts and knowledge); procedural memory (skills and habits, classical conditioning); short-term memory and a perceptual representation system (priming).

Figure 1.1 A taxonomy of long-term memory systems
(Adapted from Squire, L.R. and Zola, S.M. (1994), Structure and function of declarative and non declarative memory systems. *PNAS, U.S.A.* 93: 13515-13522).



Although the different models have a number of overlapping features, conflicts between the models are well demarcated in the literature. For example, Squire and colleagues classify priming within the non-declarative (procedural) memory system (Figure 1.1; see Squire and Knowlton, 2000 for review). By contrast, Tulving and Schacter (1990) make a distinction between procedural memory which is concerned with action systems (skill learning, conditioning) and a perceptual representation system whose function is to improve identification of perceptual objects (i.e. priming). Furthermore, Squire and colleagues view episodic and semantic memory as side-by-side systems of declarative memory which are processed in parallel and differentiated only by the kinds of information dealt with (events vs. fact) (e.g. Squire and Zola, 1996). By contrast Tulving views episodic and semantic memory as distinct systems (dependent on distinct brain structures) whose organisation at encoding is serially-mediated (episodic memory encoded 'through' semantic memory) (e.g. Tulving and Markowitsch, 1998). The different models have ramifications for the nature of dissociations that can be predicted on the basis of neurological impairment. Thus the resolution of such conflicts from a neuropsychological perspective has occupied much of the memory research (for reviews see Squire and Knowlton, 2000; Markowitsch, 2000).

Indirect and Direct Tests of Memory

The subject matter in this thesis is concerned with the division of explicit memory termed episodic memory, herein defined as long-term memory for autobiographical events embedded in a particular spatial and temporal context (Tulving, 1993b; Tulving and Markowitsch, 1998). Properties of episodic memory can be assessed by manipulating the nature of encoding and retrieval processes in memory tasks and monitoring changes in behavioural data and/or neuroimaging data. At encoding, for example, variation in depth of processing from shallow (such as counting letters in a word) to deep (such as semantically processing the word) correlates positively with subsequent memorability of an item (Craik and Lockart, 1972). Other ways of manipulating mnemonic processing (encoding and/or retrieval) are to vary the nature 'items' presented in the task or by varying the 'context' in which stimuli are presented. For example, when investigating influence of emotion upon episodic memory, the affective nature of the stimuli might be manipulated by using negative versus neutral words (e.g. Leiphart, Rosenfeld and Gabrieli, 1993). Alternatively, the emotional context in which the items are encoded might be varied independently of the valence of the stimuli (e.g. Phelps, LaBar et al., 1998).

Retrieval tasks can be broadly subdivided into three forms. 'Direct' tasks are employed to investigate conscious awareness of previously encountered events. In this type of task, reference is made in the test instructions to the prior learning episode. For example, participants might be instructed to recall studied items in any order (free recall) or in response to a fragment of the previously presented item (cued recall). Alternatively, they may be presented with copy cues (of study items) along with new items and required to make old/new judgements accordingly (recognition memory). By contrast, indirect tasks investigate how a previously encountered event influences memory where either there is no mention of the prior event, or alternatively (in order to reduce the possibility of spontaneous retrieval strategies developing as awareness arises) reference to the study episode is made but not in the task instructions. For example, in stem completion tasks participants might simply be instructed to provide 'the first word that comes to mind' or in perceptual identification tasks participants are presented with perceptually degraded (masked) old and new items that they have to categorise in some manner (e.g. as animate or inanimate). There may be a dissociation in the way the old and new items are categorised (e.g. a bias to completing word stems with studied words or faster processing times for previously encountered items), even though the participant is unaware that the item had been presented previously (i.e. priming). Finally, the retrieval task may incorporate some combination of direct and indirect tests of memory. For example, a participant's attention might be drawn to variation in items presented (e.g. old pictures versus old words) but not to any variation in the context (e.g. emotional, non-emotional) in which the encoded stimuli were presented.

Studies have shown that amnesics perform normally on indirect memory tests but have impaired performance on direct tests of memory (Weiskrantz and Warrington, 1979; Graf, Shimamura and Squire, 1985; Musen and Squire, 1992; Cave and Squire, 1992, for reviews see Shimamura, 1986; Schacter, Chiu and Ochsner, 1993). For example, in indirect completion tasks amnesics show normal priming, but they are impaired on cued recall (Graf, Squire and Mandler, 1984). Similarly, amnesic participants are impaired on recognition of homophones (e.g. hare versus hair) but still susceptible to priming effects such as bias toward spelling of the previously presented homophone (Jacoby and Witherspoon, 1982). In addition, dissociations in performance upon such tasks have been shown in a number of studies of normal participants (Jacoby and Dallas, 1981; Jacoby, 1983; Kelley, Jacoby and Hollingshead, 1989; Schacter and Church, 1992; Richardson-Klavehn, Lee, Joubran and Bjork, 1994; Kellogg, Newcombe, Kammer and Schmitt, 1996; MacLeod and Daniels, 2000). For example, changing modality between study and test typically influences performance more on indirect tests (e.g. priming is reduced) than on direct tests (Schacter and Church, 1992), whereas depth of processing manipulations have been shown to influence performance on direct tasks more than indirect tasks (Jacoby and Dallas, 1981; Kellogg et al., 1996).

Many proponents of the systems view of memory have used such dissociations in performance on direct and indirect tasks as evidence for the existence, and properties, of separate memory systems. However, this approach has received criticism. First, the 'processing view' of memory (discussed below) could provide an alternative explanation for dissociable performance on direct and indirect tasks that does not necessitate the existence of separate systems. Second, even where system models of memory are endorsed, the manner in which indirect and direct tasks are employed to investigate explicit and implicit memory gives rise to concerns that few, if any, retrieval tasks are 'process pure' (discussed below).

Processing Theories

The central tenet of the 'processing view' is that memory is dependent upon the recapitulation of processing operations performed at study, with retrieval determined by the overlap between such processing at study and test. [In general, processing theory is contrasted with activation theory whereby the presentation of a word simply automatically activates its internal representation (e.g. Graf et al., 1984)]. The two most influential processing models are encoding-specificity and transfer-appropriate processing. In the encoding-specificity principle (Tulving, 1983), memory retrieval is determined by the degree of compatibility between item representation in memory traces and the constituent features of the presented retrieval cue. Within the transfer-appropriate processing framework (Morris, Bransford and Franks, 1977) memory performance is determined by the correlation between the processing applied to the study items and the processing applied at test to the retrieval cues. In support of this proposal, Morris et al. (1977) illustrated that if at study subjects are required to make either rhyming or semantic judgements to a series of words, when subsequently tested with a standard old/new recognition task, memory performance is highest for the semantic encoding condition. By contrast, if at test they are instead required to determine whether words rhyme with those presented at study, memory performance is highest for the rhyming (shallow) encoding condition.

Some processing theorists (e.g. Roediger and Blaxton, 1987) have additionally emphasised a distinction between data-driven and conceptually driven processes. In essence, data-driven memory reflects processes based upon sensory and perceptual features of encoded information and retrieval cues. By contrast, conceptually-driven memory reflects processing dependent, at least in part, upon higher-order semantic processing, for example expectations about the nature of the presented stimuli or elaborative processing of the stimuli. Furthermore, it was further proposed that the distinction between data-driven and conceptually-driven processing could occur quantitatively (i.e. on a continuum), rather than qualitatively necessitating the existence of multiple memory sub-systems (but see Weldon, 1993). Critically, processing theory offers an explanation of the dissociations in performance across indirect and direct tasks in terms of the type of processing elicited by the task (i.e. data-driven processes generally underlie performance on indirect tasks whereas conceptually-driven processes generally underlie performance on direct tasks).

Although in its extreme the processing view offers an explanation of dissociations in performance on memory tasks that does not necessitate the existence multiple memory systems, the adoption of the processing view in this manner is rare. More generally it is proposed that processing and systems views are not necessarily mutually exclusive, and suggestions have been made to incorporate processing views within systems models (e.g. Roediger, 1990). Indeed, some researchers suggest that distinctions between memory systems and memory processes are a false dichotomy since processes operate within systems (Baddeley, 1997; Pilotti, Bergman, Gallo, Sommers and Roediger, 2000). Moreover, as outlined by Baddeley (1997) in practice distinctions between systems and processes tend to apply more to the methodological discipline in which memory is being investigated. For example, neuropsychologists frequently examine neurobiological systems (Schacter, 1994; Squire, 1998) whilst cognitive psychologists tend to examine processes operating in such systems (Roediger, Weldon and Challis, 1989; Yonelinas and Jacoby, 1995; Jacoby, 1998).

Whichever position is adopted, what remains necessary is adequate explanations of processes and the structural systems within which they operate. Unfortunately, as yet this ideal has not been achieved. Instead, controversy between systems and processing theories of memory has focused on the best manner to subdivide memory function, for example, whether 'activation' or 'processing' theories best characterise implicit memory (McAndrews, Glisky and Schacter, 1987, for reviews see Schacter, 1987; Roediger, Srinivas and Weldon, 1989; Roediger and McDermott, 1993).

Process Purity

A second criticism of using direct and indirect tasks as tools to investigate the properties of memory systems is that the approach assumes that the different retrieval tasks have a one-to-one mapping with the memory system under investigation. In practice, indirect and direct tasks may not fully exclude the contributions of qualitatively different memory systems and under such circumstances the tests cannot be assumed to be 'process pure' (Jacoby and Kelley, 1992; Jacoby, Lindsay and Toth, 1992).

One concern is that the performance on indirect tasks of memory may be contaminated by explicit memory processes (Toth, Reingold and Jacoby, 1994; see also Beauregard, Benhamou, Laurent and Chertkow, 1999). For example, the participant might become aware of the experimental manipulation and alter their behaviour in response to presented cues, either with or without volition (Schacter, Bowers and Booker, 1989). Similarly, performance on direct tasks may be contaminated by implicit memory processes. For example, performance on cued recall may result from both episodic retrieval and priming effects (Friedman, Snodgrass and Ritter, 1994). Notably, it has been proposed that two distinct processes - familiarity and recollection (which may at least in part belong differentially to implicit and explicit memory systems) subserve memory in recognition tasks (Atkinson and Juola, 1973; Mandler, 1980; Jacoby and Dallas, 1981; Jacoby and Kelley, 1992; Yonelinas, Regeher and Jacoby, 1995; discussed below in 'Theories of Recognition Memory' section). In brief, recollection characterises conscious awareness of the study episode (i.e. episodic memory) whereas familiarity is defined as memory retrieval characterised by feelings of knowing that an event has occurred but without retrieval of the context or previous occurrence of the event. Although recollection is characterised as explicit memory, familiarity-driven recognition memory may depend (at least partially) upon implicit memory processes. Thus, unless the tasks employed are designed to allow the contributions of separate memory processes such as these to be fractionated (e.g. Tulvings, 1985b, see also Rugg, Schloerscheidt and Mark, 1998c), it is clearly problematic to use the data from such tasks as evidence of the properties of the separate memory systems.

A final important consideration to note regarding the isolation of cognitive processes by memory tasks concerns the need to distinguish between 'pre' and 'post' retrieval processing (see Rugg and Wilding, 2000). That is, the distinction between processing engaged to retrieve information from memory as contrasted with processing upon the products of a retrieval attempt, for example maintaining information in working memory or the evaluating of the significance of information (Rugg and Wilding, 1996; see also Koriat and Goldsmith, 1996a). As defined further by Rugg and Henson (in press), these concepts are also distinct from the notion of 'retrieval success' (successful recovery of information) since retrieval processing may result in 'negative' memory (i.e. failures to retrieve or false memories).

Although the concept of distinct types of retrieval processing has received little emphasis in the memory literature, such a distinction has implications for the way memory tasks are employed to investigate the properties of memory systems. For example, where it is aimed that the neural correlates of retrieval are to revealed by contrasts between correctly classified retrieval cues (e.g. old vs. new words), 'retrieval' effects may be contaminated by other kinds of differential activity, for example, processing supporting retrieval orientation[1], effort and decision-making. It is only within the last decade that concepts of pre-retrieval and post-retrieval processing have been emphasised with regard to their respective isolation in cognitive tasks.

The Neuroanatomical Basis of Episodic Memory Retrieval

Anatomical accounts of memory identify neural interactions supporting memory encoding, consolidation and retrieval which, broadly speaking, can be divided into four stages (see Markowitsch, 2000 for a similar account). First, sensory uptake of information is mediated by the engagement of sensory receptors and the transmission of information up to the cortex. Second is the transient processing of information in working memory, possibly mediated by posterior association cortex (Shallice and Warrington, 1970; Butterworth et al., 1996) and also anterior regions (Casey, Cohen et al., 1995; Courtney, Petit, Haxby and Ungerleider, 1998). Third, and central to the formation of episodic memories, is the transfer of information into long-term memory and the formation of a memory trace (engram) (Thompson, 1976; Craik, 1983). This third stage is usually viewed as comprising of an initial encoding phase and subsequent consolidation of encoded information (see Baddeley, 1997 for review). The fourth stage corresponds to the retrieval of information in response to a cue (see Rugg and Wilding, 2000 for review).

By most accounts, anatomical mediation of the transfer of information into long-term memory is based upon Papez's 'limbic system' circuitry (1937) - a number of structures within the medial temporal lobe (including amygdala, hippocampus and medial thalamic nuclei) (see Markowitsch, 2000; Markowitsch, 1999). Physiological aspects of such accounts of memory formation predominantly build on Hebbian theory (1949), that is the proposal that internal and external events become

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[1] The manner in which retrieval cues are processed (Wilding and Rugg, 2000)

consolidated into memory when neighbouring synapses become more structurally and functionally connected through repeated synchronised activity (Hebb, 1949) (see Kolb and Whishaw, 1980; pp 314-317; Markowitsch, 2000; pp 787).

Of all the structures in the medial temporal lobe, it is undoubtedly the hippocampus that has received most attention regarding the anatomical locus of such Hebbian memory formation (e.g. Grasby, Frith, Friston, Frackowiak and Dolan, 1993; Hasselmo, Wyble and Wallenstein, 1996; Rempel-Clower, Zola, Squire and Amaral, 1996; Schacter, Alpert, Savage, Rauch and Albert, 1996a; Rugg, Fletcher, Frith, Frackowiak and Dolan, 1997a; Reed and Squire, 1997; Vargha-Khadem, Gadian et al., 1997; Eldridge, Knowlton, Furmanski, Bookheimer and Engel, 2000; for reviews see Squire, 1992; Tulving and Markowitsch, 1998; Aggleton and Brown, 1999, Cohen, Ryan et al., 1999). Indeed, neurophysiological studies have indicated that encoding processes correlate with bioelectrical changes (such as long-term potentiation/depression) and morphological changes in neural morphology (synaptic enlargement, dendritic spine growth etc.) in the hippocampus thus providing an experimental model of hippocampal Hebbian synapse-learning (Bliss and Gardner-Medwin, 1971; Bliss and Gardner-Medwin, 1973, Eccles, 1986; Bliss and Collingridge, 1993; see also Shapiro and Eichenbaum, 1999).

However, the extent to which the hippocampus is depended upon for memory formation is unclear. By some accounts, both the hippocampus and regions lateral to the hippocampus (perirhinal, entorhinal and parahippocampal cortices) are important for episodic and semantic memory and function collectively as an integrated (self-contained) assembly - ‘hippocampal system’ (Zola-Morgan, Squire, Amaral and Suzuki, 1989; Squire and Zola-Morgan, 1991; for reviews see Squire and Knowlton, 1999, Aggleton and Brown, 1999). By contrast, the demonstration that focal hippocampal pathology originating early in life produces pronounced episodic memory impairments (whilst sparing the acquisition of semantic knowledge) provides evidence for the view that episodic and semantic components of explicit memory are partly dissociable, with only the episodic component being fully dependent on the hippocampus (Vargha-Khadem, Gadian et al. 1997).

Although the hippocampal system is known to be important for the transfer of information into long term memory, it has proved difficult to dissociate its participation in encoding or consolidation/retention processes from any participation in retrieval processing. Reports that patients with complete bilateral medial temporal lobe lesions are able to retrieve memories acquired before the onset of the amnesia (or alternatively have temporally graded retrograde amnesia) has led to proposals that such structures are not responsible for permanently storing episodic memories and instead regions of cerebral cortex, especially association cortex have been proposed as storage loci (Knowlton and Fanselow, 1998; for reviews see Eichenbaum, 1997; Markowitsch, 2000). By this account, memory storage initially requires hippocampal system linking of dispersed neocortical storage sites, but over time the involvement dissipates. (The change in function over time is held to account for the retrograde amnesia (RA) gradients often seen in patients with medial temporal lobe damage).

By contrast, other investigators contend that remote memories are not always spared in medial temporal lobe amnesia and that medial temporal lobe damage or dysfunction may result in extensive retrograde amnesia for personal episodic memories, thus inconsistent with views limiting medial temporal lobe function to encoding and/or a temporary role in retrieval (Nadel and Moscovitch, 1997; Nadel and Moscovitch, 1998; Viskontas, McAndrews and Moscovitch, 2000). Also inconsistent with views limiting medial temporal lobe function to encoding are findings that disruption of medial temporal lobe activation at retrieval either through pharmacological intervention (Liang, Hon, Tyan and Liao, 1994; Riedel, Micheau et al., 1999) or electrical stimulation (Halgren, Wilson and Stapleton, 1985) severely impairs memory retrieval. On the basis of such evidence it was proposed by Moscovitch and colleagues that medial temporal lobe structures, specifically the hippocampus, are necessary for the retrieval of episodes and their contextual frame, and that temporal lobe-neocortical interactions contribute instead to the extraction of semantic information stored in the neocortex.

Unfortunately, the results of neuroimaging studies have been unable to resolve the whether the medial temporal lobe structures are necessary for retrieval. Compared with other regions of the cortex (posterior association cortices, prefrontal cortices), functional imaging studies (especially fMRI) have failed to consistently reveal medial temporal lobe activation at retrieval (Chapter 3; for reviews see Nyberg, 1998; Lepage, Habib and Tulving, 1998; Schacter and Wagner, 1999; Rugg and Henson, in press).

In addition to the four stages of memory outlined above (sensory uptake, transient storage, transfer into and retrieval from long-term memory); more recently a fifth stage of memory has been outlined – that is processing carried out upon the products of retrieval (for reviews see Rugg and Wilding, 2000; Rugg and Henson, in press). Although the role of the medial temporal lobe in retrieval is ill-defined, a variety of evidence suggests that the brain regions responsible for post-retrieval processing do not include medial temporal lobe structures. Instead, regions of the prefrontal cortex (especially right anterior and dorsolateral) are consistently activated across a variety of tasks involving post-retrieval processing, such as those requiring the monitoring of retrieved information, associative recall, source discriminations and temporal-order processing (Rugg, Fletcher, Frith, Frackowiak and Dolan, 1996; Rugg, Fletcher et al., 1998a; Henson, Shallice and Dolan, 1999b; Allan, Dolan, Fletcher and Rugg, 2000; Henson, Shallice and Dolan, 1999b). Furthermore, impairments that are seen in episodic memory which relate to elaborate processing supporting the retrieval of contextual information tend to follow prefrontal cortex lesions rather than medial temporal lobe lesions (e.g. Janowsky, Shimamura and Squire, 1989).

Theories of Recognition Memory

The final section of this chapter turns its attention to recognition memory, the form of memory elicited in the experiments in this thesis. Dual-process models propose that there are two routes to recognition - familiarity and recollection - which represent qualitatively different ways in which a retrieval cue can access information about a past episode (Atkinson and Juola, 1973). As defined above, the process of recollection is characterised as conscious awareness of the study episode (i.e. episodic memory). Information retrieved includes contextual details of the study episode and there is the experience of ‘remembering’ a specific past event. By contrast, familiarity defines memory retrieval characterised by feelings of knowing that an event has occurred but without any accompanying information regarding context or previous occurrence of the event. In general, dual-process models are contrasted with single-process models which postulate that a single memory system can accommodate differences between familiarity and recollection as differing points along the continuum of a memory trace (see Donaldson, 1996; Hirshman and Master, 1997; Inoue and Bellezza, 1998).

Dual-process models were quickly established as a viable framework within which to interpret results from recognition memory tasks. Perhaps the success of dual process models stems from the fact that they are, in a sense, intuitive models which accommodate our own experiences of episodic memory. For example the "where do I know you from?" phenomena of being able to recognise a person's face but unable to remember their name, or when and where you previously encountered them, is accommodated in dual-process theories by familiarity in the absence of recollection. By contrast, when we 'recollect' that person, the experience often feels qualitatively dissimilar.

However, within dual processing theories there is controversy over the nature of the cognitive processes underlying familiarity. Mandler (1980) defined familiarity as the perceptual activation of memory traces. By this account, familiarity reflects the activation of 'intra-event' information whereas recollection results from elaborative retrieval processes eliciting 'inter-event' associative information such as temporal or spatial information regarding when or where an event occurred. The perceptual activation account of familiarity has received criticism since it cannot adequately explain memory illusions such as incorrectly judging a new item in a recognition memory task to be old (e.g. Jacoby and Whitehouse, 1989; Norman and Schacter, 1997) or mis-attributions of the source of a memory (e.g. Johnson, 1997). For example, in the 'false fame' effect (Jacoby, Woloshyn and Kelley, 1989), prior exposure to a name early on in an experiment increases the probability of it being judged as famous at a later time, as long as the prior presentation is not recollected.

Jacoby and Dallas (1981), whilst viewing recollection in a similar manner to Mandler, proposed instead that familiarity is dependent upon 'attributional processing' conferred upon retrieval cues. By this account, the application of a 'fluency heuristic' when encountering retrieval cues influences judgements of familiarity. In the absence of recollection, items processed fluently are judged as more familiar than items with less fluent processing (so long as the fluency is attributed to the past rather than to some other source such as legibility or simplicity etc.). A direct prediction from attributional theories is that familiarity judgements should be affected by the ease of perceptual processing of items during a recognition memory task.[2] In support of this,

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[2] Studies which examine effects upon familiarity and recollection based recognition memory usually employ the remember/know

one study revealed that if perceptual characteristics between study and test change (e.g. masking/modality changes), then fluency is impeded and familiarity based recognition reduced (Whittlesea, Jacoby and Girard, 1990). Second, the brief presentation of a test item immediately prior to the word being presented at test (i.e. perceptually priming the retrieval cue), increases the likelihood of old judgements to both old and new words (as long as participants are not aware of the manipulation) (Jacoby and Whitehouse, 1989). In addition, conceptual fluency has also been shown to influence judgements of familiarity. For example, preceding items with a highly predictive sentence context e.g. 'He put the knife next to the FORK'; compared with a less predictive context e.g. 'He went to the shop and bought a FORK', increases the probability of judgements of the word being recognised on the basis of familiarity (Whittlesea, 1993).

A first criticism directed toward dual-process models is that some of the dissociations between familiarity- and recollection- based old judgements in recognition memory tasks may reflect variations in response criteria rather than capturing any 'true' distinction between familiarity and recollection (see Donaldson, 1996; Hirshman and Master, 1997; Inoue and Bellezza, 1998). By this account, memory is modelled as a single-process trace strength model with familiarity as a continuous variable representing evidence of an items prior occurrence (Gillund and Shiffrin, 1984). The familiarity distributions of old and new items are represented by overlapping normal probability density distributions. Dissociations between recollection and familiarity are dependent upon memory trace strength and the placement (by the self) of two decision criteria along the axis, one for old/new judgements, the second for familiarity/recollection (e.g. R/K judgements). This signal-detection theory model predicts that judgements of familiarity are inherently more unstable than judgements of recollection since shifts in the old/new criteria placement will affect the rate of familiarity responses but leave the proportion of recollection responses unaffected (see Donaldson, 1996).

A series of meta-analyses of recognition memory studies have been conducted to investigate whether such single-process models can account for findings from studies

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paradigm developed by Tulving, 1985. In this procedure, if participants are sure a retrieval cue is old but cannot recall any details regarding the items previous presentation, then they are required to give a 'know' (K) response. By contrast, if the item evokes any details of the study episode (e.g. where or when the word was presented) the participants give a 'remember' (R) response.

which have been taken as support for dual processing theory (e.g. Donaldson, 1996; Hirshman and Master, 1997). It does appear from these studies that at least some (although not all) of the dissociations between familiarity and recollection can be explained within the confines of a single-process model. Crucially, single-process models highlight weaknesses in dual-process approaches to recognition memory by providing evidence that differences in recollection and familiarity judgements may not be solely attributable to mnemonic processing but also to shifts in response criteria (which are sensitive to extraneous factors such as task instructions) (Hirshman and Master, 1997).

A second criticism directed toward dual-process models of the kind proposed by Jacoby and colleagues is that although they receive some support from cognitive psychology studies, evidence from clinical studies is less conclusive. More specifically, although episodic retrieval (recollection) is thought to engage temporal lobe structures (at least by some accounts, see above), the neuroanatomical basis of familiarity is ill-defined and thus its existence as a separate process has been questioned. If familiarity is driven by perceptual fluency akin to priming mechanisms (implicit memory) (see Jacoby, 1991), familiarity-based recognition memory should function independently of medial temporal lobe structures mediating episodic memory (e.g. hippocampus) (see Knowlton and Squire, 1995; Reed, Hamann, Stefanacci and Squire, 1997). However, evidence from studies of classical medial temporal lobe (and/or diencephalic) amnesia suggest that this is not the case (Squire and McKee, 1992; Knowlton and Squire, 1995; Reed et al., 1997, but see Aggleton and Shaw, 1996). For example, Knowlton and Squire (1995) provided evidence that familiarity judgements in tests of recognition memory depend on structures that are damaged in amnesia. Furthermore, Reed et al. (1997) provided evidence that the residual recognition memory by amnesics with medial temporal lobe damage is not due to familiarity engendered by implicit memory mechanisms.

On the basis of these findings, Squire and colleagues proposed that familiarity and recollection are both forms of declarative memory and can be accommodated for within models of recognition memory that posit a single process (see Knowlton and Squire, 1995; Knowlton, 1998; Squire and Knowlton, 1999). By this account, both familiarity and recollection are dependent upon medial temporal lobe structures that support declarative (explicit) memory but recollection additionally requires information about the context in which an item was encountered. Such additional information is dependent upon the integrity of the frontal lobes (see Moscovitch, 1992 for a similar model). Familiarity occurs when declarative information is retrieved successfully but either information about the context in which an item occurs is not available (Squire and Knowlton, 2000) or the integration of item and contextual information fails (Moscovitch, 1992). Thus, in such a framework, familiarity is viewed as weak or incomplete recollection. Poor recognition performance in amnesics occurs since declarative information is not retrieved, hence, both familiarity and recollection fail.

In contrast to the findings by Squire and colleagues, a study by Schacter, Verfaellie and Pradere (1996) appeared to provide evidence that amnesia leads to a pronounced decrement in recollection but that familiarity increases, thus suggesting that recollection and familiarity are anatomically dissociable (see also Verfaellie and Treadwell, 1993; Schacter, Verfaellie and Anes, 1997). However, it was subsequently demonstrated by Yonelinas, Kroll, Dobbins, Lazzara and Knight (1998), that the type of model chosen by researchers to analyse data critically affects the results obtained. In brief, Schacter and colleagues analysed their data sets employing a model which assumed that familiarity and recollection are mutually exclusive. Importantly, when the data were reanalysed by Yonelinas et al. (1998) with a dual-process signal-detection model (allowing for independency in the contributions of recollection and familiarity to recognition memory), it was demonstrated that familiarity and recollection are both impaired in amnesia (with impairments in recollection more pronounced).

Although Yonelinas et al., 1998 appeared to resolve the apparent inconsistencies in the literature with respect to whether familiarity-based recognition memory is impaired in amnesics, their proposals regarding the functional anatomy underlying recollection and familiarity differed from those outlined above. In the neuroanatomical frameworks proposed above by Squire et al. (1995; 1999) and Moscovitch (1992) the relationship between recollection and familiarity is one of redundancy, with familiarity processes also active during remembering. However, Yonelinas and colleagues (1998) proposed instead that recollection and familiarity are mediated (independently) by hippocampus and parahippocampal regions respectively. Furthermore, their findings were not taken to be inconsistent with ‘attributional’ models of familiarity, rather it was suggested that familiarity is likely to be multi-componential i.e. more than just 'perceptual' fluency (priming); for example, conceptual fluency might contribute to familiarity-based recognition judgements (see also Jacoby, 1991).

A similar 'independence' model of the neuroanatomy underlying familiarity and recollection has also been proposed by Aggleton and Brown (1999). In this framework efferents from the hippocampus via the fornix to the diencephalon (hippocampal – anterior thalamic axis) are proposed as necessary for recollection whereas familiarity-driven memory is proposed to be dependent upon a distinct system involving the perirhinal cortex and the medial dorsal nucleus of the thalamus. It was further suggested that deficits in both recollection and familiarity are observed in amnesics since in the majority of cases both hippocampal-anterior thalamic and perirhinal-medial dorsal thalamic systems are damaged. More specifically, it was proposed that the loss of familiarity-driven recognition memory in amnesics will be dependent upon the extent of extrahippocampal dysfunction. Furthermore, Aggleton and Brown note that, in view of the interconnections between rhinal and hippocampal regions, although recollection and familiarity are proposed to have a relationship of independence, the two components are not mutually exclusive.

The review by Aggleton and Brown helps to resolve apparent inconsistencies between familiarity as an explicit form of memory and its proposed mediation by implicit memory mechanisms of fluency (i.e. priming). In line with the argument given above, they agree that in view of familiarity and priming belonging to explicit and implicit memory systems respectively, the two processes cannot have identical neural substrates. However, it is proposed instead that priming and familiarity may share the same initial stages of processing (i.e. perceptual fluency), but that in addition familiarity requires separate mechanisms, dependent upon processing involving the perirhinal cortex, which give rise to conscious appreciation i.e. 'knowing that an event has occurred'.

Summary

The idea that memory is subdivided by a number of systems has been firmly established in psychology. Despite the many contrasting theories outlined above, there does appear to be at least some agreement as to the basic structure of memory.

This consensus has been outlined by Baddeley (1997), as consisting of a long-term memory, episodic or recollective memory system. This system is characterised by conscious awareness of (autobiographical) information retrieved from long-term memory. This is usually contrasted with implicit memory, which is proposed (somewhat negatively) as being composed of 'an array of learning mechanisms that have in common only the fact that they are incapable of generating recollective memory' (pp351).

It is been proposed that medial temporal lobe structures are the critical structures mediating the transfer of information into the long-term episodic memory system. It is possible that such structures are also active during subsequent recapitulation of such information from memory, although this proposal is not without controversy. By contrast, prefrontal cortices are recruited when the retrieval of information requires further processing such as monitoring, evaluation or other such elaborative processes.

Dual-process theories propose that old/new judgements in recognition memory can be made either on the basis of recollection or familiarity, defined as recognition memory with and without retrieval of episodic information respectively (Jacoby and Dallas, 1981; Whittlesea et al., 1990; Jacoby, 1991). Such theories have been criticised on the grounds that findings from such studies can be explained within the confines of a single-process model (Donaldson, 1996; Hirshman and Master, 1997; Inoue and Bellezza, 1998). At issue is whether familiarity is mediated by any kind of distinct system from recollection as opposed to partial recollection mediated by the same neuroanatomical substrates, and if so, whether familiarity is best categorised as an implicit or explicit (or both) memory process (see Yonelinas et al., 1998; Aggleton and Brown, 1999 vs. Knowlton and Squire, 1995; Mulligan and Hirshman, 1997). The question of whether recognition memory is supported by one or two processes will be returned to in chapter 3, wherein a number of functional imaging studies which have addressed the issue are reviewed.

CHAPTER 2

Event-Related Potentials

Background

In 1929, Berger discovered that patterns of electrical activity arising from the brain could be recorded non-invasively by placing electrodes on the scalp. Since then, studies have confirmed that this electrical activity (termed the electroencephalogram – or EEG) is the manifestation on the scalp of the activity of neural populations. Under suitable conditions, these electrical fields conduct through the brain and its covering to the scalp. Event-related potentials (ERPs) are defined as portions of the EEG waveform time-locked to a specific occurrence or event and are extracted from the ongoing EEG by means of filtering and signal averaging. The ultimate aim of ERP methodology is to be able to decompose waveforms into constituent 'components' and determine the parameters of the neural generators and psychological manipulations producing these components. Although ERPs can be analysed in both frequency and time domains, this thesis is primarily concerned with the latter, that is the employment of ERPs to index neural activity time-locked or synchronised to a specific event (for techniques regarding frequency domain analyses see Townsend, 1970; Pradhan, Dutt and Satyam, 1993).

The temporal resolution of ERP measurements is at the order of milliseconds. Thus ERPs are an accurate (in time) and non-invasive electrophysiological index of neural activity providing information about cognitive processing and brain physiology (even in the absence of overt behavioural data). Such information provided by ERPs can be used in a variety of different research purposes ranging from specific diagnoses in medicine (see Halliday, 1978; Halliday, 1980) to constraining psychological theories of neural mediation of cognitive processing (see Hillyard and Picton, 1987; Rugg and Coles, 1995). However, as with all neuroimaging methodologies, ERPs have a number of advantages and disadvantages, which are outlined in the remainder of the section. Principle advantages and disadvantages of ERP techniques as compared with haemodynamic measures are summarised in Table 2.1 (adapted from Rugg, 1998).

There are three main advantages in using ERP techniques to investigate cognitive functions.[1] The first principal advantage, high temporal resolution, is offset by a weakness in respect to spatial resolution; (as displayed in Figure 2.1, the opposite pattern is observed with haemodynamic measures, discussed further in chapter 9).

Table 2.1. Strengths and weaknesses of electrophysiological and haemodynamic measures (adapted from Rugg, 1998, Convergent approaches to electrophysiological and haemodynamic investigations of memory. *Human Brain Mapping, 6*, 394-398).

Electrophysiological	Haemodynamic
Strengths	*Event-related fMRI only
High temporal resolution	High spatial resolution
Direct, relatively unobtrusive, measure of neural activity	Homogeneous (PET) or near-homogeneous (fMRI) sampling of task-related activation
Can obtain data contingent on performance	*Can obtain data contingent on performance
Can employ randomised event-related trials	*Can employ randomised event-related trials
Weaknesses	**Not applicable to event-related fMRI
Samples only a partial and unknown fraction of activity	Indirect measure of neural activity
Poor spatial resolution	Poor temporal resolution
	Not absolute homogeneous sampling (fMRI)
	**Difficult to obtain data contingent on performance
	**Difficult to distinguish state- and item-related effects

A second advantage of ERP techniques is that it is possible to employ randomised experimental designs, whereby trials belonging to different experimental conditions can be mixed in unpredictable sequences. This ability is crucial for some psychological paradigms, for example, in the 'oddball' paradigm unexpected events need to be randomly interspersed with non-critical stimuli (e.g. Rugg, Pickles et al., 1993). Importantly, the ability to randomly intermix trials enables experimenters to avoid the pitfalls of many haemodynamic studies of neurological activity which employ blocked designs wherein measurements are made over a succession of trials constituting a single experimental condition. Blocked designs are problematic because it is difficult to distinguish between state-related and item-related effects - the former defining sustained modulations of activity that accompany engagement in a specific task, the latter defining transient changes in neural activity contingent upon

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[1] Advantages of event-related paradigms discussed also apply to event-related fMRI which has been developed over the last decade (see Chapter 9).

specific events such as presentation of a stimulus (see Rugg, 1998; Rugg and Henson, in press; see also Düzel, Cabeza et al., 1999; Donaldson, Petersen, Ollinger and Buckner, 2000).[2] Additional difficulties arise when employing blocked designs since they render it difficult to obtain data contingent upon performance.

Finally, the ability to employ event-related designs is critically important where psychological processes under investigation may change following repeated presentations of stimuli. For example, the repeated presentation of emotional stimuli in blocked studies might influence mood and thus cognitive processes such as memory and attention (e.g. Isen and Levin, 1972; Isen, Shalker, Clark and Karp, 1978; Isen, Johnson, Mertz and Robinson, 1985; Ashby, Isen and Turken, 1999). Furthermore, it is known that responses in emotion-sensitive structures in the brain (specifically the amygdala) may exhibit a quantitative response decrement (habituation) to continuously repeated presentation of stimuli (e.g. Breiter, Etcoff et al., 1996; Büchel, Dolan, Armony and Friston, 1999).

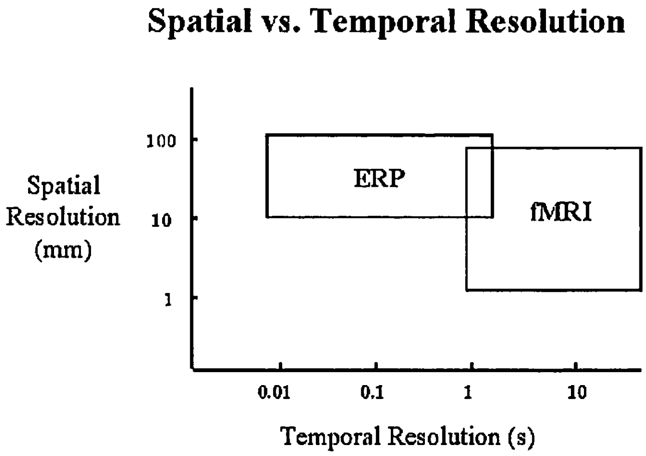

Figure 2.1 Spatial and temporal resolution in PET and fMRI (Adapted from Rugg, various).

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[2] Although attempts have been made to design blocked studies such that state- and item- related effects can be dissociated (e.g., Rugg et al., 1996; Düzel et al., 1999) as noted by Rugg and Henson, (in press) 'in practice it is difficult, if not impossible, to demonstrate that the intended fractionation was successful' p 5.

As outlined in table 2.1, there are disadvantages to ERP techniques. It has already been mentioned that ERP techniques have a relatively poor spatial resolution as compared with haemodynamic measures. However, also of concern is the relative inability of electrophysiological measures to sample the activity of the entire brain in a homogenous manner (Nuñez, 1990a). In other words such techniques are unable to detect activity with roughly equal sensitivities regardless of location in the brain or geometric configuration (Rugg, 1998). Unfortunately, these disadvantages constrain the interpretations that can be made about the neural sources and cognitive processing attributed to patterns scalp activity. For example, null effects are difficult to interpret since there may be cognitive processing mediated by structures whose neural activity is not externally observable.

Methodology

The following section is subdivided into sections outlining different aspects of ERP methodology (electrogenesis, recording, experimental design, artefact and signal averaging). Coverage of ERP methodology in literature is both extremely diverse and extensive, the following material derives mainly from Cooper, Osselton and Shaw (1980); Wood and Allison (1981); Coles, Gratton, Kramer and Miller (1986); Picton Lins and Scherg (1994); Rugg and Coles (1995); Kutas and Dale (1997) and also Picton, Bentin et al. (2000). The last-mentioned (and most recent) reference provides a set of guidelines published by a collection of leading ERP researchers with the aim of standardising ERP methodology. Where points in this section relate to the design, recording and analyses of ERP experiments it is intended that they are reasonably consistent with Picton and colleagues' (2000) guidelines. However, in the interests of conciseness, the section is fairly selective in its coverage of methodological issues, outlining only the critical points relevant to the chapters in this thesis (for a more comprehensive review of ERP publication criteria the reader is referred to the preceding references).

Electrogenesis: Potential Generation and Fields

In order to understand how ERPs can provide information about the nervous system, the relationship between such measurements and the underlying neural biology must be outlined. This section describes the relationship between evoked potentials and the properties/organisation of neurons and additionally outlines issues relating to the recording of the evoked potential from outside the scalp, as opposed to directly from neurons.

Ionic current flow across the cell membranes of neurons gives rise to potential differences between different locations in the extra cellular space (Wood and Allison, 1981; Allison, Wood and McCarthy, 1986). There are two types of transmembrane current flow: action potentials and post-synaptic potentials. The former defines current flow along the cell body to the axon terminals, the latter defines current flow in the form of graded post-synaptic potentials (excitatory or inhibitory) transmitting information between neurons (Wood and Allison, 1981). While both types of transmembrane current flow can create potential differences between different locations in the extra cellular space, there is evidence that post-synaptic potentials are the main contributor to scalp recorded ERPs (Cooper et al., 1980).

Currents flowing through neuron membranes are termed sources and sinks, depending upon their direction (outwards or inwards respectively). The summation of the individual sources and sinks (i.e. net current flow) generates the potential differences between different locations in the extra cellular space and the space in which the resulting electric potential is present is termed the potential field. The size of the potential field generated depends mainly on the neural configuration producing the sources and sinks (see Wood and Allison, 1981; Allison et al., 1986; Kutas and Dale, 1997). It has been shown (see Kutas and Dale, 1997 for review) that different neural field configurations can give rise to either 'open' or 'closed' electrical fields. An open field source configuration describes the arrangement of neurons whereby an externally observable electric field can be recorded. This is critically dependent upon the arrangement of the cells being such that the current sources and sinks generated by individual cells can summate without cancelling each other out. Physical variation between neurons (e.g. shape, size etc.,) can influence the transmission of the current and hence the size of the potential field. In addition the collective organisation (alignment, average distribution of sources and sinks, synchronicity of firing) of the neurons influences the size of the potential field.

Open field structural arrangements are typical within brain areas exhibiting laminar organisation such as the neocortex (Coles et al., 1986). The organisation of the neocortex produces open fields mainly because of the properties of its pyramidal cells, which in some accounts have been likened to dipoles with axes perpendicular to the surface of the cortex (Fourment, Jami, Calvet and Scherrer, 1965; see also Cooper et al., 1980; Mitzdorf, 1994). Though the potential produced by a single pyramidal neuron is quite weak, the potential fields produced by a patch of cortex containing hundreds of thousands of such neurons may be measured at a distance from the patch such as outside the scalp (Kutas and Dale, 1997). However, it is important to note that the size of the electric field measured at different scalp sites is influenced not only by the physical properties and the collective organisation of neurons, but also by differential conductive inhomogeneities in the intermediate brain matter between the neurons and the scalp (e.g. tissue, skull, blood and scalp).

In closed field source configurations electric potentials are self-cancelling (sum to zero) thus there is no externally observable electric potential field. As discussed by Kutas and Dale (1997), closed fields are generated if for example alternate parallel neurons have opposite orientations to each other (Fig 2.2a); or the cell bodies are clustered centrally with dendrites radiating outwards (Fig 2.2b). In these circumstances, current flow is such that the potential measured outside the structure is zero. However, even when the geometric organisation of cells is such that they have the capacity to produce an externally observable field, if the activation of neurons is temporally asynchronous (as in Fig 2.2c) the summation of potentials from individual neurons may result in a closed field.

In summary, potential differences that are recorded between electrodes result from electrical activity occurring within dispersed populations of neurons whose electric field propagates to the scalp. However, since the size of electric fields are determined by factors other than neural activity (e.g. closed/open field configurations, conductivity of matter between the neurons and the scalp), potential differences are not a complete measure of the brain's activity and as such constrain functional interpretations that can be made regarding ERP data.

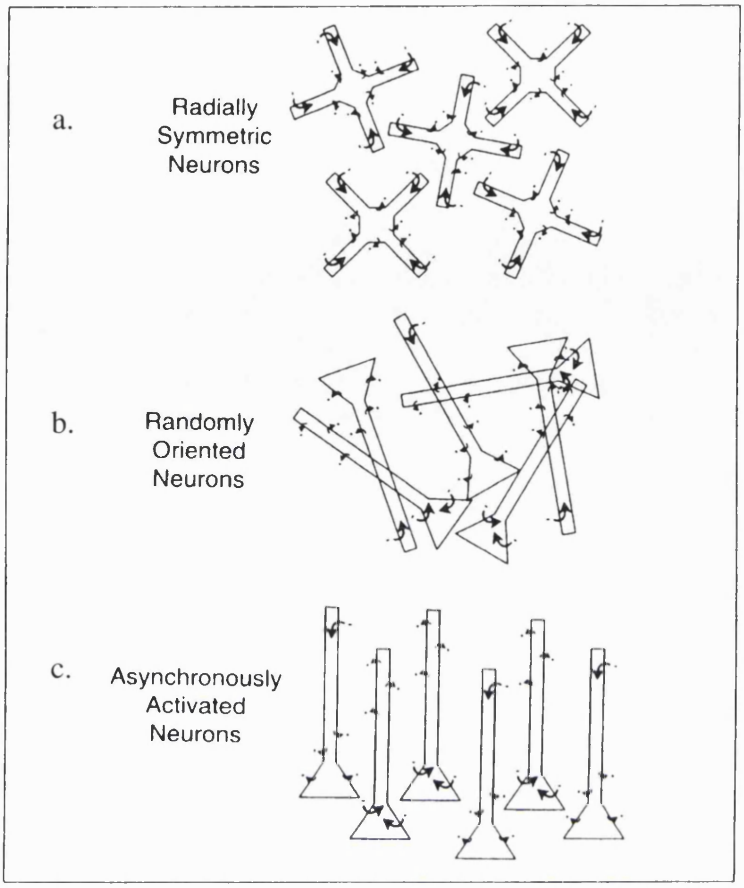

Figure 2.2. Examples of self-cancelling or closed field source configurations
Kutas, M., & Dale, A. (1997). *Electrical and magnetic readings of mental functions.* In M. D. Rugg (Ed.), Cognitive Neuroscience. East Sussex: Psychology Press.

Experimental Design

Briefly outlined in this section are points that relate specifically to the choice of using ERPs as the neuroimaging tool to investigate human cognition, as well as issues that are faced by any psychologist attempting to understand cognitive processing.

The most basic issue regarding the experimental design is whether ERPs are suitable for investigating the cognitive processing of interest. This issue necessitates the design of ERP studies such that any differential activity (for example between conditions) can be detected with adequate sensitivity. As outlined previously, there are preconditions for detecting electrophysiological signals, and hence there are likely to be circumstances in which electrophysiological methods are not sensitive to experimentally induced changes in cognitive processing. A second issue is that as far as possible, it should be ensured that any cognitive processing is process pure and not confounded by aspects of the experiment which evoke extraneous information processing (see chapter 1). For example, many aspects of cognitive processing (certainly those relating to emotion and memory) are extremely sensitive to variations in timing/order/type of stimulus presentation. Thus, to avoid confounds between such factors with experimental manipulations, parameters of the ERP experiment should be well defined, accurately measured and maintained across participants (Picton et al., 2000). Furthermore, wherever possible, counterbalancing between the experiment parameters and participants should be employed. Finally, statistical aspects of the ERP experiment such as the number of participants/trials required for the statistical tests to demonstrate an experimental effect, as well as inferences that can be made regarding any effects, should be defined prior to commencing the study.

In order to accommodate the above three issues, a clear framework to the experiment needs to be outlined prior to conducting the ERP study which should also include hypotheses and predictions regarding the experimental results in relation to the experimental parameters and the elicited information processing (refer to Picton et al., 2000 for further discussion on the above issues).

ERP Recording

The electrodes used can take many forms, but since their common purpose is to transmit electrical activity at the scalp to the amplifier they must be non-polarisable (see Cooper et al., 1980). Prior to electrode placement the skin beneath each electrode site is cleaned and slightly abraded, subsequent to electrode placement a conductive gel is inserted into the cavity between the electrode and the scalp. These steps are taken to reduce the level of impedance between electrodes and allow proper contact with the scalp. The main issues regarding recording from electrodes concern the placement of electrodes and secondly the choice of electrodes between which the potential differences are to be measured.

With regard to the first issue, locations of the electrode sites are generally standardised in order to allow easy comparisons between ERP experiments, for example many electrode montages have been based upon Jaspers' (1958) International Ten-Twenty System or more recently upon the Ten-Ten System of the American Electroencephalographic Society (1994).

Regarding the second issue, in practice voltages at each scalp electrode are typically measured with respect to a common 'reference' electrode, whereby each scalp electrode is connected to the same reference. Whilst the placement of the reference electrode varies between experiments [e.g. left or right mastoid bone, linked mastoid (based on average of left and right mastoids), chest] the main criteria for choice of placement is to minimise the influence of the signal upon the reference whilst leaving the level of background noise unaffected (for a critical review of the different referencing techniques, refer to Binnie, 1987). However, as long as the relative position of the reference remains constant with respect to each recording electrode, the resulting measure of relative differences in potentials (voltage profile) associated with experimental manipulations across electrodes is the same (Allan, 1996). Alternative reference systems which eliminate the need for a separate reference channel, for example the use of the average of all the recording sites as the reference site (average reference derivations) or the use of the weighted average of electrodes surrounding the site of interest (source derivation) as the reference, are less frequently adopted.

Following recording, there are a number steps involved in extracting the ERP from the EEG. First, voltage changes are amplified and converted to digital. Analogue filtering is usually performed concurrently during amplification with a band-pass filter in order to remove frequencies different to those which relate to brain electrical activity or outside those of experimental interest. In addition, the high cut-off frequency is set to prevent aliasing (less than one half the frequency of A/D conversion), whereas the low cut-off frequency is set at a level necessary to prevent blocking the A/D converter by slow changes in the baseline (Cooper et al., 1980; Picton et al. 2000). Offline, digital values of the amplitude of the waveform at each sampling point in time are then subsequently used to recreate the ERP waveform. (In addition, further filtering may be done to remove frequencies beyond the cut-off frequencies that were not completely removed during amplification.)

Artefact Contamination and Signal Averaging

The voltages that are recorded consist of both the signal (time-locked neural activity) and also background noise. There are basically two forms of noise: that deriving from the participant (ongoing random neural firing and electrical activity arising from e.g. eye movements and cardiovascular physiology) and that resulting from the electrical activity in the participant's surrounding (e.g. electrical activity relating to the recording equipment).

Although the signal of interest elicited by an experimental manipulation is usually extremely small compared with the level of background noise, there are a number of ways of increasing the signal-to-noise ratio. Whilst recording, noise deriving from the participant is reduced as far as possible by instructing the participant to keep movements to a minimum and surrounding electrical noise is reduced by shielding the participant from any electromagnetic fields and also by earthing the participant. Following recording, as mentioned already, filtering then removes electrical activity resulting from surrounding electrical noise (and other sources) of a different frequency to brain electrical activity.

In addition, some types of artefact can be monitored and removed. Artefacts relating to eye movements and blinks cause voltage changes at frontal scalp sites, hence many ERP researchers record the electro-oculogram (EOG - voltage changes associated with eye-movements) concurrently with the ERP, and later reject trials in which the EOG exceeds a threshold criterion (see Croft and Barry, 2000 for review). Under these circumstances the participant is additionally instructed not to blink during trials so as to minimise the number of trials rejected. Similarly, trials with EEGs outlying a pre-specified threshold (normally as a consequence of excessive muscle activity or channel drift) may also be monitored for and rejected.

Unfortunately, blink artefacts are often a major problem in ERP recording, and where trial rejection procedures have been adopted in order to remove such artefacts, this can drastically reduce the number of trials available for averaging (see below). Also, requesting participants not to blink during ERP recording imposes superfluous cognitive demands during the task they are performing. One way to alleviate this problem, whilst still reducing EOG artefact, is to accept trials with blink artefacts and to correct for their effect on the EEG. This may be done by using linear regression to estimate the contribution of blink artefact to scalp ERPs and to correct for its effects by subtracting a scaled version of the EOG (Willis, 2000; see also Croft and Barry, 2000). However, a major problem with EOG correction procedures (especially at frontal electrodes) is that artefactual potentials may not be recorded independently of the EEG and hence subtraction of a scaled version of the artefact may result in subtraction of some parts of the signal (Picton et al., 1994; see also Jervis, Coelho and Morgan, 1989; Somsen and van Beek, 1998).

Following application of noise reducing steps during recording and pre-processing of ERP data, under most circumstances averaging procedures (performed over a large number of trials recorded under conditions that are as similar as possible) are then used in order to increase the signal to noise ratio. Laws of averaging apply in that the greater number of trials contributing to the averaged ERP, then the higher the resulting signal to noise ratio (averaging procedures decrease noise by a factor of the square root of the number of trials used). Three main assumptions underlie the use of averaging in ERP analyses (Glaser and Ruchkin, 1976). First, the signal and noise must linearly sum together to produce the EEG. Second, the signal must remain constant over time / over repeated trials. Hence, researchers need to beware of employing averaging techniques when investigating psychological processes that may change rapidly over time/repeated presentation of items (e.g. habituation). Third, the background noise must be random.

If these assumptions are upheld, then averaging procedures will reduce the random background noise levels leaving the electrophysiological signal unaffected. Circumstances where the signal is inconsistent across trials (either temporally, spatially or in terms of magnitude) result in an averaged waveform unrepresentative of the original scalp activity. For example, consider the situation whereby waveforms contributing to the averaged ERP contain a peak whose latency (post-stimulus onset) differs between trials (latency jitter). The averaged waveform will exhibit a peak of reduced amplitude with a latency lying somewhere between the latencies of the original peaks present in the individual trials (Johnson, 1995; see also Mocks, 1986; Mocks, Gasser, Pham and Kohler, 1987).

Other problems in interpreting averaged ERP waveforms arise if the presence of a signal is inconsistent across trials. If the proportion of trials in which the signal occurs differs between two conditions then the resulting averaged waveforms formed for the two conditions will differ in amplitude. The seemingly graded ERP effects in the averaged waveforms could be interpreted erroneously as reflecting some variation in the level of activity in the underlying neural generators between the two conditions. The correct interpretation would be that the averaged ERP reflects the activity of the same all-or-none neural process occurring on a different number of trials between each condition.

Analytical procedures for the foregoing averaging problems have been suggested such as inspecting the individual waveforms and adjusting the data accordingly. However, since the main aim of averaging is to enhance the signal to noise ratio, inspection of the individual trials contributing to the averaged ERPs to determine the proportion of trials contributing to the signal in the averaged ERP is normally unfeasible.

Analysis and Interpretation of ERP measurements

The remainder of the chapter concerns interpretations that can be made on the basis of ERP data. Since in ERP methodology the statistical analyses employed are often dependent upon the type of interpretation that the experimenter wishes to pursue (or at least depends upon an understanding of the various interpretations of ERP data), the different interpretations of ERP data are discussed prior to the different types of data analyses.

Physiological versus Functional Approaches

The classical approach to interpreting ERP data has been to identify and name positive and negative deflections (peaks and troughs) in the waveforms with characteristic amplitudes, scalp distributions and latencies. For example the P300 describes a positive going peak with amplitude maximum at 300msec whereas the N400 describes a negative going peak with amplitude maximum at 400msec. The basic methodology is then to demonstrate how such peaks and troughs correlate with, or are sensitive to, psychological processes. On the one hand this peak analyses approach is useful since it allows cross-experimental (and cross-laboratory) comparisons of ERP effects with relative ease (so long as the nomenclature used in defining such components is relatively consistent and universally adopted). However, there are a number of reasons why this peak analysis approach is problematic.

First, the practice of using descriptive nomenclature to link deflections in the waveforms with psychological processes may be misleading. For example, the succession of two ERP peaks does not necessarily indicate two successive processing stages since there may be intermediate processing mediated by neural activity occurring in different neural configurations, but whose potential fields are unobservable (or distorted) at the scalp. Furthermore, as noted by Picton and colleagues (2000), such deflections may vary in timing or order of occurrence in a waveform as a result of external experimental factors such as age/clinical status of participants. The biggest problem with this approach however is that the ultimate aim of ERP methodology; to be able to decompose waveforms into constituent 'components' and determine the parameters of the neural generators and psychological manipulations producing these components, is often neglected. As noted by Kutas and Dale, (1997), in peak analysis it may be tempting to assume that variations in the latency of a peak at different locations on the scalp reflect the modulation of a single (non-decomposable) underlying waveform component. However, this assumption is untenable since it is highly possible that a number of individual waveform components produced by the activity of distinct generator populations are contributing to the observed ERP deflection. Hence the labelling of a specific deflection in the waveform and attachment of functional significance neglects the fact that such deflections may embody multiple components (Kutas and Dale, 1997).

Over and above difficulties inherent to the peak analysis approach, a further problem in current ERP methodology is that there is no universal treatment of ERP components contributing to observed waveform deflections (see Rugg and Coles, 1995; Picton et al., 2000). Indeed, two extreme ways of defining ERP components have developed. In one extreme, a component is taken to reflect the manipulation of a psychological process but relation to brain activation is taken as less relevant (Donchin, Ritter and McCallum, 1978). From this perspective the activity of neural populations can even be taken as irrelevant since the ultimate aim is to be able to isolate specific variations in the ERP waveforms. In the other extreme, components of the ERP are defined in terms of their relationship to a specific neural generator(s) (Nuñez, 1990a) (a non-trivial problem which will be returned to below).

Most researchers appear to have opted for a compromise position by adopting a framework that combines 'functional' and 'physiological' approaches, i.e. assessing the component of an ERP waveform as scalp activity evoked by a neural generator that is specific to a psychological function. However, although such a compromise sits well with the aforementioned ultimate aim of ERP methodology, reconciling the two approaches is potentially problematic. As already discussed only activity arising from neural generators with the proper orientation and configuration can be measured at the scalp constraining interpretations that can be made. Furthermore, the physiological approach requires a one-to-one mapping between the component and its neural generators whereas the functional approach can operate with either one-to-one mappings or one-to-many mappings between the component and its neural generator/s (under the condition that where there is more than one set of neural generators they form a homogeneous information processing system) (Rugg and Coles, 1995). These issues render it difficult to construct cohesive "physiological ⇔ functional" frameworks in which to interpret ERP data. For example, if a component's strength is used to make inferences about the brain's sensitivity to a functional process engaged by an experimental variable, assumptions may be made that the potential at an electrode is affected by an isolated generator population. However, this assumption is untenable since 'even highly localised foci of activity may produce widespread distributions at the scalp and it is highly unlikely that there would only be a single process at any given moment' (Kutas and Dale, 1997, pp 206).

Source Localisation

By the above account, patterns of electrical activity at the scalp are produced by overlapping potential fields (components) from different generator populations. The ability to map patterns of activity at the scalp onto neural generator configuration(s), when available, will make a major contribution to psychology research. Unfortunately however, although the 'forward problem' of determining the electric potential field elicited by a given set of dipoles can be expressed as a well-defined and unique solution, the 'inverse problem' of mapping from activity at the scalp onto neural sources is ill-posed mathematically (Gevins, Leong, Smith, Le and Du, 1995). The major problem is that there are an infinite number of dipole configurations within the brain which may give rise to any given pattern of electric potential fields recorded at the scalp (Nuñez, 1990a; Nuñez, 1990b).

Over the last two decades there has been much advancement in techniques enabling inferences of generator sources from scalp fields. The general procedure used is to model electric recordings as a function of dipole locations, orientations and strengths of proposed generator configurations. The potential fields of these 'equivalent current dipoles' (ECDs) are then calculated and the solutions of the real dipole locations, orientations and strengths estimated by an iterative procedure (for review see Wood and Allison, 1981; see also Scherg, 1989). In order to constrain the parameters of the

ECDs, information from neurophysiological studies (e.g. intracranial recording), neuroimaging techniques (e.g. PET, fMRI), and neurological studies is often taken into account (e.g. Scherg and Berg, 1991; Miltner, Braun, Johnson, Jr., Simpson and Ruchkin, 1994). As noted by Kutas and Dale, 1997, there are two main problems with this approach. First, it is impractical to localise more than a few dipoles using this approach since the relationship between dipole orientation/location and electrical recording is non-linear and hence difficult to model correctly. Furthermore, it is impossible to determine *a priori* what number of equivalent dipoles should be employed.

An alternative approach to the inverse problem (as outlined by Kutas and Dale, 1997) is to model the generators as a 'biologically plausible' continuous dipole distribution. In brief, this approach assumes that only cortical pyramidal cells make contributions to scalp recorded EEGs (based on prior knowledge that the EEG measured at the scalp is produced predominantly by such cells). As such the dipole distribution is modelled upon neocortical pyramidal cell geometry and location (i.e. axially symmetric, perpendicularly orientated and located within the cortical sheet) and the inverse problem reduces to estimating dipole strength over the cortical surface. This alternative approach is efficient since the relationship between dipole strength and recording is linear (hence solutions can now be determined using linear models). However, even with the highest levels of spatial sampling of the scalp electric potential the problem remains undetermined (situations arise wherein it is possible to generate multiple solutions for the same ERP data). This problem is countered by choosing the ' weighted minimum-norm solution' (which effectively provides a unique solution) but with additional constraints incorporated into the model (e.g. functional imaging data, see above) such that solution is biologically principled.

As can be seen from the above, there are problems involved in the use of source localisation models without incorporating information from other disciplines. However, the use of such information in itself may be problematic. For example source modelling constrained by neuroimaging data may produce solutions that differ in their accuracy according to the latency region employed (e.g. Mangun, 1997 cited in Donaldson, 1998; see also Donchin and Coles, 1991, for a critique of the use of information from animal models). Furthermore, even with incorporating information from other disciplines, such models can only be used to localise activity in different anatomical regions. For information about activity at the level of single neurons or between distinct cortical layers, invasive recording techniques must be employed.

Quantitative versus Qualitative Distinctions

Problems with combining functional and physiological approaches to interpreting ERPs have been outlined with respect to component analysis and source localisation. However, this by no means devastates aims to understand ERPs in terms of their relation to physiological generators in the brain and functional processing. Where the following approach to analysing and interpreting ERP effects is adopted, then patterns of ERP effects can be used to make more definitive inferences about neural activity underlying psychological processes elicited by an experimental manipulation.

In this approach, the main distinction made between differences in ERP activity across experimental conditions is between qualitative and quantitative effects. Quantitative effects reflect differences in the magnitude of ERP waveforms in different experimental conditions (but not differences in the distribution of the waveforms across the scalp). Such effects are presumed to reflect differential activity in the same pattern of underlying generators resulting from either changes in the number of activated cells or changes in the synchrony of neural firing. By contrast, qualitative effects reflect differences in the distribution of ERP waveforms over the scalp. These effects are instead presumed to reflect changes in the configuration of the neural generators such that either an additional neural generator becomes active, an active neural generator becomes inactive or active neural generators differentially increase or decrease their strength (Johnson, 1995).[3] This follows since, when recording electric fields outside the scalp, the similarity of activity from two electrode sites in the same vicinity is assumed to be due to the electric field being driven by a common open field generator configuration, or in the case of multiple generators, because there are extensive interconnections between the generators (see Cooper et al., 1980).

Since it is generally assumed that different brain states indicate different functional states, qualitative differences are usually taken as evidence for the engagement of different functional processes. By contrast, quantitative differences, in the absence of

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[3] With the use of a large number of recording electrodes an informed choice can be made as to which of the three above scenarios is responsible for alterations in activity at the scalp (Johnson, 1995).

qualitative differences, are presumed to reflect differential levels of engagement of the same cognitive processes (albeit with the caveat that accompanies conclusions based on a null result in ERP analysis, i.e. that there may be differential neural populations activated whose configuration is such that they do not produce an externally observable field). All things considered, when the qualitative/quantitative distinction is adopted, ERPs do provide information about the poise of activity in the brain and the ability to monitor when this activity changes, and hence offer insights into functional processing underlying human behaviour.

Data Analysis

In many ERP studies of cognitive processing, recordings are made of the participant's behaviour (reaction time, response type) simultaneously with the ERP recordings. Behavioural data can then be used, where required, for categorising trials post-hoc. In addition, information gained from the behavioural data may provide information about cognitive processing, thus helping evaluation of ERP data within the context of the theoretical framework (Picton et al., 2000).

ERP data can be analysed in a variety of ways. However, instigated in most methods is the quantification of waveform amplitude with respect to a pre-stimulus baseline. This in itself is problematic since it is difficult to ascertain what cognitive processes are engaged during the pre-stimulus baseline periods between events. For example, the participant might still be engaged in cognitive processing in response to the preceding event. Over and above this, in order to characterise statistical effects, waveforms from different experimental conditions can be either contrasted directly against each other, or alternatively, waveforms are assessed independently as to whether they differ reliably from the pre-stimulus baseline. For the following reasons (adapted from Rugg and Henson, in press), of the two types of contrasts, those between different experimental conditions within the same task (or the same types of experimental conditions across tasks) are preferred.

Consider the situation wherein waveforms from different conditions are being compared individually against a pre-stimulus baseline. Any conclusion that the two conditions differ significantly (based upon the finding that the waveforms from only one experimental condition differ reliably from the pre-stimulus baseline) requires the acceptance of the null hypothesis (i.e. that the waveforms from the second experimental condition do not differ from the baseline). In addition, measures of waveforms associated with an experimental condition relative to a pre-stimulus baseline are difficult to interpret in investigations of higher cognitive processing since 'responses reflect a mixture of 'low-level' processes common to all tasks, task-specific processes common to all item-classes, and processes specific to the item-class eliciting the response' (Rugg and Henson, in press, p7). Thus processes specific to conditions are best revealed by contrasting directly ERPs from different conditions.

Univariate statistics (such as ANOVA) can be used to assess whether the waveforms differ significantly across experimental conditions. ERP waveforms can be analysed either in terms of their magnitude (amplitude measures with respect to the pre-stimulus baseline), or alternatively in terms of their topography (the scalp distribution associated with different experimental conditions is assessed). In analysis of the magnitude of ERP effects, the amplitude of ERP waveforms from differential conditions are contrasted either at the time point and electrode site of a specified peak/trough, or alternatively, the mean amplitude of the waveform is measured across a number of time points (epoch) and/or electrode sites. (Where more than one epoch/electrode site is employed, such additional variable/s can be factored into the analyses.) In analysis of the topographical distribution of ERP effects over the scalp, subtraction waveforms (between experimental conditions) are calculated across a number of sites and used to provide information about the scalp distribution associated with different sets of experimental conditions.[4]

Analyses employing amplitude measures are particularly suitable for data containing particularly well-defined ERP effects, or in experiments wherein the parameters of the ERP effects have been well defined *a priori.* Alternatively, the analyses can be more exploratory in nature, although under such circumstance where mean latencies and sites for analyses have not been selected *a priori,* results may be difficult to characterise or worse still, unwittingly affected by experimenter bias - especially if ERP effects are not well defined (see Donchin and Heffley, 1978). A further problem concerning analyses which involve measuring the amplitude of the waveforms is component overlap, wherein the portion of the waveform being measured may in fact be receiving contribution from a number of electrical dipoles that are affecting its voltage leading to difficulties in interpreting the data (although as discussed above,

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[4] For problems concerning the use of subtraction techniques to isolate cognitive functions in imaging experiments refer to Friston

this is of little concern if a functional approach is adopted) (see Donchin and Heffley, 1978).

Concerning the employment of univariate statistics to analyse ERP data, problems may arise if assumptions underlying the use of such univariate statistics are violated. For example, in circumstances where several ERP effects (e.g. peaks) are incorporated into an analysis as an experimental variable, it may be difficult to establish that the effects are independent of one another. Furthermore, where ANOVA is employed to analyse amplitude differences in ERP waveforms across multiple electrode sites, it is probable that the sphericity assumption is violated. This is because the covariance in data between electrode sites which are close together will almost certainly be smaller than that between electrode pairs which are further apart (non-sphericity). While the ANOVA model is robust in the face of minor violations of the sphericity assumption, where necessary, non-sphericity in ERP data can be corrected for by application of the Greenhouse-Geisser technique which provides an estimate of the degree to which the assumption is violated, and reduces the degrees of freedom accordingly (Keselman and Rogan, 1980).

Topographic analyses suffer from additional problems concerning the fact that changes in the strength of neural generators may have multiplicative (as opposed to additive) effects upon voltage measurements made at electrode sites. Unless this issue is addressed, interactions between experimental factors and electrode sites may arise leading to the erroneous interpretation that ERP effects reflect differences in the location of underlying generators rather than differences in strength in the underlying generators. Fortunately, ERP data can be rescaled to remove confounding effects of magnitude differences on the scalp distribution of the effects (McCarthy and Wood, 1985). Such methods of rescaling data maintain the relative size of ERP effects at different electrode sites (and across different conditions) whilst removing differences due to amplitude, therefore allowing any resulting interactions to be interpreted as differences in the composition of neural generators (or differential activation of dissociable generators) (but see also Haig, Gordon and Hook, 1997) .

Regardless of the above drawbacks, where amplitude analyses can be employed they often are - perhaps because they correspond well to visual inspection procedures used

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et al., (1996).

when forming an impression of trends in the data. However, it should be emphasised that magnitude and topographic analyses represent complementary methods of amplitude analyses and, although under many circumstances the distinction proves to be extremely useful (as demonstrated in abundance by Rugg and colleagues), such a distinction is not always made. Furthermore, situations may arise whereby amplitude analyses are a less appropriate method for analysing ERPs and an alternative approach must be adopted. For example, in the quantification of slow wave potentials (steady increases or decreases in the amplitude of the ERP waveform such as the contingent negative variation) (for general review of the alternative analyses techniques see Donchin and Heffley, 1978).

Summary

This section has proposed that electrical activity at the scalp consists of a series of electrical potentials elicited by event-processing in the brain. The latency, amplitude and scalp distribution of these electric potentials can be quantified time-locked to events (the event-related potential - ERP). Information on an ERP's latency can be related to experimental manipulations providing accurate time-course monitoring of brain activity associated with psychological processes. In addition, information on the balance of activity at the scalp can provide information relating to the configuration of neural generators.

Chapter 3

Event-Related Neuroimaging of Memory

This chapter provides a selective review of studies employing neuroimaging techniques (ERPs and fMRI) to investigate human episodic memory retrieval. The first section of the chapter is devoted primarily to ERP studies whereas the latter part addresses the findings of efMRI studies. Neuroimaging studies of the retrieval of emotional information are discussed in the following chapter.

ERP studies of Memory

ERPs are useful for studying memory for a number of reasons which are summarised briefly as follows (see also preceding chapter). First, high temporal resolution enables accurate time-course monitoring of brain activity. Second, ERPs can 'covertly' measure processing in the absence of overt behaviour. Third ERP waveforms can be formed off-line after experiments have been completed according to the participants behaviour. Fourth, and more generally, ERP studies provide a non-invasive and relatively inexpensive way to study memory.

The majority of ERP studies of episodic memory are conducted using direct memory tasks (frequently recognition) wherein participants are presented with words and later presented with unstudied retrieval cues (new items) and retrieval cues related in some way to the studied items (old items). There are at least two types of recognition memory paradigms. In continuous recognition tasks, participants are presented with items in a single series and required to make old/new judgements with the study and test items integrated together. More commonly, the study and test phases are kept separate (hence termed the study-test procedure) as in recognition memory tasks or cued recall tasks. The experimenter either categorises trials *a priori* as old or new items, or alternatively, trials may be categorised *post hoc* according to the participant's behaviour during a memory task (for example as remembered or forgotten).

Whilst both old and new retrieval cues should elicit neural activity correlated with processes subserving retrieval attempt (pre-retrieval processing, see chapter 1), relative to old retrieval cues, new retrieval cues should be associated with minimal successful retrieval of episodic information (Rugg and Wilding, 2000). Thus, activity subserving successful episodic retrieval is usually revealed by comparisons between activity elicited by unstudied retrieval cues relative to activity elicited by studied retrieval cues (e.g. old versus new words in a recognition memory task). The main assumption is that if two kinds of old/new contrasts are associated with qualitatively different patterns of scalp electricity, this signifies the engagement of at least partially non-overlapping neural populations (Rugg and Coles, 1995; see also Chapter 2).

An established finding in both study-test and continuous recognition paradigms is a positive-going amplitude shift of the ERP that is elicited by previously studied words relative to new words during memory tests. It appears that this old/new shift may comprise at least three topographically distinct old/new effects. The first of these three old/new effects to be established is termed the left parietal 'old/new' effect (Johnson, Pfefferbaum and Kopell, 1985; Wilding, Doyle and Rugg, 1995; Wilding and Rugg, 1996; Rugg, Mark, Gilchrist and Roberts, 1997b, for review see Rugg and Allan, 2000). This effect, held to be the electrophysiological index of episodic retrieval (recollection), reflects the elicitation of a phasic positivity (ca. 500 – 1000 msec) with maximum amplitude over parietal electrode sites (usually left lateralised) by old relative to new words. A second, less-established, old/new effect involves an earlier (ca. 300-500 msec) bilateral shift with a frontal distribution. This effect has been held by some authors (e.g. Rugg, Mark et al., 1998b; Curran, 2000) to be the electrophysiological index of familiarity. However, as discussed later, its elicitation is relatively inconsistent in studies of recognition memory. Finally, a third old/new effect onsets quite late (ca. 500-700 msec), is distributed over the right frontal scalp site and is held to reflect processes operating on the products of memory retrieval (e.g. Wilding and Rugg, 1996) or, more recently, retrieval processes in the service of task demands (Rugg, Allan and Birch, 2000).

The Left Parietal Effect

When reports of a parietally-based ERP old/new effect were first published, a number of concerns were raised that it could simply reflect the modulation of a number of overlapping components which support processes non-specific to memory (e.g. Karis, Fabiani and Donchin, 1984; Neville, Kutas, Chesney and Schmidt, 1986). Amongst a number of non-specific processes that might have influenced ERP amplitudes in memory tasks were categorisation effects; target effects; confidence; latency of old versus new response; stimulus probability and priming.

Specifically, the effect was initially reported to onset at around 300 msec (with a duration of 500-1000 msec) and investigators were concerned that the early portion (300-500 msec) was simply a modulation of other ERP components present within that latency range, such as the P3 and N400 (see Johnson, 1995 for review). Notably, the P3 is sensitive to the aforementioned variables, especially target effects, categorisation effects and stimulus probability (see Donchin and Coles, 1988). Thus, following suggestions that old words in recognition memory tests are associated with a lower 'subjective' probability and a higher 'targetness' than new words, it was conceivable that the memory evoked shift simply reflected elicitation of a P3-type positivity by the old words.

Addressing these concerns, a number task manipulations were conducted in order to establish the functional significance of the parietal old/new effect. Evidence from a number of studies suggested that the parietal old/new effect was not simply a modulation of the P3 component. For example, varying the ratio between old and new words in a continuous recognition memory task, Friedman (1990) demonstrated the old/new effect did not interact with stimulus probability. Similarly, a sensitivity of the old/new effect to retrieval from long-term memory but not to target effects was demonstrated by Smith and Guster (1993) who employed an oddball recognition memory paradigm. Furthermore, by employing a paradigm which eliminated invariant mapping between repetition and response requirement, Rugg, Brovedani and Doyle (1992) demonstrated that the effects of word repetition on ERPs were not a consequence of facilitated decision/response processing for repeated items.

However, various studies contrasting the parietal old/new effect with the N400 component (known to be sensitive to semantic priming in word repetition without explicit retrieval; see Smith and Halgren, 1987; Rugg, 1990; Besson, Kutas and Van Petten, 1992) revealed that whilst the latter portion of the old/new effect (post- 500 msec), could be dissociated from the N400 by virtue of its time course, the early portion of the old/new effect (ca. 300-500msec) was found to respond to many variables in a similar manner to the N400. As reviewed by Johnson (1995, pp 149) the early-portion of the old/new effect was found to be sensitive to repetition of legal words but not to repetition of illegal words (Rugg and Nagy, 1987) and furthermore the early portion of the effect did not appear to reflect long-term memory since it 'disappears when the lag between the repeated items increases' (Nagy and Rugg, 1989; Karayandis, Andrews, Ward and McConaghy, 1991). Finally, evidence suggested that scalp distributions of the early component of the old/new effect were not dissociable from that of the N400 (Besson et al., 1992).

In summary, reasonably strong evidence was provided that the latter portion (ca. 500 msec onwards) of the parietal old/new effect is systematically elicited when memory tasks require retrieval from long-term memory, and in addition is functionally, temporally and topographically dissociable from components such as the N400 and P3 (Johnson, 1995). However, it is important to note that although many possible confounds have been investigated, there may still be differences in the responses elicited by old and new items that do not reflect cognitive operations supporting, or contingent upon, successful episodic retrieval (Rugg and Wilding, 2000).

Old/new Effects and Dual Processing Models

Until the late 1980's, the old/new shift in ERP studies of memory had been predominantly reported as constituting a single 'retrieval-related' or 'word-repetition' effect. However, it was unknown whether the old/new effect was related to any particular psychological construct that had been previously defined in the memory literature (e.g. familiarity versus recollection, see chapter 1 for definitions). This issue was addressed in a number of ERP studies, employing a variety of operational definitions of familiarity and recollection. The majority of such studies aimed to manipulate recognised items according to whether they were recognised on the basis of familiarity or on the basis of recollection. If old/new effects formed separately for memory retrieval on the basis of recollection and familiarity were associated with qualitatively distinct scalp distributions, then this would provide evidence that the two processes are supported by functionally distinct cognitive operations. By contrast, if the old/new effect was found to vary only in terms of magnitude then this would lend support to single process models.

As outlined below, although the results of the initial studies addressing this issue were consistent with the parietal old/new effect indexing retrieval-related processing, reports were inconsistent regarding the type of retrieval processing indexed.

Furthermore, for nearly a decade, such studies failed to provide any evidence for the existence of neurally dissociable processes contributing to memory retrieval.

In one experiment Smith and Halgren (1989) reported an absence of the parietal old/new effect in patients after unilateral anterior temporal lobectomies, thus they interpreted their findings as evidence that the parietal ERP old/new effect reflected activity subserving episodic retrieval (recollection) – 'the word-repetition effect on ERPs might be aptly characterised as directly reflecting the integration of a retrieval cue with trace information during the reconstruction of a past event' (pp 58). This proposal was subsequently contradicted by Potter, Pickles, Roberts and Rugg (1992) upon evidence that administration of scopolamine impaired recognition memory tasks whilst leading to an increase in the magnitude of old/new effects. The authors concluded that, since recollection is partly dependent on cholinergic transmission in medial temporal lobe structures, the increase in the size of the old/new effects must instead reflect an increase in familiarity-driven processing as compensation for the deterioration of recollection-driven processing.

A problem with both of these studies is that they assume that disruption of medial temporal lobe activity has a selective influence on recollection, however as discussed in chapter 1 (see also Aggleton and Brown, 1999), this assumption may be untenable. Furthermore, in the study by Potter et al., scopolamine may have had detrimental effects upon other processes mediating recognition memory (mediated in brain regions outside of the medial temporal lobes) whilst instead sparing recollective processes.

Avoiding issues regarding the anatomical locus of recollection and familiarity, another study employed word-frequency effects to assess the functional significance of the parietal ERP old/new effect (Rugg and Doyle, 1992). The study was predicated upon the assumption that recognition advantages for low frequency words result from familiarity-driven processing. It was found that only recognition of low-frequency words elicited a left-parietal effect, thus the authors concluded that the parietal ERP old/new effect was sensitive to the familiarity-driven recognition memory (Rugg and Doyle, 1992). However, it was subsequently established that recognition advantages for low frequency words are carried predominantly by recollection-driven processing (cf. Gardiner, Java and Richardson-Klavehn, 1996) thus the conclusion from this study was later discredited.

A major problem with many of the preceding paradigms was that the experimental manipulations did not allow a straightforward dissociation between items recognised on the basis of familiarity and those recognised on the basis of recollection. Remedying this, Smith (1993) employed Tulvings' (1985b) remember/know procedure which allowed trials to be more easily dichotomised according to whether recognition was associated with the presence or absence of recollection (see chapter 1). The study revealed that memory effects associated with R responses (recollection) were larger than those associated with K (familiarity) responses.

The main criticism of this experiment is that, since the Remember/Know procedure employed was conducted with a single response [i.e. remember-know-new decision rather than an old-new recognition followed by remember-know judgement (binary response)], the differential ERP effects to familiarity and recollection may have reflected differences in confidence/ proportion of guesses, rather than dual processes. Specifically, it has been demonstrated that relative to old-new judgements or binary response judgements the simultaneous consideration of three alternatives at once results in a 'markedly liberal response bias both in recognition detection and in the ascriptions of remember and know judgements' (Hicks and Marsh, 1999, pp 117). However, it should also be noted that that single response R/K procedures may have an advantage over binary response procedures since contrasts between old and new items are not confounded with differential response requirements (Rugg and Henson, in press). More specifically, whereas classifying items as 'new, remember or know' might emphasise a quantitative distinction between recollection and familiarity, whereas direct classification of remember/know in a binary response procedure might emphasis a qualitative distinction.

Subsequent to this study, convincing evidence that the left parietal old/new effect does indeed index recollection was provided in a series of studies by Rugg and colleagues employing source memory and associative recognition paradigms. These paradigms operationalise recollection (R) as the ability to retrieve 'contextual' or 'source' information, for example, information about the recognised item's spatio-temporal context or the modality (auditory, visual) in which it was initially presented, or alternatively, information about the items that retrieval cues were paired with at study (cf. Jacoby, 1991). Familiarity is operationalised as recognition without retrieval of contextual information. Such paradigms have an advantage over R/K procedures in dissociating familiarity and recollection since the categorisation of trials is less dependent upon introspective judgements made by the participants. However, a disadvantage of source judgements is that they may not index an 'absolute' measure of recollection as remember judgements do since remember judgements can be made on the basis of any type of retrieved information (e.g. temporal position of item in study episode, not just on the basis of information about a source specified by the experimenter), (see Mulligan and Hirshman, 1997).

In the first of such studies, Rugg, Cox, Doyle and Wells (1995) modified their (aforementioned) word frequency study such that as well as the word frequency manipulation, items were also presented in one of two contexts at study. Consistent with the results of the previous study, the authors found that low frequency words were better recognised than high frequency words (although here the findings were taken in light of evidence from Gardiner et al. (1996) that recollection processes are responsible for word frequency effects). In addition they found that such words were also more likely to be assigned their correct study context than high frequency words. As predicted, ERP old/new effects were larger for recognised low frequency items relative to recognised high frequency items and this was interpreted to reflect differential levels of cognitive processing subserving recollection.

Following this, Wilding and colleagues reported two studies wherein recognition memory effects contingent upon accurate and inaccurate source memory were directly contrasted. In their first study, the source attribute was sensory modality (visual or auditory) (Wilding et al., 1995). In the second study the source attribute was speaker's voice (male or female) (Wilding and Rugg, 1996). In both studies, ERP memory effects over left parietal scalp sites were larger for recognised words that had been assigned the correct study context (figure 3.1)[1]. On the basis of their results, Wilding and Rugg (1996) provided a more comprehensive definition of the cognitive operations generating parietally-based ERP old/new effects (hereafter know as the left-parietal effect). They proposed that the left parietal effect indexed operations supporting retrieval of item and contextual information from memory, as mediated by medial temporal lobe structures (see also Squire, 1992; Chapter 1).

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[1] A second topographically distinct old/new effect with a right frontal scalp distribution was additionally revealed to be sensitive to retrieval of context , this will be returned to later.

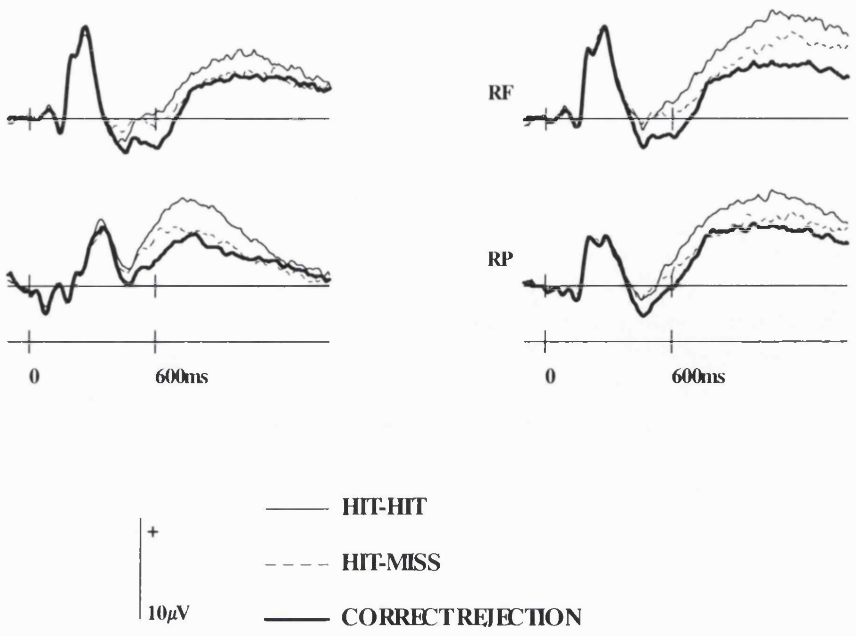


Figure 3.1 Example of left parietal and right frontal old/new effects
ERPs from lateral frontal and parietal electrodes elicited by words correctly classified as new (correct rejections), recognised and assigned to incorrect study contexts (hit-miss), or recognised and assigned to the correct study context (hit-hit).
(Adapted from Wilding and Rugg, 1996. An event-related potential study of recognition memory with and without retrieval of source. *Brain,* **119**, 889-906).

A following study by Donaldson and Rugg (1998) provided further evidence that the left parietal effect supports the retrieval of contextual information. This study used an associative recognition paradigm to dissociate familiarity-driven and recollection-driven processing. In this paradigm, participants make recognition judgements on item (usually word) pairs that are new, re-presentations of pairs studied in a preceding study task or re-pairings of study items. It is assumed that items that maintain their pairing between study and test (*same* pairs) will elicit more recollection than items whose pairings change between study and test (rearranged pairs), which are likely to be recognised as old on the basis of familiarity. In line with the findings of Wilding and colleagues, Donaldson and Rugg found that the left parietal ERP memory effect was larger for conditions eliciting greater recollection than for those eliciting predominantly familiarity-driven processing.

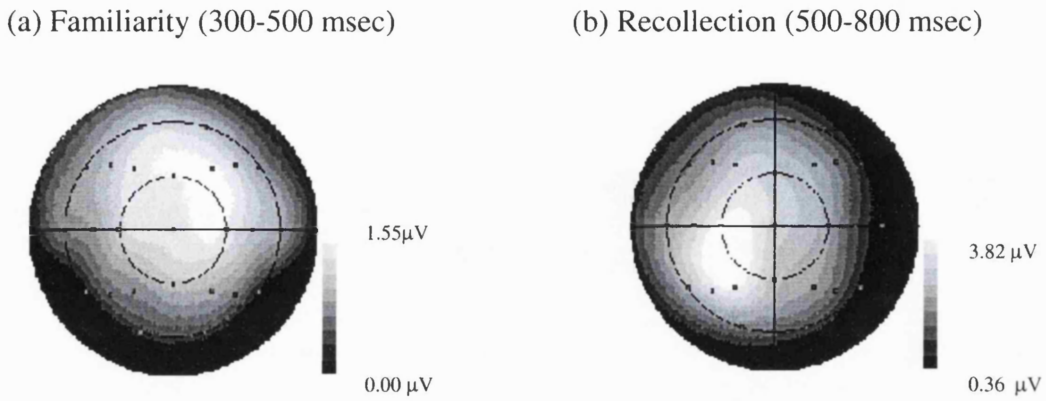
The proposal by Rugg and colleagues that the left parietal effect is dependent upon retrieval operations supported by the medial temporal lobe is consistent with neurophysiological evidence that following lesions to the temporal lobes parietal old/new effects are abolished or attenuated (e.g. Smith and Halgren, 1989; Rugg, Roberts, Potter, Pickles and Nagy, 1991). In addition the proposal is consistent with the results of neuroimaging studies (PET, fMRI) which have indicated that retrieval of item information associates with medial temporal lobe activity (Lepage et al., 1998; Schacter and Wagner, 1999). However, it is unlikely that generators of the effect are situated within the medial temporal lobes since the organisation of the hippocampus and adjacent structures is such that their potential fields make, at best, a very modest contribution to scalp-recorded activity. Instead, Rugg and colleagues further suggested that the effects probably reflect changes in activity in cortical structures that receive input from the medial temporal lobes following hippocampally mediated 'reactivation' or 'reinstatement' of retrieved information activity (see McClelland, McNaughton and O'Reilly, 1995).

The findings of the R/K, source localisation and associative recognition ERP studies were all interpreted as consistent with the hypothesis that the magnitude of the left parietal old/new effect indexes the degree to which recollection-driven processing is operating. However, in view of the absence of any evidence that the effects elicited in the recollection condition differed qualitatively from those elicited in the familiarity condition, such findings offered little support for dual process models of recognition memory. Rather the findings were suggestive of familiarity depending on the same processes as those supporting recollection, with the left parietal effect for familiarity simply reduced in size (cf. Moscovitch, 1992; Moscovitch, 1995). Thus the experiments provided support for the view that familiarity reflects weak or partial recognition, enough to allow correct recognition but not enough to support episodic retrieval.

However, it is possible that in these studies, trials contributing to the familiarity condition were contaminated by 'non-familiarity' processes. As mentioned, in the one-stage R/K procedure, trials might have been contaminated by differential proportions of guess trials thus distorting the ERP effects. In addition, in the source paradigms it is possible that when items were recognised but source recollection failed, familiarity trials included trials wherein participants had recalled other 'non-criterial' aspects of study context (Yonelinas and Jacoby, 1996). Finally, any conclusion that recollection and familiarity are not mediated by distinct neurobiological systems based upon the absence of dissociable ERP effects is of course accompanied by the caveat that accompanies null results in ERP studies, namely that negative findings may reflect an insensitivity to the neural activity supporting the condition of interest, here familiarity. Indeed, evidence was to follow in two later studies that recollection and familiarity under certain experimental conditions do associate with qualitatively dissociable scalp conditions.

The first study to show such a dissociation was conducted by Düzel, Yonelinas, Mangun, Heinze and Tulving (1997). These authors reported electrophysiological dissociations between familiarity and recollection (as indexed by R/K judgements) in terms of scalp topography from approximately 300 -1000 msec. As already noted by Rugg and Allan, 2000, the findings by Düzel et al. should be treated with caution for two reasons. First, the number of trials forming the ERPs associated with know judgements was very low in some participants, raising concerns about signal quality in this condition (see chapter 2). Second, they did not rescale their data in order to reduce the confounding effects of magnitude differences (McCarthy and Wood, 1985) (see chapter 2).

The second study to suggest that familiarity and recollection are supported by distinct cognitive operations was provided by Rugg et al. (1998b) (Figure 3.2). In this study, participants studied a series of words under either deep (sentence generation) or shallow (alphabetic judgement) conditions. At test, ERP trials were categorised according to whether items were recognised (hits) or not recognised (missed) if old, or alternatively correctly rejected if new. Sensitivity to the depth of processing in the ERPs to recognised items was used to index whether items were recognised on the basis of familiarity or recollection. This assumption was predicated on theories that depth of processing exerts its effects exclusively through recollection (Gardiner et al. 1996). Between 300 and 500 msec ERPs at frontal sites were more positive going for recognised old words relative to correctly rejected new words and missed items (Figure 3.2a). This frontal effect was equivalent in magnitude and scalp topography in both the deep and shallow processing conditions and could be topographically dissociated from a later prominent left parietal effect which was present only for recognised deeply processed items relative to new items (Figure 3.2a). It was concluded that the findings provided evidence for familiarity and recollection having distinct neural correlates. Problematically for this interpretation however, depth of processing may not exert its effects exclusively through recollection (cf. Toth, 1996).


(a) Familiarity (300-500 msec)

(b) Recollection (500-800 msec)

Figure 3.2 Topographic maps showing old/new effects proposed by Rugg and colleagues to reflect (a) familiarity and (b) recollection

(Adapted from Rugg et al. 1998(b), Dissociation of the neural correlates of implicit and explicit memory. *Nature,* **392**, 595-598).

Finally, in an experiment by Curran (2000), participants performed a recognition memory task in which they had to discriminate between new, old and similar words (similar words changed plurality between study and test). It was proposed that studied and similar words would be recognised as old on the basis of familiarity but that recollection would be necessary to discriminate between studied and similar words (cf. Hintzman and Curran, 1994). It was discovered that a frontal N400-like (similar to that described by Rugg et al., 1998c) was sensitive to the relative familiarity of words (i.e. was equivalent in size for recognised studied and similar words). The parietal old/new effect was found to associate with recollection.

Summarising the above, the ERP left parietal appears to be sensitive to the amount of contextual information retrieved about a past event and thus reflect the cognitive operations associated with recollection of episodic events (episodic retrieval). In addition, whilst the result of the majority of studies suggested that familiarity is synonymous with incomplete or partial recollection, there does appear to be at least some evidence that dissociable neural processes contribute to recognition memory.

The Right Frontal Effect and Retrieval Processing

The above review has described two old/new effects, - a left parietal effect (ca. 500-1000 msec) that has been linked to recollection and an earlier bilateral frontal effect (ca. 300-500 sec) that has been linked to familiarity-driven recognition memory. Importantly, a number of these studies also revealed a third topographically distinct effect which appears to be connected with processes subserving episodic retrieval. More specifically, the third effect appears to be prominent in tasks which cannot be performed on the basis of old/new recognition alone.

The third old/new effect first came to light in the aforementioned Wilding and Rugg (1996) study investigating source memory. As described above, an old/new effect with amplitude maximum over left parietal scalp sites was elicited by items associated with both correct and incorrect source judgements, but was larger for old words assigned to the correct study modality. Notably however, as can be seen in figure 3.1 recognised old words assigned to correct and incorrect study modality also elicited a more positive going ERPs over right frontal sites relative to new words. This 'right frontal' old/new effect onset around the same time as the left parietal effect but was sustained until the end of the recording epoch. Similar to the pattern observed with the left parietal effect, correct source judgements associated with a larger right frontal effect than incorrect source judgements.

Wilding and Rugg (1996) interpreted the right frontal effect to reflect processing carried out upon retrieved episodic information necessary to assign the retrieval cue to the correct source (for example, maintenance, verification and evaluation) (see also chapter 1). The proposal that the right frontal effect indexes post-retrieval processing has since received support from a number of studies employing recognition tasks with demands that exceed those of simple yes/no recognition. For example, a similar sustained frontal positivity has been found to accompany the left parietal effect for R Judgements in the Remember/Know task (Düzel et al., 1997; Rugg et al., 1998c) and also right frontal effects have been found in studies of associative recognition (Donaldson and Rugg, 1998).

By way of digression, it is of interest to note that the study by Rugg et al. (1998) compared the two main ways of operationalising recollection, that is recollection defined by the ability to make accurate source judgements and recollection defined as the subjective experience of remembering. ERPs were obtained in two experiments, one employing a source memory procedure similar to that employed by Wilding and Rugg, 1996; the second employing a remember/know paradigm similar to that employed by Smith, 1993 but with a binary response procedure. In both experiments, as with Wilding and Rugg (1996), two temporally and topographically distinguishable old/new effects were elicited. However, although the old/new effects elicited in the remember/know paradigm were larger than those elicited in the source discrimination paradigm, the scalp topographies of the old/new effects in the two tasks did not differ statistically across the two experiments, hence evidence was provided that recollection as defined by the ability to make accurate source discriminations and recollection as the subjective experience of remembering are neurally and functionally equivalent.

Recent reports that prominent right frontal effects are elicited by old items associated with little or no recollection (as indexed by low confidence judgements) relative to those associate with confidently recollected information (Rugg et al., 2000) suggest that, under some circumstances at least, the right frontal effect is not simply indexing further processing dependent upon successful recovery of episodic information. Instead it may also index processes operating upon the products of the retrieval attempt prior to recognition decisions regardless of the amount or nature of the information retrieved. Multiple interpretations of the cognitive function indexed by the right frontal effect are accounted for by the suggestion that the right frontal effect reflects activity in functionally heterogeneous regions of the prefrontal cortex, and therefore may index a number of kinds of post-retrieval processing (Rugg and Henson, in press). It has further been noted that the functional interpretation by Rugg et al. (2000) of the right frontal effect elicited by their paradigm is reminiscent of post-retrieval processing suggested by Rugg and Henson, (see below) to operate on the products of a retrieval attempt and to be mediated by dorsolateral prefrontal activity. By contrast, the functional interpretation of the right frontal effect proposed by Wilding and colleagues, resembles post-retrieval operations proposed by Rugg and Henson (see below) to be engaged when a retrieval attempt culminates in the successful recovery of episodic information and to be mediated by anterior prefrontal cortex (refer to Rugg and Henson, in press, for further discussion of these analogies).

The proposal that the retrieval operations indexed by the right frontal old/new effect are mediated by prefrontal cortex is based upon three convergent streams of evidence. First, the scalp distribution of the right frontal effect is suggestive of prefrontal cortex activation. Second, as mentioned, neuroimaging studies have shown that right dorsolateral and anterior prefrontal cortices are important for studies of episodic memory requiring additional processing such as source discriminations or monitoring (for review see Cabeza and Nyberg, 2000). Third, lesions to the prefrontal cortex are frequently noted to result in severe memory impairments such as the ability to retrieve source information (Janowsky et al, 1989; Wheeler, Stuss and Tulving, 1995).

Finally, in some studies, ERP activity during tasks that require monitoring and control processes rather than the reactivation of studied information during retrieval have additionally revealed left lateralised frontal activity. In two experiments by Ranganath and Paller (2000), brain potentials were recorded whilst participants performed tests of memory for objects. In both experiments, activity was compared between a 'general task' wherein participants were required to differentiate studied from unstudied objects, and also a 'specific task', wherein participants made perceptual judgements about whether objects were larger or smaller at study. In both experiments, brain potentials recorded over the left prefrontal scalp sites were enhanced during the specific test relative to the general test (for both unstudied and studied objects), thus being consistent with comparative processing rather than simply the reactivation of studied information (Ranganath and Paller, 2000). The findings were interpreted as reflecting the engagement of both left and right prefrontal regions when demands to retrieve and evaluate perceptual information increased. More specifically, the left frontal retrieval effects were proposed to reflect activity in left frontal regions which have been shown by some studies, especially efMRI studies, to be more important in retrieval processing than their right hemisphere counterparts. However, their functional interpretation of the left frontal effect as reflecting retrieval processing can be criticised since the left frontal ERP effect may have instead reflected task-dependent differences in either 'effort' (Schacter, Savage, Alpert, Rauch and Albert, 1996) or in retrieval 'orientation'(see Rugg & Wilding, 2000, chapter 1).

Event-Related fMRI

This section focuses on the results of studies that have used event-related fMRI to investigate episodic memory retrieval. Similar to ERP studies of memory retrieval, most of the studies reported below have employed variants of the 'yes/no' recognition task to elicit episodic retrieval, employing contrasts between recognised old words and rejected new words. The review is reasonably succinct as its primary purpose is to provide a background to the final efMRI study (in terms of regions activated by old/new contrasts). Where relevant, the findings from previous 'blocked' methodologies are also addressed (for reviews of blocked studies see Fletcher, Frith and Rugg, 1997; Buckner and Koutstaal, 1998; Desgranges, Baron and Eustache, 1998; Lepage et al., 1998; Nolde, Johnson and Raye, 1998; Cabeza and Nyberg, 2000).

In light of the findings of the previous ERP studies and blocked haemodynamic studies of episodic retrieval it was something of a surprise that the earliest efMRI studies of episodic memory retrieval using a recognition memory paradigm failed to reveal clear old/new effects in the haemodynamic response (Schacter, Buckner, Koutstaal, Dale and Rosen, 1997; Buckner, Koutstaal et al., 1998b). However, both studies employed long inter-trial intervals which may have encouraged processing that have interfered with episodic retrieval. In addition such long inter-trial intervals may have resulted in a lack of statistical power due to the small numbers of trials obtained (Josephs and Henson, 1999; Meizin, Maccotta, Ollinger, Petersen and Buckner, 2000; Burock, Buckner, Woldorff, Rosen and Dale, 2000) .

Consistent with the results of blocked studies, subsequent efMRI studies of episodic retrieval [which have employed reduced inter-trial intervals more suitable for detecting event-related responses (i.e. rapid trial presentation Dale and Buckner, 1997)] have revealed old/new effects in prefrontal and parietal regions (e.g. Konishi, Wheeler, Donaldson and Buckner, 2000; Donaldson et al., 2000). As with ERP studies of episodic retrieval, efMRI studies have also employed either R/K or source judgements to assess regions associated with recollection as opposed to familiarity. These studies have revealed a fairly consistent pattern of regions sensitive to episodic retrieval including left anterior prefrontal cortex, left inferior and superior parietal cortex and medial parietal cortex (including precuneus and posterior cingulate) (e.g. Henson, Rugg, Shallice, Josephs and Dolan, 1999a; Henson, Rugg, Shallice and Dolan, 2000; Eldridge et al., 2000; Ranganath, Johnson, and D'Esposito, 2000; see Rugg and Henson, in press for review). Less consistently reported regions include left dorsolateral, left ventral, right anterior prefrontal cortex and right inferior parietal cortex.

Prefrontal Cortex

The finding of prefrontal cortex activity (specifically anterior and dorsolateral regions) during episodic retrieval in the efMRI studies is consistent with the findings of the majority of neuroimaging studies of episodic retrieval which employ blocked designs (for reviews see Fletcher et al., 1997; Desgranges et al., 1998; Nolde et al., 1998). However, for reasons that remain unclear, the prefrontal activity revealed by the efMRI is most frequently left-lateralised, whereas the prefrontal activity revealed by blocked studies had been predominantly right-lateralised (paralleling findings of a right-frontal effect in ERP studies of episodic retrieval). Indeed, the pattern of right prefrontal cortex activity during episodic retrieval in the blocked studies was so consistent it led to the proposal of a hemispheric encoding/retrieval asymmetry model of memory (HERA - Tulving, Kapur, Craik, Moscovitch and Houle, 1994).

According to this model, the left and the right prefrontal lobes are part of an extensive network that subserves episodic remembering, but with left prefrontal cortices involved in encoding novel aspects of retrieved information into memory, and right prefrontal regions specifically tuned to episodic retrieval. However, although the results of the efMRI studies are obviously inconsistent with predictions made from the HERA model, it should be noted that on occasions left lateralised activity has been revealed in episodic retrieval studies employing blocked designs, but this tends to be when contrasts are between demanding retrieval tasks (e.g. retrieval of complex information) relative to less demanding tasks (e.g. Hunkin, Mayes et al., 2000; see Nolde et al., 1998 for review).

Regardless of the various contrasting patterns of dissociable activity during retrieval, evidence of lateralisation contingent upon different task designs/ retrieval contrasts suggests functional heterogeneity in prefrontal regions. The main problem of course is establishing the nature of retrieval processing subserved by the different regions in the prefrontal cortex. With regard to this issue, a long standing controversy has been whether right lateralised activations in blocked designs reflect processing contingent upon the reactivation of stored information or generalised processing associated with retrieval tasks i.e. item- or state-related processing (Rugg et al., 1996; Rugg et al., 1998a; Buckner, Koutstaal, Schacter, Wagner and Rosen, 1998a vs. Nyberg, Tulving et al., 1995; Kapur, Craik et al., 1995).

By one account the right prefrontal cortex activity during episodic retrieval is proposed to reflect processing subserving retrieval attempts such as monitoring of information or discrimination processing in order to make old/new judgements. By this scenario the right prefrontal activity reflects state-related processing and its functional role is characterised as supporting the maintenance of a ‘retrieval mode’, that is the adoption of a state of retrieval during presentation of all types of retrieval cue i.e. task-dependent state-related activity independent of whether a retrieval attempt is successful or unsuccessful (e.g. Nyberg et al., 1995; Kapur et al., 1995; Lepage, Ghaffar, Nyberg and Tulving, 2000).

By an alternative account, the retrieval processing reflected by the right prefrontal cortex activity is proposed to operate selectively on the products of information retrieved in response to a retrieval cue, for example, processing evaluating the context of the retrieved information (e.g. Rugg et al., 1996; Rugg et al., 1998a). In this scenario - the 'retrieval success' hypothesis - the right prefrontal cortex activity is not task-dependent but item-related, a proposal receiving support from some electrophysiological studies (see above). As noted by Donaldson et al. (2000) these processes differ not only cognitively, but also neurally such that the time course of changes in neural activity associated with state- and item- related processes should be sustained and transient respectively.

Even though attempts have been made to circumvent limitations of blocked designs, for example by manipulating the proportions of old and new items across blocks (e.g. Rugg et al., 1996) such controversy regarding the functional significance of prefrontal cortex during episodic retrieval is difficult to resolve using blocked paradigms. Unfortunately, as outlined below efMRI studies have not resolved the controversy as easily as anticipated in the wake of such designs.

At first sight, findings from event-related studies that the most common frontal regions associated with retrieval success are left lateralised (specifically left anterior prefrontal cortex, and to a lesser extent left dorsolateral and left ventrolateral anterior regions) suggests that much of the diffuse right-prefrontal cortex observed in blocked studies was not reflecting item-related activity. However, this conclusion should be treated with caution since at least three event-related studies (Henson et al., 1999a; Konishi et al., 2000; Henson et al., 2000) have reported enhanced right prefrontal cortex activity during episodic retrieval (specifically right anterior). Furthermore, the failure of the other event-related studies to reveal right prefrontal cortex activity may reflect an inflated rate of type 2 errors resulting from employment of inappropriate data analyses in investigations of event-related responses in this region (see Meizin et al., 2000). Notably, regions of right prefrontal cortex may exhibit event-related responses that are delayed in time with respect to responses elicited in other brain regions (e.g. temporal cortices), and as such be best revealed by modelling data with a response function that is delayed in time relative to standard haemodynamic response functions (HRFs). This proposal is proffered on the findings of event-related studies which revealed activity in right prefrontal cortex during episodic retrieval when data were modelled with a delayed HRF (e.g. Henson et al., 2000, see also Schacter et al., 1997, Buckner et al., 1998b) (see Meizin et al. 2000; Rugg and Henson, in press for further discussion on the above issues).

Turning now to the functional significance of anatomically localised regions of prefrontal cortex revealed in the efMRI studies, this is best revealed through examination of the relationship between recognition paradigms employed and memory effects obtained in efMRI studies of episodic retrieval (e.g. Henson et al., 1999a; McDermott, Jones, Petersen, Lageman and Roediger, 2000; Henson et al., 2000; Eldridge et al., 2000; Ranganath et al., 2000; Cabeza, Rao, Wagner, Mayes and Schacter, in submission). In the case of left anterior prefrontal cortex, McDermott et al., (2000) found that the left anterior cortex is activated by correctly recognised old items and correctly rejected lure[2] items relative to new words. On the assumption that correct rejection of lure items is contingent upon recollection of the original study episode being strong enough to oppose spurious familiarity/recollection, these authors proposed that left anterior prefrontal cortex is sensitive to episodic retrieval. Furthermore, Henson et al., (1999a) revealed that activity in this region is enhanced for Remember judgements relative to Know judgements, thus suggesting that this region is activated when retrieval of contextual information is strong (i.e. high levels of episodic retrieval). As proposed by Rugg and Henson, taken together the findings of these two studies suggest that processing supported by anterior prefrontal cortex is engaged when a retrieval attempt culminates in successful episodic retrieval.

The results of at least two efMRI studies challenge this proposal. First, Ranganath et al., (2000) (employing a similar paradigm to their ERP study - described above) found left anterior prefrontal activation in an inter-task comparison between the specific task (greater) and the general task, however they did not find anterior prefrontal cortex activity in any of the old/new contrasts. On the basis of these results, the authors suggested that left anterior prefrontal cortex may support monitoring and/or evaluation operations carried out on the products of retrieval attempt engaged

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[2] Unstudied items which are in some manner related to old items and engender false recollection

preferentially when retrieval tasks require a higher level of cognitive processing (but the criticisms discussed regarding their earlier ERP study can be applied here also). The results of an R/K study by Eldridge and colleagues (2000) present more of a problem for the proposal by Rugg and Henson that left anterior prefrontal cortex reflects processing contingent upon recollection since, in contrast to Henson et al., (1999a), these authors found greater anterior prefrontal activation for Know relative to Remember responses.

Another region of prefrontal cortex activity that has been linked extensively with post-retrieval processing by the above reviewed studies is dorsolateral prefrontal cortex. In lieu of this region being predominantly activated by studies requiring further processing, such as retrieval of episodic information (Henson et al., 1999a; Henson et al., 2000; Eldridge et al., 2000), the discrimination between lure items and new items (Cabeza et al., in submission) or the degree of decision processing elicited by the retrieval cues (McDermott et al., 2000; Henson et al., 2000), rather than simply the successful retrieval of information, Rugg and Henson (in press) proposed that the type of retrieval processing supported by dorsolateral prefrontal cortex probably relates to generic monitoring and evaluation processes that operate on the products of a retrieval attempt but are less concerned with the nature of the information in mind (old/new).

Finally, most efMRI studies of episodic retrieval report activations in other frontal regions including ventral, medial and frontopolar regions. These latter activations may reflect processes specifically associated with differences in task requirement rather than retrieval processing per se (see Fletcher et al., 1997 for review).

Parietal Cortex

The finding of parietal cortex (medial and lateral) during episodic retrieval is consistent with the majority of studies of episodic retrieval using blocked designs (see Fletcher et al., 1997; Desgranges et al., 1998). As yet, theories regarding the functional significance of parietal cortex have been relatively sparse. This probably reflects the relative ease with which activity in parietal cortex is activated rendering it difficult to assign function on the basis of inter-task or inter-contrast comparisons.

It is suggested that the parietal cortex is sensitive to the amount of information retrieved (Rugg and Henson, in press). This proposal is proffered upon evidence of greater parietal activity (both medial and lateral) for Remember relative to Know judgements by Henson et al. (1999a). Furthermore, this proposal is supported by the finding of parietal cortex in contrasts between true (greater) and false recollection (Cabeza et al., in submission). However, Rugg and Henson's proposal is weakened by findings of greater parietal activity (medial) conditions associated with minimal episodic retrieval (e.g. K relative to R judgements, Henson et al., in press). Plausible roles for the parietal cortices may include the modulation of attentional processes triggered by successful episodic retrieval (Rugg and Henson, in press; see also Coull, Frith, Büchel and Nobre, 2000; Kastner and Ungerleider, 2000), the support of visual imagery (Fletcher, Frith et al., 1995, but see Krause, Schmidt et al., 1999) or the retrieval of memory associations (Krause et al., 1999). However, on the basis of the results of neuroimaging studies there seems little evidence of which of the three roles is correct.

Medial Temporal Lobe

Turning now to the medial temporal lobes, surprisingly, despite extensive neuropsychological evidence of medial temporal lobe involvement in episodic memory (see chapter 1), and in addition, findings of previous functional neuroimaging studies employing blocked designs (especially PET, for reviews see Nyberg, McIntosh, Houle, Nilsson and Tulving, 1996; Lepage et al., 1998; Cabeza and Nyberg, 2000), medial temporal lobe activity in efMRI is only conspicuous by virtue of its predominant absence (but see Eldridge et al., 2000; Cabeza et al., in submission).

However, recently Eldridge and colleagues (2000) have reported hippocampal activity during recognition accompanied by episodic retrieval (R judgements) relative to remembering without retrieval of episodic information (K judgements), consistent with suggestions that neural activity in hippocampus increases as a function of the amount of information recovered (Schacter et al., 1996a; Rugg et al., 1997a; Stark and Squire, 2000) and thus that the hippocampus is involved in the recovery of stored memory traces (Nyberg et al., 1995). However, when employing the same procedure, Henson and colleagues (1999a) failed to reveal medial temporal lobe activity.

The failure in the other efMRI studies to reveal retrieval-related medial temporal lobe activity could be due to a number of reasons. First, recognition memory tasks employed in such studies are process impure (see chapter 1). As discussed previously, recognition judgements may be made on the basis of familiarity-driven processing relative to recollection. It is therefore of interest to note that Eldridge et al., (2000) found hippocampal activation when employing a procedure that avoided the above confound by contrasting activity between items associating with recollection relative to familiarity. Second, medial temporal lobe regions are known to be activated during encoding (for reviews see Lepage et al., 1998; Schacter and Wagner, 1999) which could account for the absence of medial temporal lobe activation in straightforward old-new contrasts. By this account, when old-new subtraction designs are used to investigate structures activated at retrieval, medial temporal lobe activity during presentation of novel items (encoding) may sometimes conceal hippocampal activity during presentation of old items (retrieval). Finally, medial temporal lobe activity may occur during episodic retrieval but its apparent absence as revealed by efMRI studies may reflect an inflated rate of type 2 errors here resulting either from vulnerability in such regions to susceptibility artefact or retrieval-related activity not giving rise to detectable BOLD signals. Unfortunately, the lack of findings in efMRI studies of medial temporal lobe activity during episodic retrieval entails that only a minimal contribution from these efMRI studies has been made regarding the function subserved by such regions.

Summary

This section has described three topographically distinct ERP old/new effects; an early bilateral frontal effect which may represent familiarity driven processing, the left parietal old/new effect which reflects recollection, and the right frontal old/new effect which reflects sustained processing on retrieved information (e.g. monitoring and evaluation processes). Comparisons of the paradigms employed in ERP and fMRI studies (blocked and event-related) suggests that the functional operations indexed by the left parietal and right frontal old/new effects map fairly directly onto the operations subserved by medial temporal lobe and prefrontal cortex activity.

It has been suggested that retrieval operations supported by frontal cortex can be dissociated according to whether they are contingent upon the successful retrieval of episodic information or not, (subserved by anterior and dorsolateral prefrontal cortex respectively) (see Rugg and Henson, in press). Suggestion of functional roles for parietal cortex activity during episodic retrieval include attentional processing, the support of visual imagery and the retrieval of memory associations. However, perhaps in part related to the ease with which parietal cortex is activated during retrieval, it has been difficult to make a firm conclusion regarding the role of parietal cortex during episodic retrieval. Finally, it is somewhat of an anomaly that medial temporal lobe is infrequently activated by efMRI studies of episodic retrieval relative to the earlier blocked studies. Paradigms which succeeded in eliciting medial temporal lobe activity (Cabeza et al., in submission, Eldridge et al., 2000), indicate that such activity is not undetectable by efMRI methods, hence it is hoped that the improvement of paradigms used in future investigations will be more productive in determining the role of medial temporal lobe structures in episodic retrieval.

Chapter 4

Memory and Emotion

Introduction

This chapter provides a background to how emotion modulates memory. Provided first is a synopsis of definitions of emotion. The second section of the chapter then turns its attention to a specific form of emotional memory - the 'Conditioned Emotional Response'. This section is included in order to outline the (amygdala-centred) neurocircuitry which underlies 'arousal-mediated' emotional memory. As described in the third section- 'Emotional Episodic Memory'- this neural circuitry may also account for some of the findings of emotional enhancement of episodic memory reported in the literature.

The third section of this chapter primarily addresses episodic memory for emotional information. Distinctions are made in this section between the two main ways in which emotion can influence episodic memory; either through mechanisms of semantic cohesion or through mechanisms of physiological arousal. The chapter then moves on to propose which non-amygdala structures may be important in emotional memory for episodic information. This fourth section – 'Beyond the Amygdala' - provides a review of structures (and their putative functions) sensitive to emotional content of presented information or to aspects of emotional behaviour. Such structures are (at least at encoding) good candidates for forming parts of the circuitry that mediate the modulation of memory for emotional information.

Of these structures, the frontal cortex plays an extensive role in emotional behaviour and is thus warranted a section of the chapter to itself. In that section various aspects of prefrontal cortex function in emotional behaviour are defined along with their underlying neural mechanisms. Although the frontal cortex has not been as extensively linked with emotional memory as has the amygdala (reinforcement-related emotional learning excepted), the section highlights how frontal cortex function in emotional behaviour may be integral to modulating memory for emotional information.

The penultimate section discusses the results of previous ERP studies and is included to inform the reader of established ERP findings in the field of affective neuroscience. Finally, the last section in the chapter discusses retrieval of information with emotional content. Outlined are issues relating to (and criticisms of) the minimal neuroimaging literature which has attempted to uncover neurocircuitry underlying episodic retrieval of emotional information. The section also illustrates how issues relating to the retrieval of emotional episodic memory are addressed in the series of experiments in this thesis.

Defining Emotion

Difficulties in defining and classifying emotions can be seen throughout writings on the topic. It appears that although we all know what it is to experience emotion, we cannot define the phenomena. As a result, coherent overviews of what emotions are (taxonomy, functions, terminology used) are minimal. This section attempts to summarise the general consensus and disagreements in the literature with respect to how emotions should be defined.

Obstacles to providing a comprehensive definition of emotion arise from a variety of sources. First, there appear to be an abundance of equivocal definitions of emotion in the literature. This abundance has been attributed to 'the imprecise way linguistic terms map onto human experience'- there are over 600 words in English referring to affective experiences, certainly too many for a one-to-one correspondence with the range of emotional states (Bower, 1992, p8). Bower further notes that this imbalance has resulted in much confusion between 'proper' and 'spurious' emotional terms in the literature, thus resulting in emotion being ill-defined. For example, terms like lonely, guilty and safe refer to factual descriptions of a person's situation or behaviour, but it is debatable as to whether the terms themselves should be classified as emotions.

Second it is unclear how (or indeed whether) mental and non-mental (physiological) reactions should be dissociated when defining emotions. For example, whether disgust should be investigated in isolation from nausea, or anger from physiological arousal (see Ortony, Clore and Foss, 1987). It has been suggested that physiological reactions dissipate on a longer time scale relative to emotions which instead are defined in terms of a reaction; 'brief, spasmodic, intense experiences of short duration' (Bower, 1992, p11). However, by other accounts non-mental states (e.g. physiological arousal) are themselves integral to emotions (Lang, Greenwald, Bradley and Hamm, 1993; see below).

A third problem is that emotions are also often confounded with 'mood' – that is the prolonged maintenance of an emotional disposition. Typically, moods are considered as states or frames of minds as opposed to reactions to events (see Berner, 1988; Bower, 1992; Mandler, 1992). In general, with exception perhaps of their differing time-course, emotion and mood are not systematically differentiated between in the literature.

Over and above these issues there does appear to be some consensus as to what defines an emotion. Few would deny that there is a biological and evolutionary basis for emotion, thus in general emotions are regarded as 'biosocial' phenomena. The main problem in the literature appears to be how to apply a more specific definition to emotion.

One popular approach is to define a set of basic or 'prototypical' emotions which can be systematically investigated and their neural substrates identified (e.g. see figure 4.1). These basic emotions are usually classified according to whether they are positive or negative and may be further subdivided into subordinate categories. This approach has led to the development of a variety of techniques for inducing, detecting and investigating emotions [e.g. from the analysis of facial expressions (e.g. Ekman and colleagues); imaging brain responses to emotional stimuli (e.g. Dolan and colleagues) or stimulating emotion centres in the brain (e.g. LeDoux and colleagues)].

There is no doubt that this approach has contributed to our understanding of the neurobiology of emotions. However, perhaps as an inevitable result of the employment of such a variety of techniques, the major problem with this approach is that there appears to be little consensus across the field as to what constitutes a basic emotion [cf. Ekman, (1992) vs. Panksepp, (1992) vs. Shaver, Schwartz, Kirson and O'Connor, (1987)]. For example, Ekman designates six basic emotions (happiness, anger, surprise, fear, disgust and sadness) (cf. figure 4.1). It had been hoped that such different approaches might converge upon a set of basic emotions; unfortunately this has not been the case. A second problem with the basic emotions approach is that it ignores commonalties amongst different emotions. Finally, this approach does not characterise particularly well the extensive range of human emotions, for example complex emotions (such as guilt, pride, jealousy) are of lesser importance (subordinate). Thus, it could be argued that this approach neglects the richness of emotions in human life.

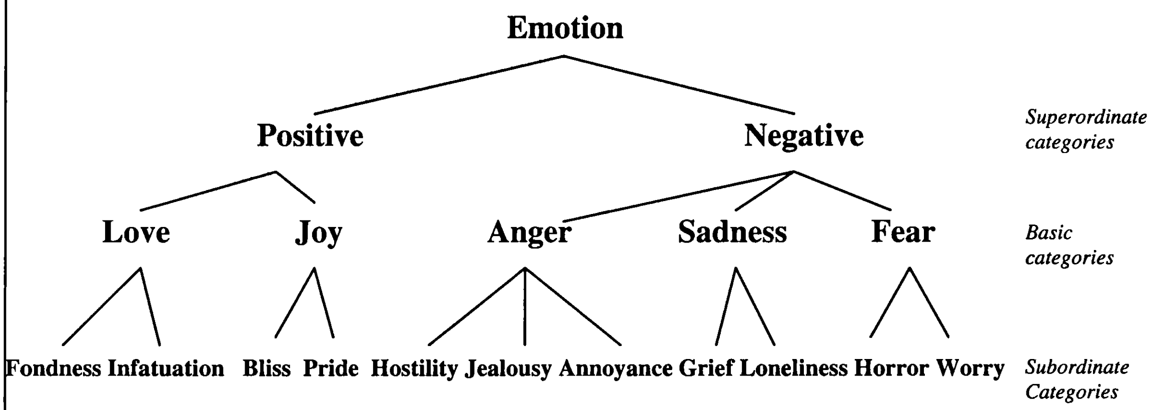

Figure 4.1 A taxonomy of emotion
(as defined by Shaver et al. (1987) (not all subordinate emotions are included). Adapted from Bower,G.H. (1992). How emotions affect learning. In S. A. Christianson (Ed.), _*The Handbook of Emotion and Memory: Research and Theory.* (pp. 3-32). Hillsdale, New Jersey: Lawrence Erlbaum Associates Inc.Bower, 1992).

A second approach is to view emotions in a framework where 'elements' across emotions as opposed to basic emotions are studied and defined. In this approach, two components of emotion have been defined – 'approach' and 'avoidance'. Crucially, these components may be shared by diverse emotions such as anger, sadness and joy (Ortony and Turner, 1990; Turner and Ortony, 1992; Armony and LeDoux, 2000; see also Lang, Bradley and Cuthbert, 1990; Davidson, Ekman, Saron, Senulis and Friesen, 1990; Lang, Bradley and Cuthbert, 1998; Neumann and Strack, 2000). Avoidance behaviours minimise the effects of eliciting stimuli whereas approach behaviours maximise the effects of eliciting stimuli. The usefulness of studying emotions in this manner was demonstrated in a study by Fox and Davidson (1988) in which it was revealed that patterns of brain activity depended, not upon different categories of emotions but upon whether stimuli elicited avoidance or approach responses. However, this approach has been criticised since, by itself, it does not adequately explain for the apparent universality of distinct basic emotions [as suggested in studies of facial expressions, (see Ekman, 1992) or neurobiological data of separate brain systems mediating affective-emotional processes (see Panksepp, 1992)]. Thus, component approaches to defining emotion also appear insufficient to account for the complexity and richness of emotions in humans.

A third approach to defining emotion is to address the motivational states emotions play in human and animal evolution. As defined by Bower (1992), in this approach humans and animals are considered as biological machines ‘endowed’ with systems whose roles include, a) detection of needs and motive states; b) prioritisation of needs according to their importance; c) construction of action sequences to pursue ‘satisfaction’ (i.e. of needs/motive) and d) sensory monitoring of internal and external environmental signals in order to be able to modify stimulus-goal contingencies. By this account, a system with such components ‘will exhibit emotions as a by-product of translating its concerns into goal-directed actions’ such that events appraised as achieving motivational states (or alternatively the absence of anticipated negative events) will produce positive emotions, whereas as events appraised inhibiting motivational states (or alternatively the absence of expected positive goals) produce negative emotions (Bower, 1992, pp5).

A final approach reduces variance in emotions to a two-dimensional framework organised by the axes of valence (negative-positive) and arousal (calm-aroused) (Lang et al., 1993). Valence refers to the direction of the emotion (i.e. positive vs. negative, relative to a neutral position), for example whether the emotion is pleasant or unpleasant [e.g. achievement vs. inhibition of motivational state (approach 1); happiness vs., anger (approach 2); approach vs. avoidance (approach 3)]. By contrast, arousal is proposed to refer to the ‘intensity’ of the emotion, ranging from calm to physiologically aroused.

Even though aspects of the various approaches are reconcilable, researchers tend to investigate emotion employing a definition specific to their stance with definitions across approaches are rarely combined . However, as will become clear in the remainder of the chapter, the term emotion incorporates many aspects of the above approaches. Thus, summarising the above synopsis, emotion can be defined as behavioural, hormonal and autonomic responses to either the outcome of an event or to a presented object or agent. Furthermore, basic emotions may be subserved by integrated neurobiological sub-systems (e.g. subserving approach, avoidance or arousal) as well as by specific neural mechanisms sensitive to emotion type (e.g. happiness vs. anger).

The Conditioned Emotional Response

Approach and avoidance behaviours form the basis of emotional memory (and research thereof) in that they are both modified by experience. In investigations of the neuroanatomical basis of emotional memory, as revealed by approach and avoidance behaviours, it is undoubtedly the influence of emotion on the conditioned emotional response (CER) that has received the most attention. The CER characterises an emotional response (avoidance or approach) to a previously neutral stimuli which has acquired affective significance through its temporal pairing with emotional experience (positive or negative) (Pavlov, 1927). One particular type of CER, fear conditioning, has been studied more extensively than any other. Fear conditioning is the elicitation of a fear behaviour e.g. freeze or flight (conditioned fear response; CFR) to a conditioned stimuli (CS) following the association of a neutral stimuli (US) with fear or danger such that it is 'conditioned' to signify threat or danger.

The results of such research provide extensive evidence that the amygdala plays a critical role in fear conditioning in humans [LaBar, LeDoux, Spencer and Phelps, 1995; LaBar, Gatenby, Gore, LeDoux and Phelps, 1998; Phelps et al., 1998; Büchel et al., 1999, for reviews see Büchel and Dolan, 2000; Aggleton, 2000 (for investigations at the cellular level see LeDoux, Iwata, Cicchetti and Reis, 1988; Davis, 1992; LeDoux, 1993; Armony, Quirk and LeDoux, 1998, and Armony and LeDoux, 2000 for reviews)]. The amygdala appears to subserve three main functions in fear conditioning; first 'evaluation' – (of the affective significance of stimuli); second 'control' of physiological responses (- to affective stimuli) and third 'memory' (- sensitising the nervous system to the eliciting stimuli in future events) (see McGaugh, Cahill and Roozendaal, 1996; Cahill, Weinberger, Roozendaal and McGaugh, 1999 *vs* Davis, 1997; Fanselow and LeDoux, 1999; LeDoux, 2000 for variations on this view). Certainly the amygdala is ideally situated for such a function having connections with; a) sensory (Iwai and Yukie, 1987; LeDoux, Cicchetti, Xagoraris and Romanski, 1990; Turner and Herkenham, 1991; for reviews see

Amaral, Price, Pitkanen and Carmichael, 1992; Kapp, Whalen, Supple and Pascoe, 1992; LeDoux, 2000); b) autonomic (for reviews see LeDoux et al., 1988; see Kapp et al., 1992); and c) memory (Aggleton, Burton and Passingham, 1980; Porrino, Crane and Goldman-Rakic, 1981; Aggleton, 1986; Izquierdo, Medina et al., 1993; Maren and Fanselow, 1995) systems.

Evidence that the amygdala plays a role in evaluating the affective significance of stimuli is provided by neuroimaging studies revealing amygdala activity during presentation of stimuli which contain or evoke fear (e.g. Morris, Friston et al., 1998). Furthermore, neuropsychological studies have also revealed that bilateral amygdala damage impairs processing of fear content in stimuli (e.g. fearful facial expressions, Adolphs, Tranel et al., 1999). Notably, the amygdala receives direct input from early stages of sensory processing and projects to virtually all sensory related cortical areas, thus suggesting that the amygdala can modulate sensory processing at a very early stage (see Amaral et al., 1992). It is suggested that back projections to early visual association cortices mediate reinforced processing of behaviourally salient visual cues (Friston, Tononi, Reeke, Jr., Sporns and Edelman, 1994; see also Kosslyn, Shin et al., 1996; Taylor, Liberzon et al., 1998).

With respect to the second putative function of the amygdala in fear conditioning (control of physiological responses), where environmental cues are arousing functional connections between the amygdala and regions responsible for autonomic response (e.g. hypothalamus and brain stem) control the expression of the fear response such as freezing, changes in blood pressure and the release of stress hormones (e.g. adrenaline).

That the amygdala plays a role in memory formation for fear inducing stimuli has been evidenced by studies that patients with bilateral amygdala damage are impaired on tests of fear conditioning (fail to acquire conditioned skin conductance responses) (Phelps et al., 1998) but perform normally on tasks of episodic memory (see LaBar et al., 1995)[1a]. Crucially, as revealed by Bechara, Tranel et al. (1995) this pattern of

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[1a] Although patients with lesions limited to bilateral amygdala may have relatively normal episodic memory, they do not show normal enhanced episodic memory for the emotional material (Adolphs et al., 2000)] (see following section, p 85).

memory impairment is reversed with hippocampal damage (i.e. impaired explicit memory but conditioned autonomic responses are preserved).[1b]

Convergent evidence that the amygdala plays a role in memory formation for fear inducing stimuli has been provided following the advent of efMRI studies which (through permitting mixed-trial classical conditioning paradigms) more readily enable detection of amygdala activity during conditioning. Indeed, whereas many early neuroimaging studies employing blocked paradigms failed to find any evidence of amygdala activation (e.g. Fredrikson, Wik, Fischer and Andersson, 1995; Hugdahl, Berardi et al., 1995, but see Morris, Ohman and Dolan, 1998), event-related neuroimaging studies have been far more successful (e.g. Büchel, Morris, Dolan and Friston, 1998; LaBar et al., 1998; Büchel et al., 1999). (The failure of the earlier studies employing blocked paradigms to reveal amygdala activity during fear conditioning may under some circumstances have resulted from habituation to the CFR following repeated presentation of the CS.)

Regarding functional connections with regions responsible for memory, it is suggested that the function of amygdala-hippocampal pathways is context-conditioning[2] (Maren and Fanselow, 1995), whereas orbitofrontal-amygdala pathways have been proposed as involved in reinforcement learning (Rolls, 2000 see below). The main mechanism proposed to underlie modulation of the amygdala-hippocampal memory system is arousal - specifically the influence of peripheral adrenergic systems upon the cholinergic, optoid peptidergic and GABA-ergic systems in the amygdala (McGaugh, Introini-Collison et al., 1993; McGaugh and Cahill, 1997; Cahill and McGaugh, 1998). For example, changes in β-adrenergic neurotransmission between the amygdala and the hippocampus have been shown to affect LTP formation in hippocampal cells (Ikegaya, Saito and Abe, 1994; Ikegaya, Nakanishi, Saito and Abe, 1997) or at hippocampal-amygdala synapses (Maren and Fanselow, 1995). In addition, a 'braking' system which retards acquisition and facilitates extinction of the CER is proposed as being provided by inhibitory influence of glutamanergic input from prefrontal cortex (specifically medial and orbital regions) onto GABA neurons

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[1b] Relative to controls, temporal lobectomy patients with relative sparing of the amygdala have impaired episodic memory but still show a similar level of enhanced level of recall for emotional relative to neutral information (Phelps et al., 1997; Hamann et al., 1997a; Hamann et al., 1997b) (see following section, p85).

[2] the association between a US and the context in which the Pavlovian memory is formed, the context itself may then subsequently form part of the emotional memory

in the amygdala (Morgan, Romanski and LeDoux, 1993; Morgan and LeDoux, 1995; Rolls, 1996; Rolls, 2000). However, whether the amygdala is the site of plasticity for fear conditioning, or whether it plays a purely modulatory role on memory systems elsewhere in the brain (e.g. hippocampus) has been a source of debate (e.g. see Fanselow and LeDoux, 1999 vs. Cahill and McGaugh, 1998).

Although amygdala involvement in the processing of emotion has been defined predominantly by studies of fear conditioning, more recent evidence suggests that the amygdala is also activated when the emotion is not fear, but some other high-arousal emotion, such as anger (e.g. Scott, Young et al., 1997; Morris et al., 1998, but see Blair, Morris, Frith, Perrett and Dolan, 1999). Indeed, recently amygdala activation has been associated with arousing positive stimuli (Dolan, Lane, Chua and Fletcher, 2000). By contrast, it is rare for emotions which have a lower-level of autonomic arousal (e.g. disgust and sadness) to elicit amygdala activation (e.g. see Lane, Reiman, Ahern, Schwartz and Davidson, 1997; Phillips, Young et al., 1997; Phillips, Young et al., 1998, but see Blair et al., 1999). Although this pattern is consistent with the proposal that the critical factor in (amygdala-mediated) emotional memory is arousal, it appears to contradict earlier themes that the amygdala has a specific role in aversive, if not fear, conditioning. However, this apparent inconsistency may well be accounted for by functional heterogeneity in differential amygdaloid nuclei (see Everitt and Robbins, 1992; see also Kesner, Walser and Winzenried, 1989).

Emotional Episodic Memory

The CER is usually classified as a form of implicit memory since conscious awareness of the prior episode in which the CS was encountered appears to be of limited significance for the expression of the CER (but see Morris et al., 1998). However, in addition to its effects on implicit memory, emotional experience may also influence episodic memory. We are familiar with this influence through personal experience, such as enhanced memory for details central to a traumatic event. Such effects of emotion on implicit and explicit memory have been termed 'emotional memory' and 'memory for emotion' respectively (LeDoux, 1996). However, this description is somewhat misleading since, as outlined below, evidence suggests that emotion influences implicit and explicit memory, at least in part, by the same mechanism i.e. arousal-mediated amygdala activity. For this reason in this thesis, where a distinction between kinds of emotional memory is necessary, the word ‘emotional’ is simply added as a prefix before the appropriate memory system i.e. emotional implicit memory, emotional episodic memory and so on.

At least three kinds of evidence suggest that physiological mechanisms akin to those subserving the CER also mediate the enhancement of explicit memory. First, neuropsychological studies provide evidence of a double dissociation between medial temporal lobe impairment with and without amygdala damage and emotional and non-emotional episodic memory. Relative to controls, temporal lobectomy patients with relative sparing of the amygdala have impaired episodic memory but show a similar level of enhanced recall for emotional events (Phelps, LaBar and Spencer, 1997; Hamann, Cahill and Squire, 1997a; Hamann, Cahill, McGaugh and Squire, 1997b). By contrast, patients with lesions limited to bilateral amygdala have normal episodic memory but do not show normal enhanced memory for the emotional material (Adolphs, Cahill, Schul and Babinsky, 1997; Phelps et al., 1998; Adolphs, Tranel and Denburg, 2000). Second, β-adrenergic antagonists abolish facilitation of episodic memory by emotion in humans, without altering ratings of emotional valence of stimuli (Cahill, Prins, Weber and McGaugh, 1994). Third, neuroimaging studies suggest that amygdala activity during encoding of emotional episodic information predicts how well information is subsequently retrieved (Cahill, Haier et al., 1996; Hamann, Ely, Grafton and Kilts, 1999).

The above studies thus indicate that the amygdala (and physiological arousal) is important in emotional episodic memory as well as in the formation of the CER. In addition, and not inconsistent with this proposal, lateralised amygdala activity may dissociate emotional explicit memory and emotional implicit memory. This follows from evidence that the right amygdala’s response to a CS is significantly enhanced if the stimulus is masked (i.e. when the emotional memory is unconscious) whereas the left amygdala's response is enhanced when then CS is unmasked (i.e. when there is a degree of awareness to the emotional memory) (Morris et al., 1998).

However, as well as having an influence on memory through amygdala-mediated physiological arousal, emotion may in other circumstances influence episodic memory by virtue of valence, that is the emotional tone associated with information (Phelps et al., 1998). In this scenario, emotion may influence memory by virtue of emotional information belonging to a relatively cohesive semantic group as compared with neutral information (cf. Deese, 1959). The above issue, which is often neglected in the literature, has specific relevance for studies employing emotional words in investigations of emotional episodic memory. By the foregoing analysis, emotionally valenced words may not exert their effect on memory by virtue of their emotionality *per se*. Rather they may do so because emotionally valenced words have, on average, stronger inter-item associations than do sets of unselected neutral words. Thus memory for emotional words may not always be mediated by systems or processes to which these items have privileged access, such as the above described arousal-mediated amygdala-hippocampal system. Instead, memory for emotional words may be mediated by the same cognitive operations that support memory for non-emotional material. [3]

A number of lines of evidence suggest that emotional words may show an advantage over neutral words through mechanisms of semantic cohesion. This evidence, which is discussed in more detail in the introduction to the first experiment (Chapter 5), can be briefly summarised as follows. First, although affective words are not consistently arousing for participants (as measured by skin conductance responses) they are recalled better than neutral words (Rubin and Friendly, 1986; Danion, Kauffmann-Muller, Grange, Zimmermann and Greth, 1995; Phelps et al., 1997). Second, enhancement effects of emotion on memory as observed in tests of recall do not always extend to tests of recognition (Leiphart et al., 1993; Danion et al., 1995), consistent with such effects being mediated by 'semantic cohesion' (cf. Roediger and McDermott, 1995). Finally, when the semantic cohesiveness of items is controlled for, the recall advantage for emotional words is removed (Phelps and LaBar cited in LaBar and Phelps, 1998).

Beyond the Amygdala

Investigations of arousal-mediated emotional memory have focused predominantly on fear (or non-specific negative affect). To date there is comparatively little research into the cognitive neuroscience of memory for other types emotions such as happiness, disgust, sadness and anger. However, it is probable that structures activated by perception of emotion-inducing affective stimuli, or those which when lesioned lead to impairments of processing of emotion-inducing stimuli, also form

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[3] n.b., This classification of emotional words does not include taboo words. Where taboo words and neutral words give rise to differential forgetting rates (indicating that emotion influences memory consolidation in humans) this is proposed to reflect arousal-mediated mechanisms (LaBar and Phelps, 1998; see also Phelps et al., 1998).

part of the circuitry that mediate memory for the stimuli (at least at encoding). Such structures can play a 'direct' role in emotional memory, i.e. the structure is the site of the modulation of memory by emotion. Alternatively such structures may play a more 'indirect' role, wherein the activity of the structure (at encoding) is upstream or downstream from the site of the emotional memory interaction, but nethertheless necessary for interactions between memory and emotion to occur. Furthermore, some structures can be classified as playing a 'generalised' role in emotional memory since they appear to be activated indiscriminately by the different types of emotions (the amygdala being a case in point - but see Broks, Young et al. (1998) for example of amygdala specificity to fear), whereas other structures are sensitive to the nature of the emotion (e.g. fear vs. disgust).

By the above account, structures activated frequently by emotionally salient stimuli (regardless of type of affect) which are involved in autonomic and motor responses (such as the hypothalamus and basal ganglia respectively) (e.g. see Smith, DeVito and Astley, 1990) have a generalised but indirect role in emotional memory. By contrast, structures activated frequently by emotionally salient stimuli (regardless of type of affect) which have a direct role in emotional memory are proposed to include retrosplenial cortex and the anterior temporal pole (see Maddock, 1999 for review, but see also Vogt, Absher and Bush, 2000).

The proposal that retrosplenial cortex has a direct role in mediating the interaction between emotion and memory arose from the observation that, as well as being frequently activated by emotionally salient stimuli, retrosplenial cortex is also frequently activated during episodic retrieval (e.g. Grasby, Frith et al., 1993, Donaldson et al., 2000, see Maddock, 1999). The proposal is further supported by findings of a significant correlation between retrosplenial cortex activity by emotionally salient words and the enhancement of recall for these words (Maddock and Buonocore, 1997). Maddock (1999) notes that the retrosplenial cortex is well positioned anatomically for integrating the emotional significance of events and episodic memory formation. It receives afferent input from the anterior cingulate, orbitofrontal cortex and superior temporal sulcus (all of these regions have extensive connections with amygdala and thus are a potential source of information about the emotional significance of an event), whereas its efferent pathways connect with parahippocampal and entorhinal regions (thus retrosplenial cortex can influence episodic memory processing). The same author also postulates an alternative wherein the retrosplenial cortex implements emotional memory processing following earlier emotional-memory [amygdala-entorhinal/(hippocampal) cortex] interactions. The reader is referred to Vogt et al. (2000) for further discussion regarding the role of the retrosplenial cortex in the interaction between emotion and memory.

A direct role in emotional memory has similarly been proposed for the anterior temporal cortex of imparting affective tone to experience (Dolan et al., 2000). In their study, Dolan and colleagues investigated directly which regions subserve retrieval of emotional episodic memory. Evidence was provided that (in addition to the amygdala) the anterior temporal cortex was sensitive to the emotional nature of the retrieved items. It was proposed therein that the anterior temporal cortex activity reflected the (tonic) psychological ‘set’ or state associated with modulating emotional memory as opposed to (phasic) item-related activity (criticisms of this study are addressed in the final section).

Some structures have been classified as playing a role ‘specific’ to a type of emotion. Notably, studies investigating the perception of emotion have revealed that the anterior insula and basal ganglia have been linked to disgust (and sometime sadness), but not usually fear. For example, neuropsychological studies have revealed impaired recognition and experience of disgust following injury to either insula or basal ganglia (Sprengelmeyer, Young et al., 1996; Gray, Young, Barker, Curtis and Gibson, 1997; Halligan, 1998; Calder, Keane, Manes, Antoun and Young, 2000). Furthermore neuroimaging studies have revealed increased activity in such structures during presentation of either disgusting images or facial expressions of disgust (Phillips et al., 1997; Phillips et al., 1998). However, it should be noted that the pronounced vagal response associated with disgust might in part be responsible for anterior insula activity during perception of disgust (Cacioppo et al., 1993 cited in Davidson, 2000).

Frontal cortex

Much of the chapter so far has focused upon structures mediating ‘reflex like’ behaviour to ‘primary’ emotions including sensory, motor and autonomic structures. One other region of the brain that has been linked with emotional memory, predominantly through neuropsychological studies is the frontal cortex. Indeed, the neuropsychology of emotional behaviour began last century with the case study of Phineas Gage who exhibited marked changes in social behaviour and personality following an accident which resulted in a lesion to his frontal lobes. Since then an extensive literature has developed addressing the effects of frontal lobe lesions on human behaviour. An exhaustive survey of such effects are beyond the scope of this thesis, instead the major findings are presented so that the reader will be in a position to connect aspects of frontal lobe function with emotional memory.

It has been documented that patients with frontal lobe damage often show altered emotional and social behavioural such as impulsiveness, jocularity, irritability, inappropriate sexual advances and misinterpretation of people's moods (Damasio, Tranel and Damasio, 1990; Rolls, Hornak, Wade and McGrath, 1994; Hornak, Rolls and Wade, 1996). There is some suggestion that positive emotion processing is lateralised to left hemisphere whereas negative emotion processing is lateralised toward right hemisphere, (see Gemar, Kapur, Segal, Brown and Houle, 1996; Canli, Desmond, Zhao, Glover and Gabrieli, 1998), and that left and right frontal cortex lesions produce differential abnormalities in social behaviour. Consistent with this 'valence hypothesis' decreases in the activity of left prefrontal cortex (as revealed by neuroimaging studies) have been found to accompany negative mood states/ depression (e.g. Bench, Friston et al., 1992; Bench, Friston, Brown, Frackowiak and Dolan, 1993; George, Ketter and Post, 1993) and recovery from depression is associated with normalisation of left frontal blood flow (e.g. Bench, Frackowiak and Dolan, 1995). Furthermore 'pseudodepression' (apathy, indifference, loss of initiative, reduced sexual drive, little overt emotion) secondary to brain injury is most prevalent after left frontal lobe lesions (e.g. Sackeim, Decina and Malitz, 1982; Sackeim, Greenberg et al., 1982; Robinson and Chait, 1985, for reviews see Downhill, Jr. and Robinson, 1994; Davidson and Irwin, 1999; Davidson, Abercrombie, Nitschke and Putnam, 1999). By contrast, 'pseudopsychopathy' (impulsiveness, irritability, mania, elation, lack of restraint, coarse language, inappropriate sexual advances, social inappropriateness, jocularity) is often observed after right-sided lesions (e.g. Cohen and Niska, 1980; Sackeim et al., 1982; Gillig, Sackellares and Greenberg, 1988, for reviews see Downhill, Jr. and Robinson, 1994; Davidson and Irwin, 1999; Davidson et al., 1999).

Findings indicate that damage to orbitofrontal/ventral regions of the frontal lobe are associated with more dramatic changes in personality than is damage to dorsolateral regions (Zangwill, 1966 cited in Kolb and Whishaw, 1980). Ventral prefrontal cortex damage has been observed to produce specific impairments in the identification (e.g. Hornak et al., 1996) and production (e.g. Angrilli, Palomba, Cantagallo, Maietti and Stegagno, 1999) of facial emotional expression as well as abnormal autonomic responses to socially meaningful stimuli, even though autonomic responses to elementary UCS (e.g. loud noises) are normal (e.g. Damasio et al., 1990). Furthermore ventral prefrontal (orbitofrontal) cortex activity has been linked to the instantiation and regulation of mood both through neuropsychological studies of mood disorders (Drevets, Videen et al., 1992; Drevets, Price et al., 1997) and neuroimaging studies of induced mood (Pardo, Pardo and Raichle, 1993; Baker, Frith and Dolan, 1997).

The role of the frontal cortex in emotional behaviour certainly includes an influence on emotional memory. Evidence from neurophysiological studies suggest that when such an influence relates to habituation of a CER, dorsolateral and medial prefrontal cortex regions are responsible (e.g. Morgan et al., 1993; Morgan and LeDoux, 1995; Morgan and LeDoux, 1999). By contrast, the primary focus for reinforcement processing (e.g. reward-related learning) appears to be more ventrally located in orbital regions (e.g. Rolls et al., 1994; see Rolls, 2000 for review).

Frontal cortex may influence some types of emotional memory through its role in cognitive processing (for review see Heilman and Gilmore, 1998). For example, by contrast with avoidance and approach in the CER, avoidance and approach behaviours in operant conditioning (reinforcement-learning) usually require higher-levels of cognitive processing, for example when consequences of actions are delayed and representations of behavioural-consequence contingencies must be maintained (see Elliott, Dolan and Frith, 2000 for review; see also Rolls, 2000). Hence, functions of orbitofrontal cortex such as the suppression of irrelevant memory traces (see Schnider, Treyer and Buck, 2000) or the control of persevarative responses (see Rolls et al., 1994) may be the critical factors in reinforcement learning rather than emotion processing per se. More generally, where higher-level cognitive functions are necessary for the expression of the emotional memory (e.g. subsequent monitoring, evaluation or classification of retrieved information), the emotional memory will be highly dependent on whichever region of frontal cortex subserves the cognitive function.

The role of the frontal cortex in emotional memory is complicated further since it is known that regions of the frontal cortex are differentially activated by the processing of emotional versus neutral information in cognitive tasks involving decision making (Isen, Rosenzweig and Young, 1991; Bechara, Damasio and Damasio, 2000), planning (Partiot, Grafman, Sadato, Wachs and Hallett, 1995; Elliott, Frith and Dolan, 1997; Elliott, Baker et al., 1997), attention (Elliott, Rubinsztein, Sahakian and Dolan, 2000); language (George, Parekh et al., 1996) and memory (Ashby et al., 1999; Bechara et al., 2000). Thus, where cognitive processes are necessary for production/expression of emotional memory, the type of processing may interact with the type of information retrieved (e.g. positive, negative, neutral). A similar concept has been discussed by Damasio and colleagues with their 'somatic marker hypotheses' (Damasio, 1996; Bechara et al., 2000). By this account functions of the frontal lobe (such as working memory, decision making) may be influenced (either consciously or unconsciously) by marker signals (in 'bio-regulatory processes') that are expressed in emotions and feelings.

From the above account it can be seen that the frontal cortex is critical for normal functioning emotional memory. For example, in circumstances where subsequent processing is required upon retrieved information or in situations where the influence of prefrontal cortex on subcortical structures is crucial (as in the extinction of the CER). Finally, it should be noted that memory processing for complex emotions such as guilt, spite, satisfaction, shame is almost certainly dependent on frontal cortex function since these emotions involve a higher level of cognitive (inter-personal) processing relative to the archetypal basic emotions.

ERPs and Emotion

The general theme of the chapter so far has been that where memories are to be formed for emotional stimuli relative to neutral stimuli different brain regions may be involved. It should also be noted that on numerous occasions it has been suggested that right hemisphere structures are more sensitive to affect than their left hemisphere counterparts (see Schwartz, Davidson and Maer, 1975; Blonder, Bowers and Heilman, 1991; Cimino, Verfaellie, Bowers and Heilman, 1991; Wheeler, Davidson and Tomarken, 1993; George et al., 1996). However there are some studies which fail to find a right hemispheric sensitivity in the processing of affect (Ferry and Nicholls, 1997; Hagemann, Naumann, Becker, Maier and Bartussek, 1998; Schapkin, Gusev and Kuhl, 2000; see Borod, Haywood and Koff, 1997 for review). Furthermore, right hemisphere sensitivity may reflect the emotional stimuli in psychological tests being predominantly negative and thus reflect a valence effect rather than an emotionality (positivity/negativity) effect. As discussed earlier, activity of right prefrontal cortex has been found to accompany negative mood states and depression whereas lesions of the right frontal cortex may result in symptoms of pseudomania such as excessive jocularity and elation.

Perhaps, the strongest support for right hemisphere sensitivity to emotional stimuli has arisen from ERP investigations of how the perception of emotion modulates neural activity (e.g. Laurian, Bader, Lanares and Oros, 1991; Kayser, Tenke et al., 1997; Kayser, Bruder, Tenke, Stewart and Quitkin, 2000, but see Schapkin et al., 2000). In addition, such studies have noted that scalp-recorded P2 and P3 amplitudes are enhanced during presentation of emotional stimuli relative to neutral stimuli (e.g. see Johnston, Miller and Burleson, 1986; Johnston, Burleson and Miller, 1987; Lang, Nelson and Collins, 1990; Naumann, Bartussek, Diedrich and Laufer, 1992; Palomba, Angrilli and Mini, 1997; Kayser et al., 1997; Schapkin et al., 2000; Kayser et al., 2000; Schupp, Cuthbert et al., 2000, but see Carretie, Iglesias, Garcia and Ballesteros, 1997), such effects extending on occasions into a sustained slow (positive) wave potential (400 msec and beyond – usually to around 1200 msec post-stimulus onset) (e.g. see Vanderploeg, Brown and Marsh, 1987; Naumann et al., 1992; Diedrich, Naumann, Maier, Becker and Bartussek, 1996; Palomba et al., 1997; Schapkin et al., 2000; Cuthbert, Schupp, Bradley, Birbaumer and Lang, 2000). Furthermore, such positive shifts in the waveforms observed are accentuated for stimuli of high emotional intensity/arousal (Cuthbert et al., 2000).

The procedures generally employed in such experiments involve the presentation of emotional (positive or negative) and neutral stimuli (words or pictures) in a random sequence with critical items appearing with an equal probability. In general, interpretations of the effects are fairly consistent. Early positivity in the ERP waveforms to emotional stimuli (around 200msec - P2 enhancement) has been suggested to reflect evaluation processes specific to the detection of emotional stimuli (see Schapkin et al., 2000; Cuthbert et al., 2000). Modulation of these early potentials may reflect activity in low level avoidance/approach systems and thus be an index of the emotional reaction/orienting complex (cf. Halgren and Marinkovich, 1995).

Subsequent modulation of the P3 component (around 300msec) is suggested to index task-relevant processing of emotional stimuli following detection (for example target effects, oddball effects, see Donchin and Coles, 1988) and is highly influenced by cognitive as opposed to emotional (and/or sensory) variables (Carretie et al., 1997; Schapkin et al., 2000, but see Naumann et al., 1992). Notably, a study which controlled for such cognitive variables (specifically a relevance-for-task effect) did not elicit differential P3 responses for emotional relevant to neutral stimuli (Carretie et al., 1997). On the basis of their findings Carretie and colleagues' suggested that the P3 is not an appropriate variable for monitoring emotional reactions to emotional stimuli, however surprisingly this counsel has been relatively ignored in the literature (e.g. Kayser et al., 2000).

The slow positive wave is suggested to reflect a generalised increase in information processing for emotional stimuli as compared to neutral stimuli, for example increased motivational engagement and commitment of attentional resources to the emotional stimuli (Naumann et al., 1992; Schupp et al., 2000; Cuthbert et al., 2000). As noted by Cuthbert et al. (2000), theory regarding sustained modulations of waveforms has traditionally been more concerned with negative waves (which are hypothesised to reflect higher-order conceptual activity). They suggest that the positive slow waves during emotional stimulus presentation may instead reflect sustained information processing linked with perceptual and memory function (see also chapter 3; Ritter and Ruchkin, 1992).

It has been noted previously that the positive slow wave and the P3 reflect similar processes (Kok, 1997), however, unlike P2/P3 modulation, the positive slow wave appears to be insensitive to affective direction (positive, negative) of stimuli (Cuthbert et al., 2000). This emphasises the importance of emotional salience in its elicitation rather than it reflecting processing simply relating to categorisation effects. Nethertheless, it does appear that the positive wave is still sensitive to cognitive processing relating in some manner to the evaluation of the emotional content of stimuli, since it is not elicited if the participants' attention is directed away from the affective content of the stimuli, for example if they are required to structurally process words (Naumann et al., 1992, but see Diedrich et al., 1996).

Retrieval of Emotion

The above synopsis regarding emotional episodic memory has addressed primarily the neural circuitry underlying the encoding of emotional stimuli relative to the encoding of neutral stimuli. Surprisingly, although the literature regarding systems underlying the encoding of emotional stimuli is extensive, the neurological basis of the retrieval of information with emotional content has been relatively ignored.

There are obviously two possibilities regarding the underlying mechanisms of the retrieval of emotional information. One possibility is that a common neural network is responsible for retrieval of both emotional and neutral information. By this scenario, the effects of emotion upon memory act at the time of encoding or consolidation. Certainly, as reviewed above, there is evidence that emotion influences memory consolidation in humans (e.g. LaBar and Phelps, 1998; see also Phelps et al., 1998). However, the alternative possibility is that, in addition to its effects at encoding and during consolidation, emotion modulates retrieval processing through the engagement of emotion-sensitive structures such as those reviewed above which were 'directly' involved in the interaction between emotion and memory during encoding (Dolan et al., 2000; LeDoux, 2000).

It has been suggested that regions involved in the retrieval of emotional memory have been revealed by studies which use recall of emotional episodic events as a means of generating emotional mood (e.g. Pardo et al., 1993; George, Ketter et al., 1995; Lane et al., 1997; Reiman, Lane et al., 1997; Kimbrell, George et al., 1999). Such studies have revealed increased activity for recall of emotion information relative to recall of neutral information in regions including temporal pole, anterior insula, cingulate, frontal cortex (orbital and medial regions), brainstem, thalamus, putamen limbic structures (e.g. temporal pole). However, it is inappropriate to use such studies as evidence of which regions are involved in the retrieval of emotional information. First, it is impossible from such studies to distinguish between mood- related effects and effects related specifically to the retrieval of emotion (see Berner, 1988; Bower, 1992; Mandler, 1992, for discussion of the distinction between mood and emotion) . Second, where emotional autobiographical events are recalled (e.g. Pardo et al., 1993; George et al., 1995; Kimbrell et al., 1999) it is difficult to dissociate memory effects related to the 'emotionality' of the recalled event and those related to the 'distinctiveness' of the recalled event.

More recently, the question of whether emotion influences retrieval processing has been the subject of studies employing functional neuroimaging methods to investigate specifically the neural correlates of emotional and non-emotional memory retrieval. The results from these studies are inconclusive with regard to whether the same structures mediating memory for emotionally neutral information also modulate memory for emotional information. Using PET, Taylor et al. (1998) found that relative to recognition memory for neutrally-toned pictures, recognition judgements on emotionally negative pictures was associated with enhanced activation in occipital cortex (lingual gyrus). Taylor et al. (1998) concluded that while retrieval of emotional information did not recruit the same emotion-sensitive structures (e.g. amygdala) involved at the time of encoding, it was associated with enhanced processing in sensory regions. By contrast, in the PET study by Dolan et al. (2000) (discussed earlier) recognition memory for emotional relative to neutral pictures was associated with activation in the amygdala and anterior temporal pole, leading these authors to conclude that emotional memory retrieval did indeed recruit regions specialised for the processing of emotion.

Three problems arise from the methodology employed in these two studies. First, both studies employed a block design rendering it difficult to distinguish between state-relate and item-related effects (see chapter 2). Thus as with the aforementioned autobiographical studies, there is a confound between mood and emotion. This has implications especially for the study by Dolan and colleagues since it was proposed therein that the anterior temporal cortex activity reflected (tonic) psychological 'set' or state associated with modulating emotional memory as opposed to (phasic) item-related activity. However, although a target-density manipulation was employed, no substantial evidence was provided that the anterior temporal cortex activity was not item-specific (as might be revealed through the employment of an event-related paradigm).

A more serious criticism relates to the employment of emotional vs. non-emotional stimuli (pictures or words) as retrieval cues. The first problem with this is that the properties of neutral and emotional stimuli differ on more psychological dimensions than just 'emotionality'. As discussed above, emotional stimuli, unlike emotionally neutral items, tend to belong to categories that are semantically cohesive, that is categories in which the constituent items share strong inter-item associations (Phelps, LaBar et al., 1998). There is also evidence that emotional items are more imageable but less concrete than neutral items (Campos, Marcos and Gonzalez, 1999). Therefore emotional stimuli may influence retrieval-related brain activation by virtue of their high levels of semantic cohesion, high levels of imagability and low levels of concreteness, factors which may act independently of emotion per se.

The third problem with employing emotional and non-emotional items as retrieval cues is that the nature of the test items is confounded with the nature of the information to be retrieved. As a result of this confound, differences in activity elicited between the emotional and non-emotional conditions could not be attributed to emotion-specific differences in retrieval processing. This third criticism, which is endemic to all studies that employ emotional and neutral stimuli as retrieval cues in investigations of the neural circuitry underlying emotional memory, is addressed in the final three experiments in this thesis. The issue (and relevant literature) is thus returned to in the introductions to these chapters.

The question of whether the mechanisms underlying the retrieval of information with emotional content are the same as those mediating retrieval of emotionally neutral information has also been addressed in an ERP study by Leiphart et al. (1993). This study investigated the ERP correlates of recognition memory for high- and low-emotional words. Although there were effects of emotionality in the behavioural data (more high- than low-emotion old words were correctly recognised and more low- than high-emotion new words were correctly rejected), and the ERPs were revealed to be sensitive to the old/new status of the words, there was no interaction between the old/new status of the words and the emotionality of the words in the ERP data. However the experiment used as stimuli high-emotion and low-emotion words which had been classified according to an emotional scale from 1.36 to 6.23 with an emotionality value of 3.2 being the cut-off point between high and low emotion words. This implies that all words used had some emotional content. As a result, when averaging across trials to form the ERPs, differences in emotional content of high- and low- emotional words may have been insufficient to elicit ERP emotionality effects.

A final issue relating to the retrieval of emotional information relates to a distinction between the retrieval of emotional items and retrieval of emotional context (see chapter 1 for definition of the distinction between items and context). The above studies investigated the retrieval of information wherein the emotion source was intrinsic to the stimuli employed. However, it is also known that emotion in the environment that is not intrinsic to a particular stimulus may still lead to enhanced recollection of that stimulus. For example, neutral words encoded in emotionally toned sentences are subsequently remembered better (as indexed by free recall) than neutral words encoded in neutral sentences (Phelps et al., 1997; Phelps et al., 1998). In addition, studies have shown that arousal due to white noise (Berlyne, Borsa, Craw, Gelman and Mandell) or physical exercise (Baron and Moore, 1987) will lead enhanced recall for neutral words. The neural circuitry and cognitive processing mediating the effects of emotional context on memory retrieval investigated in the final three experiments.

Proposed Experiments

The key points of the above review are summarised as follows. In general, emotion has an enhancing effect upon episodic memory. In some circumstances emotion enhances episodic memory through arousal-mediated amygdala activity. Alternatively, the valence of the emotional stimuli may affect retrieval processing, for example through mechanisms of semantic cohesion, accounting for the effects of emotion upon episodic memory. As yet, little is known about the neuroanatomical mediation of either of these types of influence at retrieval. There are two ways in which emotion might modulate neural activity mediating episodic retrieval of information. First, there might be enhancement of activity in networks supporting episodic retrieval of neutral information. Second, there might also be enhanced activity in regions known to be activated when emotional information is encountered in the environment.

As discussed in Chapter 3, brain activity associated with episodic memory for neutral information has been extensively investigated and such studies have resulted in a number of well-defined (haemodynamic and electrophysiological) memory effects. The results of this previous research allow for the manner in which emotion influences the neural circuitry underlying episodic retrieval to be directly investigated. Surprisingly, in light of the abundance of neuroimaging research investigating the neural circuitry underlying episodic retrieval, there is a virtual absence in the neuroimaging literature of studies investigating the neural circuitry underlying 'retrieval' for emotional vs. neutral events. The experiments in this thesis thus employ ERP and fMRI techniques to investigate memory for emotional information with the hope of redressing the imbalance in the literature. However, unlike the few aforementioned studies, the investigations are based upon a theoretical framework wherein emotional episodic memory is viewed as being subserved by dissociable mechanisms which; a) have been defined previously in either the memory and/or emotion literature and b) have quantifiable electrophysiological or haemodynamic indices/effects. The effect of emotion on established neuroimaging effects are addressed in the following experiments. The specific aspects of the influence of emotion upon memory which are to be investigated are summarised as follows.

The first distinction made is between memory for emotion mediated by 'arousal' and that mediated by 'valence'. This issue, which has been neglected in the neuroimaging literature, must be addressed if one wishes to interpret effects elicited in experiments investigating memory for emotional information. This issue is investigated in experiments 1 and 2 (chapters 5 and 6). In brief, old/new effects (specifically the left parietal effect) are sensitive to the semantic cohesiveness of stimuli employed and can therefore be used to index the extent to which emotion-modulated retrieval processing is driven by semantic cohesion.

A second distinction that is addressed intermittently throughout all of the experiments is between recognition memory driven by familiarity and that driven by recollection, and whether these processes differentially interact with emotionality manipulations employed. The influence of emotion specifically on recollection is addressed in experiment 4.

A final distinction made in this thesis is between memory for emotional items (i.e. whereby previously studied materials themselves have an emotive nature) and that for emotional context (i.e. whereby it is the environment in which a previously encountered stimuli was encountered that carries the emotionality) manipulation. Whereas (as with the previous neuroimaging experiments) experiments 1 and 2 investigate memory for emotional items, it will be shown in due course that a more optimal way of investigating memory for emotional information is to investigate memory for emotional context (thus avoiding confounds between the nature of the retrieval cue and the nature of the information to be retrieved).

Memory for emotional context is investigated in experiments 3 to 5 (chapters 7, 8 and 10). In brief, as discussed earlier, emotionally toned contexts enhance memory for pre-experimentally neutral stimuli (Phelps et al., 1997; Phelps et al., 1998). The main issue addressed in experiments 3 to 5 is whether retrieval of contextual emotional information enhances activity in the same neural systems that support the conscious recollection and subsequent retrieval processing of neutral information. This issue is addressed firstly by monitoring the effects of the emotionality manipulation on established ERP old/new effects (experiments 3 and 4). In addition the issue is addressed by employing fMRI (experiment 5) to assess whether activity in regions subserving the initial retrieval of episodic information (medial temporal/posterior cortical regions) (see Nyberg et al., 1996) and regions supporting the subsequent monitoring and evaluation of the retrieved information (e.g. prefrontal cortices; see Rugg et al., 1996) is increased during the retrieval of emotional relative to neutral information. Also addressed is whether emotion modulates retrieval processing through the engagement of emotion-sensitive structures which have been previously linked with processing (e.g. perceptual, encoding) of emotional information.

Chapter 5

Experiment 1: Electrophysiological correlates of Recognition Memory for Emotionally Negative and Neutral Words

Chapter Summary

Scalp recorded ERPs were used to investigate the neural activity elicited by emotionally negative and emotionally neutral words during performance in a recognition memory task. Behaviourally, the principal difference between the two word classes was that the false alarm rate for negative items was approximately double that for the neutral words. Correct recognition of neutral words was associated with three topographically distinct ERP memory 'old/new' effects: an early, bilateral, frontal effect which is hypothesised to reflect familiarity-driven recognition memory; a subsequent left parietally distributed effect thought to reflect recollection of the prior study episode; and a late onsetting, right-frontally distributed effect held to be a reflection of post-retrieval monitoring. The old/new effects elicited by negative words were qualitatively indistinguishable from those elicited by neutral items and, in the case of the early frontal effect, of equivalent magnitude also. However, the left parietal effect for negative words was smaller in magnitude and shorter in duration than that elicited by neutral words, whereas the right frontal effect was not evident in the ERPs to negative items. These differences between neutral and negative words in the magnitude of the left parietal and right frontal effects were largely attributable to the increased positivity of the ERPs elicited by new negative items relative to the new neutral items. Together, the behavioural and ERP findings add weight to the view that emotionally valenced words influence recognition memory primarily by virtue of their high levels of 'semantic cohesion', which leads to a tendency for 'false recollection' of unstudied items.

Introduction

Numerous studies have demonstrated that performance on episodic memory tasks is influenced by the emotional nature of the test items. Notably, recall of emotionally negative material (and, in some studies, positive material also) is enhanced relative to the recall of neutral items (e.g. Rubin and Friendly, 1986; Danion et al., 1995; Phelps et al., 1997). It has been suggested that differences in memory performance for emotional and non-emotional material arise through multiple mechanisms, two of the most important of which are ‘arousal’, and ‘semantic cohesiveness’ (Phelps et al., 1998). Items that are arousing (i.e. items that elicit significant autonomic responses as indexed, for example, by skin conductance) gain a mnemonic advantage over non-arousing items through the enhancement of their encoding and consolidation in memory. This advantage seems likely to be mediated at the neural level by the modulatory influence of the amygdala on hippocampal and cortical components of the network supporting episodic memory (Phelps et al., 1998; Hamann et al., 1999). By contrast, non-arousing emotional items (e.g. words with negative emotional valence) influence memory largely because, unlike emotionally neutral items, they tend to belong to categories that are semantically ‘cohesive’, that is, categories in which the constituent items share strong inter-item associations.

The foregoing distinction provides a useful framework in which to view findings of studies comparing memory for emotionally valenced and emotionally neutral words. With the exception of certain classes of item such as ‘taboo’ words, emotional and non-emotional words differ little in their arousing properties (LaBar and Phelps, 1998) raising the possibility that differences in memory for these two word classes are due mainly to differences in semantic cohesiveness. Consistent with this possibility, Phelps and LaBar (cited in LaBar and Phelps, 1998) found that when inter-item associations were controlled, the recall advantage normally found for emotionally valenced words over neutral items was eliminated. Also consistent are findings showing that the above-mentioned recall advantage does not extend to tests of recognition memory (e.g. Leiphart et al., 1993; Danion et al., 1995). In one of these studies (Danion et al., 1995), discrimination (d') between studied (old) and unstudied (new) words was lower for emotional than for neutral items (hit and false alarm rates were not reported). In the second study (Leiphart et al., 1993), emotional words were associated with a higher hit rate but, because this effect was offset by an equivalent elevation of the false alarm rate, recognition accuracy did not differ for the two word types.

The disparate pattern of findings for recall and recognition fit well with the idea that emotional valence exerts much of its effect on memory for words through the mechanism of semantic cohesion. The fact that emotional words generally belong to a relatively 'closed' semantic category means that recall for these items benefits for the same reasons that underlie the recall advantage for words from any semantically categorised set relative to uncategorised words (Baddeley, 1997). In the case of recognition, the findings of Leiphart et al. (1993) suggest that emotionally valenced words may act like the 'related lures' that elicit high false alarm rates in studies of 'false recollection'. In these studies (e.g. Roediger and McDermott, 1995; Robinson and Roediger, 1997; Schacter et al., 1997, see Johnson and Rye, 1998 for review) participants typically study lists of semantically related items and subsequently attempt to discriminate between these items and two kinds of new word - semantic associates of studied words (related lures), and words semantically unrelated to items that had been shown at study (unrelated lures). Relative to unrelated lures, related lures generate high false alarm rates, with participants reporting many of these responses to be based on a recollection of the lure as a member of the study list ('Remember' responses, e.g. Roediger and McDermott, 1995). Neuroimaging and electrophysiological evidence suggest that the illusory recollection of related lures relies on much of the same neural circuitry that underlies veridical recollection (Schacter, 1996; Johnson, Nolde et al., 1997; Düzel et al., 1997; Schacter et al., 1997). Since sets of emotionally valenced words tend to be semantically and associatively related, it is easy to see how these items might also engage processes supporting false recollection.

According to the foregoing analysis, therefore, emotionally valenced words do not exert their effect on memory by virtue of their emotionality *per se*. Rather, they do so because emotionally valenced words have, on average, stronger inter-item associations than do sets of unselected neutral words. Thus, memory for emotional words is mediated not by systems or processes to which these items have privileged access, but by the same cognitive operations that support memory for non-emotional material.

In the present experiment, the foregoing proposal is assessed by investigating the neural correlates of recognition memory for emotionally valenced and neutral words using event-related brain potentials (ERPs). In general terms, the proposal that recognition memory for the two classes of word engages equivalent cognitive operations can be assessed by determining whether the memory-related ERP effects they elicit differ with respect to scalp distribution. If the effects for emotional and neutral words do differ in this respect, it would indicate that memory for the two kinds of material is neurally (and, therefore, most likely functionally) dissociable (Rugg and Coles, 1995). Such a finding would be inconsistent with the proposal that memory for emotional and neutral words relies on functionally equivalent memory mechanisms.

The results of previous research investigating the ERP correlates of recognition memory allow predictions arising from the 'semantic cohesiveness' hypothesis to be addressed more specifically. It has long been known that, relative to new words, ERPs elicited by correctly classified old words in tests of recognition memory are more positive-going – the so-called ERP 'old/new' effect (see Rugg, 1995 for review). Recent work (for review see Rugg and Allan, 2000; see also Rugg et al., 1998b) has led to the identification of three old/new effects which appear to index functionally distinct aspects of recognition. For present purposes, the most important effect is one which onsets around 400-500 msec post-stimulus, and is maximal over the left parietal scalp (the 'left parietal' old/new effect). The effect appears to be a neural correlate of the episodic retrieval (recollection) of study items (Wilding, 2000) and, in studies of false recollection (e.g. Johnson et al., 1997; Düzel et al., 1997) is elicited by both genuinely old words and related lures. Another old/new effect involves an earlier (ca. 300-500 msec), bilateral shift with a frontal distribution. Rugg et al., (1998b) proposed that this effect was a neural correlate of familiarity-based recognition. This is a form of recognition memory held by some authors to be independent of recollection, and to underlie recognition judgements associated with 'Know' rather than 'Remember' responses (Tulving, 1985b; Gardiner et al., 1996). The third old/new effect onsets quite late (ca. 500-700 msec), persists for a second or more, and is distributed over the right frontal scalp (Wilding and Rugg, 1996; Donaldson and Rugg, 1998). The 'right frontal' old/new effect is held to reflect processes that operate on the products of memory retrieval (Rugg and Allan, 2000).

If, as suggested above, unstudied emotionally valenced words in tests of recognition memory act like associative lures in studies of false recollection, these items should be difficult to discriminate from studied emotional items because of their tendency to elicit 'recollection' of their study presentation. As a consequence, unstudied emotional items should be associated with an elevated false alarm rate relative to unstudied neutral words. Furthermore, even in trials on which unstudied emotional items are correctly classified as new, the tendency of these items to elicit illusory recollection might be expected to both impede the decision to respond 'new' and, critically, to be manifest in a pattern of neural activity – the left parietal ERP effect – signifying the engagement of neural systems supporting episodic retrieval. Thus, relative to the left parietal old/new effect elicited by neutral words, the effect elicited by emotionally valenced words should be smaller in magnitude. Furthermore, the difference in the magnitude of the left parietal effects elicited by the two word types should be carried mainly by the ERPs elicited by new items, those elicited by emotional words exhibiting the greater positivity.

These predictions were tested by recording ERPs while participants discriminated between studied and unstudied emotionally negative and neutral words. For the reasons already noted, it was expected that negative words would give rise to an excess of false alarms, a smaller left parietal old/new effect, but that there would be no evidence for the recruitment of memory mechanisms additional to those engaged by neutral items. Further, to the extent that emotional valence influences recognition memory exclusively through its effects on recollection, the ERP old/new effect held by Rugg et al. (1998b) to index familiarity-driven recognition should be unaffected by this variable.

Method

Participants

20 young male and female right-handed participants were employed in the study. Each participant gave informed consent prior to participation in the study and all were remunerated at the rate of five pounds per hour. 4 participants' data were discarded prior to data analysis due to excessive electro-oculographic artefact leading to a failure to provide 16 or more artefact free trials for one or more of the ERP categories. The 16 participants whose data were analysed consisted of 11 females and 5 males.

Experimental Material

The critical stimuli consisted of 224 words selected from The Balanced Affective Word Project (a corpus of words normed for emotional valence; Siegle, 1998). Half of these words were emotionally negative (e.g. FRIGHT), whereas the remainder were emotionally neutral (e.g. MENTION). Five neutral buffer words were also used. The words varied in length between three and nine letters. All words were semantically distinct from each other in the sense that derivatives of words from a common root were not used.

Two study lists (A and B) were created, each containing a set of 56 negative and 56 neutral words. The words in the study lists were randomly ordered and a neutral buffer word was added to the beginning and end of each list. Two test lists (1 and 2) were created using all 224 negative and neutral critical words in two randomised orders, with a buffer word added to the beginning of both lists.

Procedure

The experiment took the form of a single study-test cycle. The combination of study and test list used was counterbalanced across participants, thus ensuring there was no correlation between word type and old/new status.

The stimuli were presented in central vision on a computer monitor (white upper case words on a dark screen). Each word subtended a maximum vertical visual angle of approximately 0.4 degrees and a maximum horizontal angle of approximately 1.2 degrees. Study words were presented with their first letter replacing the fixation character. Test words were presented with the third letter replacing the fixation character.

Participants were tested in a sound attenuated recording booth. Prior to the experiment, participants were fitted with an electrode cap. Participants were informed that the experiment consisted of two parts but they were not informed that the second part would involve a memory test. An interval of around 5 minutes separated the study and test phases, and during this time participants were instructed to relax.

Study Phase

Each trial consisted of a presentation of the word for 300 msec, followed immediately by the restoration of the fixation character. This character remained in view until the next trial was initiated (see below). Participants were required to give an affective rating to each study word using a scale that ranged from –3 (negative) through 0 (neutral) to +3 (positive). They were instructed to make positive ratings to words they associated with feelings of happiness, content or satisfaction, negative ratings to words they associated with unpleasant feelings of sadness, anger or anxiety, and neutral ratings for words which were neither negative nor positive. The experimenter initiated each trial after recording the response to the preceding item.

Test Phase

Participants were presented with one of the two test lists. Each trial consisted of the presentation a fixation character for 2100msec, followed by a 124msec period during which the screen was blank. This period was followed by the display of a test item for 300msec, following which the monitor was blanked for 2700msec. Participants were required to judge whether or not each word had appeared previously in the study phase. Responses were made by button press using one or other index finger. The mapping of keys to response type was counterbalanced across participants. Participants were instructed to relax, to keep body movements to a minimum, and to blink only when the fixation character was in view. The test phase was computer controlled. Responses faster than 300msec or slower than 2500msec were treated as errors.

ERP Recording

EEG was recorded from 25 tin electrodes embedded in an elasticated cap and from an electrode placed on the right mastoid process. All channels were referenced to a left mastoid electrode, and re-referenced off-line to represent recordings with respect to linked mastoids. EOG was recorded bipolarly from electrodes placed above the supraorbital ridge of the right eye and on the outer canthus of the left eye. EEG electrode locations were based upon the International 10-20 system (Jasper, 1958). Scalp electrodes were located over the midline (Fz, Cz, Pz), and at the following additional locations: lateral frontal (FP1/FP2, F3/F4, LF/RF (75% of the distance from Fz to F7/8), and F7/F8), central/anterior temporal (C3/C4, LT/RT (75% of the distance from Cz to T3/4), and T3/T4), parietal/posterior temporal (P3/P4, LP/RP (75% of the distance from Pz to T5/6), T5/T6), and occipital (O1,O2) (Figure 5.1) Data were sampled at a rate of 8msec per point and digitised with 12 bit resolution. The duration of the recording epoch was 2048msec with a 104msec pre-stimulus baseline period.

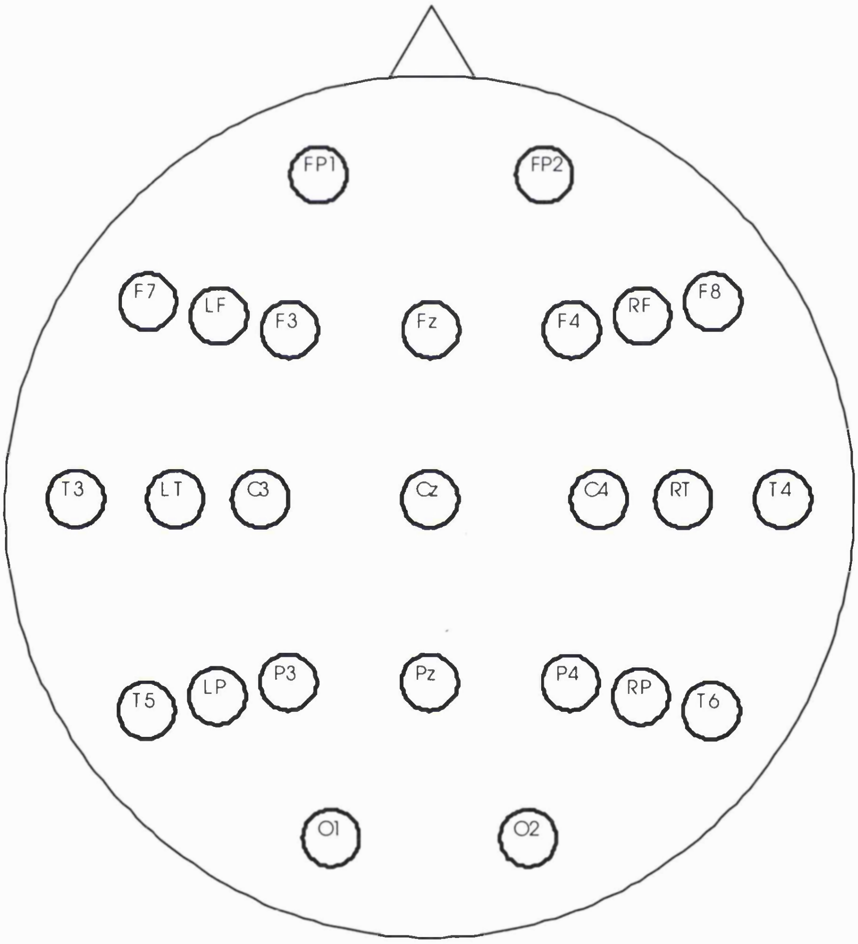


Figure 5.1 Electrode montage of the 25 sites employed in Experiments 1 to 3

All channels were amplified with a bandpass of 0.032-35Hz. Trials on which base to peak EOG activity exceeded 98 microvolts were rejected, as were trials on which A/D saturation occurred, or on which baseline drift across the recording epoch (i.e.

amplitude of the first point minus the amplitude of the last point of the epoch) exceeded ±55 microvolts in any EEG channel.

ERPs were formed for 4 response conditions: Correctly recognised old neutral words (neutral hits); correctly rejected new neutral words (neutral correct rejections), correctly recognised old negative words (negative hits), and correctly rejected new negative words (negative correct rejections). The waveforms were smoothed with a 5 point binomally weighted filter. There were insufficient trials to form ERPs to items associated with error trials (i.e. misses and false alarms).

Results

Behavioural Data

The mean rating assigned to the negative words was -1.73, (across participant sd = 0.35; range –2.38 to -1.07) whereas the mean rating for the neutral words was 0.52, (across participant sd = 0.40; range -0.04 to 1.30). These means differed reliably (t15 = 15.28, $p < 0.001$). For every participant the mean rating given for the negative words was significantly lower than that given for the neutral items (minimum t110 = 11.66, $p < 0.001$).

Hit and correct rejection rates for the neutral and negative items, along with discrimination (pH-pFA, or 'Pr') and bias ('Br') indices (Snodgrass and Corwin, 1988), are shown in table 5.1. Pr for neutral items was significantly greater than that for negative items (t15 = 5.01, $p < 0.001$). Bias also differed significantly between word types (t15 = 7.45, $p < 0.001$), such that participants were more willing to respond 'yes' to negative items. Additional t tests revealed that hit rates and false alarm rates were both significantly greater for negative items (t15 = 2.93, $p = 0.01$, and t15 = 6.28, $p < 0.001$ respectively).

Table 5.1 Experiment 1: Accuracy data.
Columns 1 and 2: Mean proportion (standard deviation in brackets) of hits and correct rejections to each word type. Column 3 and 4: Discrimination Index (Pr) and bias indices (Br).

WORD TYPE	HIT	CR	Pr	Br
NEUTRAL	0.83 (0.10)	0.86 (0.12)	0.73	0.41
NEGATIVE	0.89 (0.07)	0.66 (0.14)	0.57	0.72

Reaction time (RT) data are shown in table 5.2. ANOVA of the RTs for hits and correct rejections revealed main effects of response type (F(1,15) = 10.32, $p < 0.01$), valence $(F(1,15) < 17.90, p = 0.001)$, and an interaction between these factors $(F(1,15) = 17.46, p < 0.001)$. Tukey HSD tests revealed that RTs were faster for correct rejections to the neutral rather than the negative items, and that RTs for hits were faster than those for correction rejections in the case of the negative items only. A further test revealed that RTs to false alarms were faster for negative words ($t15 = 2.81, p < 0.01$).

Table 5.2 Experiment 1: Reaction time data (msec)
Mean reaction times (standard deviations in brackets) for hits, correct rejections and false alarms to each word type.

WORD TYPE	HIT	CR	FALSE ALARM
NEUTRAL	999 (242)	1097 (267)	1313 (272)
NEGATIVE	975 (249)	1184 (268)	1188 (292)

ERP Data

The mean numbers of trials (range in brackets) contributing to the ERPs for neutral hits, neutral correct rejections, negative hits and negative correct rejections were 38 (22-49), 39 (23-50), 38 (20-50) and 29 (18-38) respectively. The proportion of trials lost because of artefact was 18%, 19%, 22% and 20% respectively. These proportions did not differ significantly. Grand average waveforms from selected lateral and midline sites are shown overlaid according to response category and valence in figures 5.2 and 5.3 respectively. ERPs begin to diverge as a function of response category and word type from around 300msec post-stimulus onset. ERPs to old words become more positive-going than those to new words, and ERPs to negative items become more positive-going than those to the neutral items. From approximately 500 msec post-stimulus, old/new effects demonstrate a left posterior maximum. From around 800 msec post-stimulus, the old/new effects for negative words are no longer evident, whereas those for neutral words begin to exhibit a right frontal maximum which extends for approximately a further 500 msec.

ERPs were quantified by measuring (with respect to the mean of the pre-stimulus baseline) the mean amplitudes of 4 consecutive latency regions (300-500 msec, 500-800 msec, 800-1100 msec, 1100-1400 msec). These intervals correspond closely with the regions chosen for analysis in previous studies (e.g. Wilding and Rugg, 1996; Donaldson and Rugg, 1998).

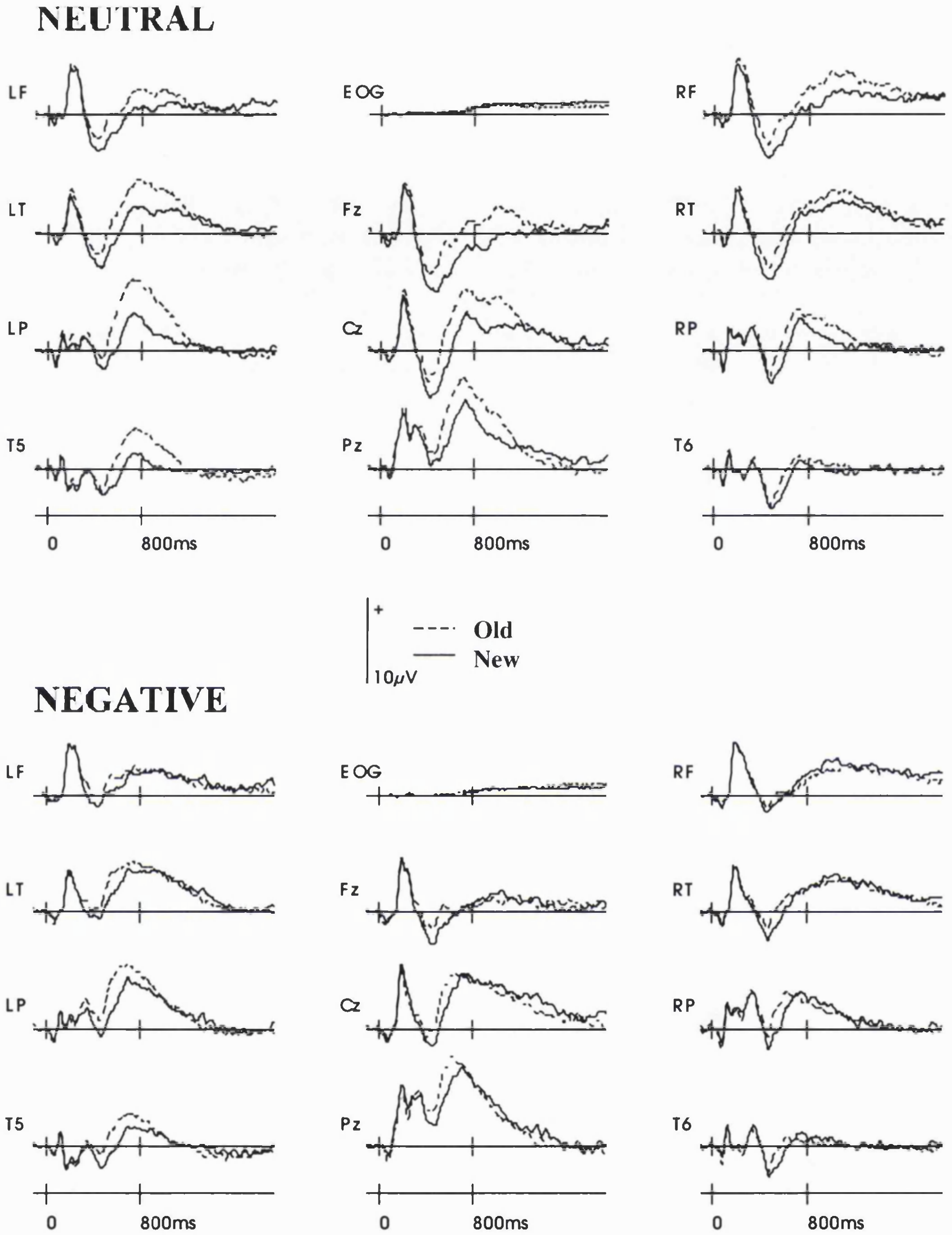
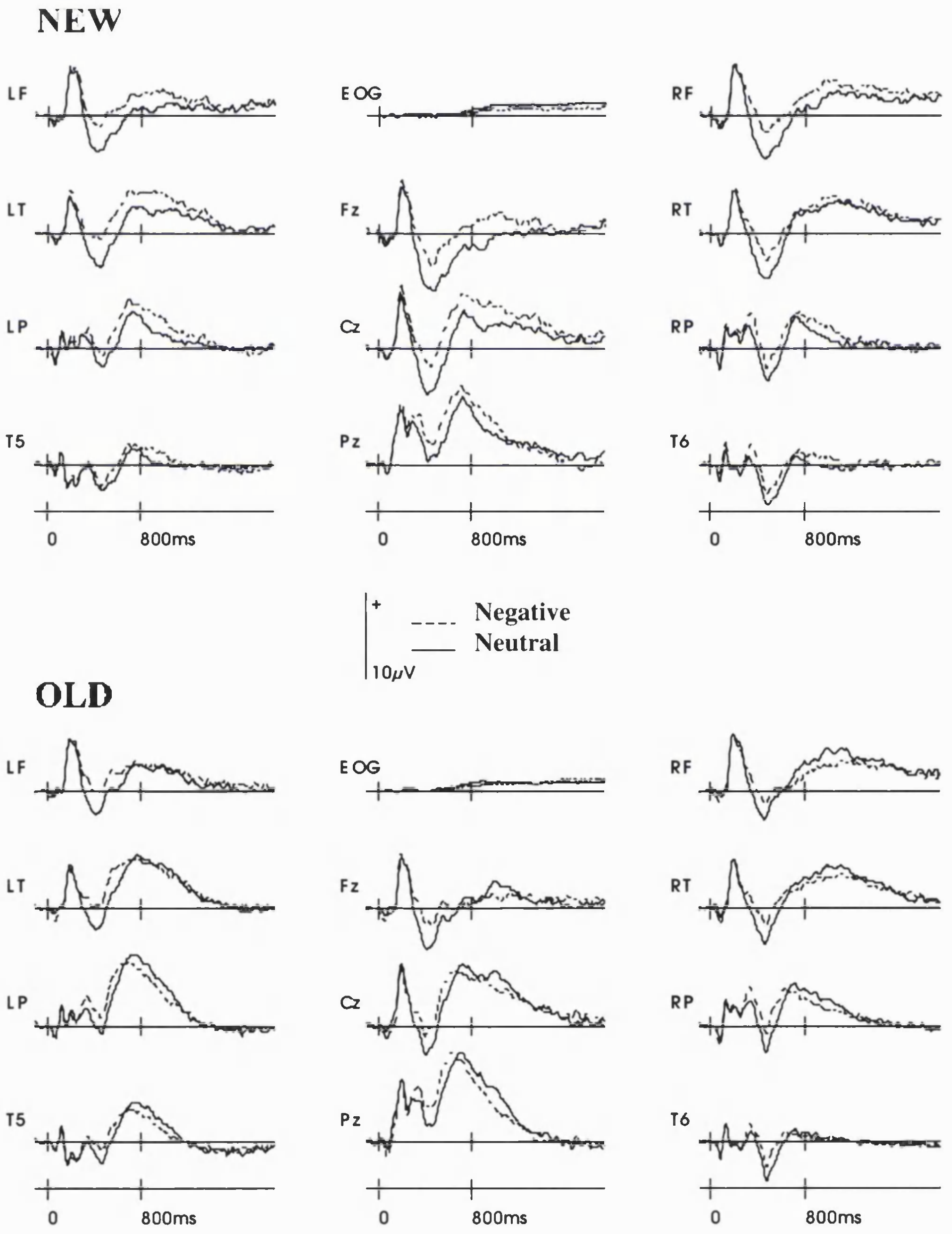


Figure 5.2. Experiment 1: Top: Grand average ERP waveforms elicited by correctly classified old and new neutral words. Bottom: Grand average ERP waveforms elicited by correctly classified old and new negative words.
Electrode locations are described in the text. Gain for the EOG channel is x5 lower than for the EEG.

Two sets of analyses were performed on these data. The first set investigated differences in the amplitude of ERP effects associated with the factors of valence and category. The second set tested for differences in the scalp distribution of the effects, and whether the distribution of these effects changed over time. In all ANOVAs degrees of freedom were corrected for non-sphericity by application of the Greenhouse-Geisser procedure (Keselman and Rogan, 1980) and F ratios are reported with corrected degrees of freedom. Data employed in the topographic analyses were rescaled to eliminate the confounding effects of between-condition and between-epoch differences in amplitude (McCarthy and Wood, 1985).

Figure 5.3. Experiment 1: Top: Grand average ERP waveforms elicited by correctly classified neutral and negative new words. Bottom: Grand average ERP waveforms elicited by correctly classified neutral and negative old words.
Gain for the EOG channel is x5 lower than for the EEG.



Mean Amplitude analyses

To assess amplitude differences between the conditions, ANOVAs were conducted for each latency region on the data from lateral frontal (F7/8,LF/RF, F3/4), temporal/central (T3/4, LT/RT, C3/4), and parietal (T5/6, LP/RP, P3/4) electrode sites, employing the factors of valence (negative vs. neutral), response category (hit vs. correct rejection), hemisphere, location (frontal, temporal/central, parietal) and site (inferior, middle, superior). The results of these ANOVAs with respect to the valence and response category factors are shown in table 5.3. The ANOVAs were followed up by additional subsidiary ANOVAs as reported below.

As can be seen in table 5.3, analysis of the 300-500 msec latency range revealed effects of valence and response category, reflecting the greater positivity of ERPs elicited by negative words and hits respectively. Crucially, while the factor of valence interacted with the factors of location, hemisphere, and site (see table 5.3), it did not interact with response category (maximum F = 1.57).

Table 5.3 Experiment 1: Mean amplitude analyses, significant effects summary
Table summarising the results of ANOVAs during the 4 latency intervals shown. Only significant effects involving the condition factors (word type, response category) are reported. ON = old/new (response category), NE = neutral/negative (valence), CH = frontal/anterior/temporal location, HM = hemisphere (left, right), ST = electrode site (Inferior, Mid-lateral, Superior).
Significant F values of interactions involving the factors of valence and response category are shown in bold.

	300-500msec	500-800msec	800-1100msec	1100-1400msec
NE	F(1,15)=31.6,p<0.001	F(1,15)=8.4,p<0.025	-	-
ON	F(1,15)=6.9,p<0.025	F(1,15)=11.1,p=0.005	-	-
NExON	-	**F(1,15)=4.2,p=0.058**	**F(1,15)=14.3,p<0.0025**	-
NExCH	F(1.6,24)=19.6,p<0.001	-	-	-
ONxHM	-	F(1,15)=22.1p<0.001	F(1,15)=7.4,p=0.01	-
ONxST	-	F(1,15.4)=6.5,p<0.025	F(1.1,16.1)=4.7,p<0.05	-
NExONxST	-	**F(1.1,16.2)=9.9,p=0.005**	**F(1,15.7)=8.5,p=0.01**	-
NExCHxHM	-	F(1.9,28.5)=7.3,p<0.005	F(1.5,22.6)=4.3,p<0.05	-
NExCHxST	F(2.6,38.4)=6.6,p<0.005	-	-	F(2.5,37.2)=3.1,p=0.05
NExHMxST	F(1.8,26.9)=6.6,p<0.01	F(1.5,22.9)=5.9,p=0.01	F(1.4,20.4)=5.1,p<0.05	-
ONxCHxHM	-	F(1.7,25.3)=6.7,p<0.01	-	-
NExONxCHxHM	-	**F(1.4,21.5)=6.0,p=0.01**	**F(1.7,25.5)=9.5,p=0.001**	**F(1.3,19.9)=4.5,p<0.05**

A further ANOVA was conducted on the data from the 300-500 msec latency region. This focused on the three sites – F3, Fz, F4 - at which the putative ERP correlate of familiarity described by Rugg et al. (1998b) was of maximum amplitude in that study.

The waveforms from these sites are shown in figure 5.4. The ANOVA revealed significant effects of valence ($F(1,15) = 26.53$, $P < 0.001$) and response category ($(F(1,15 = 7.67$, $p < 0.025$), but no interaction between these factors (max $F(1.6\ 24.4) = 2.27$, $p > 0.1$). Separate ANOVAs showed that the effect of valence was reliable for both old and new items ($F(1,15) = 18.21$, $p < 0.001$ and $F(1,15) = 18.68$, $p = 0.001$ respectively), and that the effect of response category was reliable for both neutral and negative items ($F(1,15) = 5.95$, $p < 0.05$, and $F(1,15) = 5.14$, $p < 0.05$, respectively).

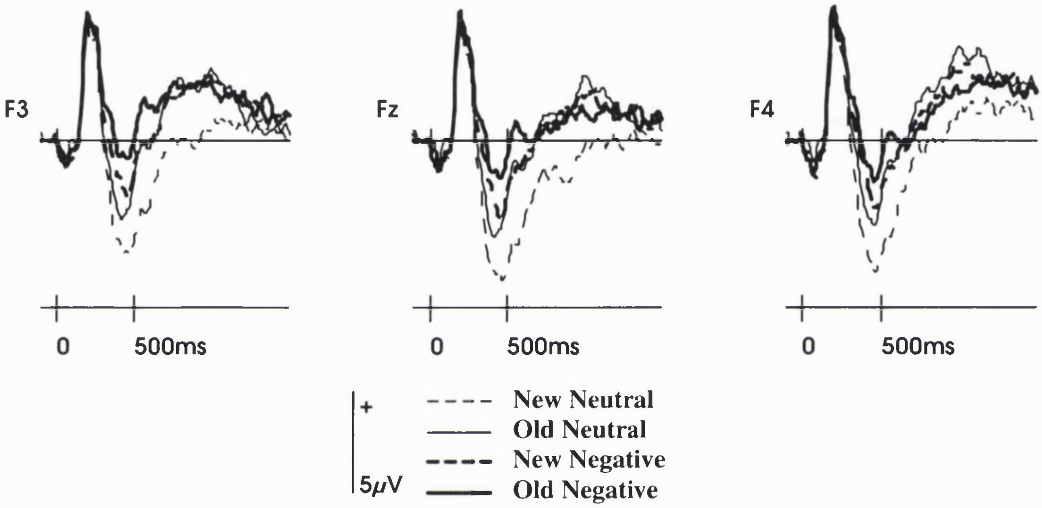
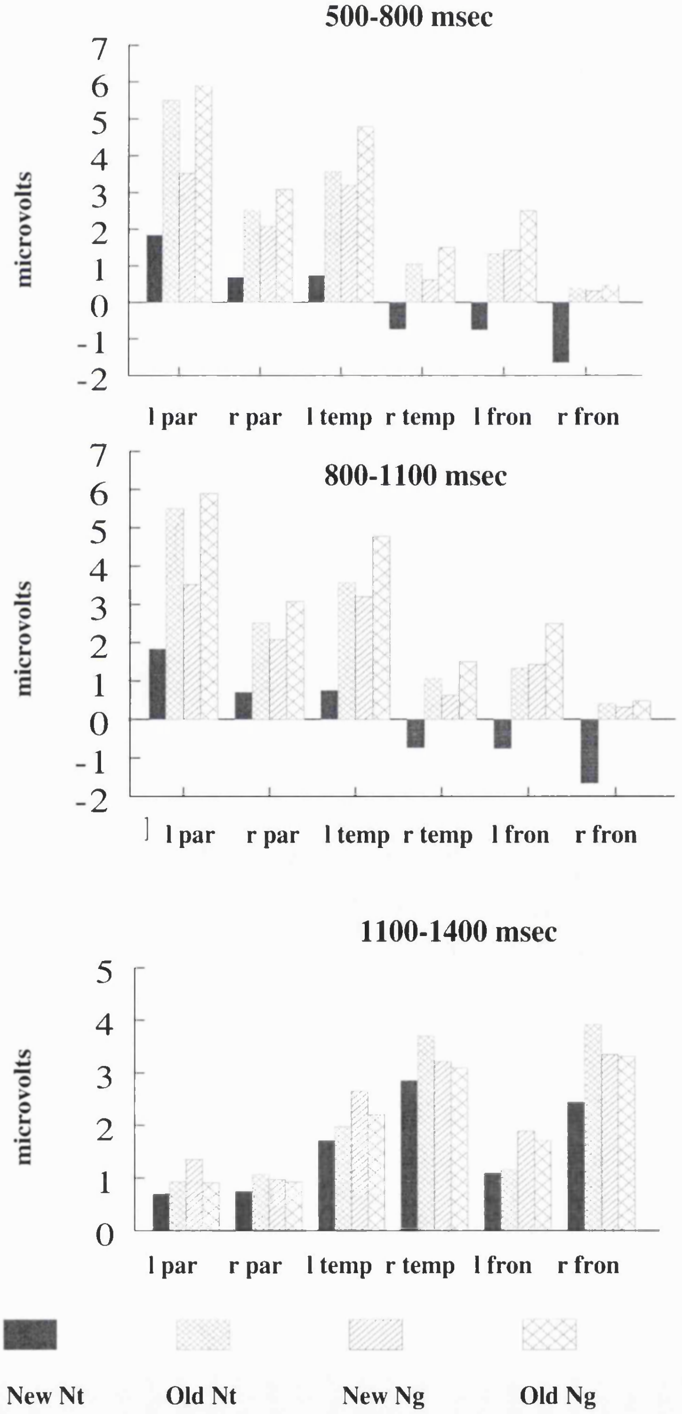


Figure 5.4 Experiment 1: Grand average waveforms for all word types (neutral; negative; old; new) from a subset of frontal electrode sites (F3, Fz, F4).

Table 5.3 shows that the ANOVA of data from the 500-800 msec region revealed main effects of valence and response category, along with three interactions (one of marginal significance) involving these factors. As can be seen in figure 5.4, old/new effects in this latency range showed a left posterior maximum for both classes of word. Furthermore, while old/new effects were larger for the neutral than for the negative words at all scalp regions, the disparity between the effects varied across regions.

In order the assess the reliability of the old/new effects elicited by each class of word, separate ANOVAs were conducted on the data for the neutral and negative items. The ANOVA for the neutral items revealed a main effect of response category ($F(1,15) = 20.64$, $p < 0.001$), an interaction between response category and hemisphere ($F(1,15) = 15.10$, $p = 0.001$), and a three way interaction between response category, location and hemisphere (F(1.5, 22.2) = 12.33, p = 0.001). The effects reflect the robust nature of the old/new effects elicited by the neutral items, and their left posterior maximum. ANOVA of the data for the negative items revealed interactions between response category and hemisphere (F(1,15) = 8.36, p = 0.01), and between response category and location (F(1.3,19.7) = 4.35, p < 0.05). These effects reflect the tendency for the old/new effects elicited by these items to be left lateralised, and in addition to show an anterior-posterior gradient (see figure 5.5).

Figure 5.5. Experiment 1: Differences in mean amplitude for old negative minus new negative, and old neutral minus new neutral, for the 500-800 msec, 800-1100 msec, and 1100-1400msec epochs.



Amplitude measures are averaged over the electrode site indicated and the sites immediately adjacent to it.

A final set of analyses were conducted on the data from the 500-800 msec latency in order to focus specifically on the left parietal old/new effect, the putative ERP signature of episodic retrieval (see introduction). An ANOVA was conducted on the data from the left parietal electrode alone. This revealed effects of valence ($F(1,15 = 5.40$, $p < .05$) and response category ($F(1,15) = 33.90$, $p = 0.001$), as well as a marginally significant interaction between these factors ($F(1,15) = 4.32$, $p < 0.06$). Separate ANOVAs revealed that the effects of response category were reliable for both the neutral and negative items ($F(1,15) = 50.05$, $p < 0.001$, and $F(1,15) = 12.89$, $p < 0.005$, respectively). Two further ANOVAs revealed that the waveforms elicited by the new negative words were more positive than those for the new neutral items ($F(1,15) = 7.09$, $p = 0.025$), whereas no such effect was evident for the ERPs to the two classes of old item ($F(1,15) < 1$).

As shown in table 5.3, ANOVA of data from the 800-1100 msec region revealed three interactions between the factors of valence and response category, including the four-way interaction between these factors, location and hemisphere. As shown in figure 5.5, these effects reflect the left posterior maximum of the old/new effects in this latency range and the apparent absence of such effects in the ERPs to negative words.

As for the previous latency region, old/new effects in the 800-1100 msec region were assessed separately for neutral and negative words. ANOVA of the data for the neutral items revealed a main effect of response category ($F(1,15) = 8.62$, $p = 0.010$), and interactions between response category and hemisphere ($F(1,15) = 7.04$, $p < 0.025$), and between response category, location and hemisphere ($F(1.7,25.8 = 8.56$, $p < 0.005$). The effects reflect the left posterior distribution of the old/new effects for these items. ANOVA of the data for the negative items revealed no effects involving the factor of response category.

Once again, a further set of analyses was directed toward the left parietal electrode alone. An initial ANOVA revealed a significant effect of response category ($F(1,15) = 19.12$, $p = 0.001$), and a response category x valence interaction ($F(1, 15) = 14.62$, $p < 0.01$). Further ANOVAs revealed a reliable old/new effect for the neutral items ($F(1,15) = 38.88$, $p < 0.001$) but not for the negative items. A final pair of ANOVAs indicated that the ERPs for new negative words were more positive than those for new neutral items ($F(1,15) = 8.63$, $p = 0.01$), whereas the reverse pattern was found for the ERPs to old words ($F(1,15) = 9.02$, $p < 0.01$); (see figure 5.5).

ANOVA of the 1100-1400msec data revealed yet another four way interaction between valence, response category, anterior/posterior locality and hemisphere (table 5.3). Figure 5.5 shows that old/new effects in this latency region were confined largely to ERPs elicited over the right anterior scalp by neutral words. In keeping with the impression given by the figure, a further ANOVA confined to data from the frontal sites alone gave rise to an interaction between valence, response category, and hemisphere ($F(1, 15) = 8.46, p < .025$), as well as to an interaction between valence, response category and site ($F1.3,19.8 = 4.62, p < .05$). ANOVAs performed on these data for the two word classes separately revealed, for the neutral items, interactions between response category and hemisphere, and response category and electrode site ($F1,15 = 8.56, p < .01$, and $F1.3,18.9 = 4.18, p < .025$, respectively). These effects reflect the tendency for the old/new effects elicited by these words to be greater over the right than the left hemisphere, and at superior rather than inferior sites. For the negative items, the ANOVA revealed no effects involving the factor of response category.

Topographic Analyses

Four sets of topographical analyses were performed. The first set compared the scalp distributions of the old/new effects (i.e. the differences in voltage between the ERPs elicited by correctly classified old and new words) for negative and neutral words between 300 and 500 msec. These distributions are illustrated in figure 5.6. ANOVA (factors of electrode site and valence) of these data revealed no evidence of a valence x site interaction ($F = 1$), indicating that the two scalp distributions are statistically equivalent.

A second analysis contrasted the topographies of the foregoing old/new effects with the effects of valence in the same latency range, that is, over the time interval in which the analyses of the mean amplitudes between 300 and 500 msec suggested that old/new and valence effects were additive. The old/new effects consisted of difference scores (old-new) collapsed over the factor of valence. Valence effects consisted of the difference scores (negative – neutral) collapsed over the factor of response category. The topographies of the two effects are illustrated in figure 5.7, where it can seen that each displays a mid-frontal maximum.

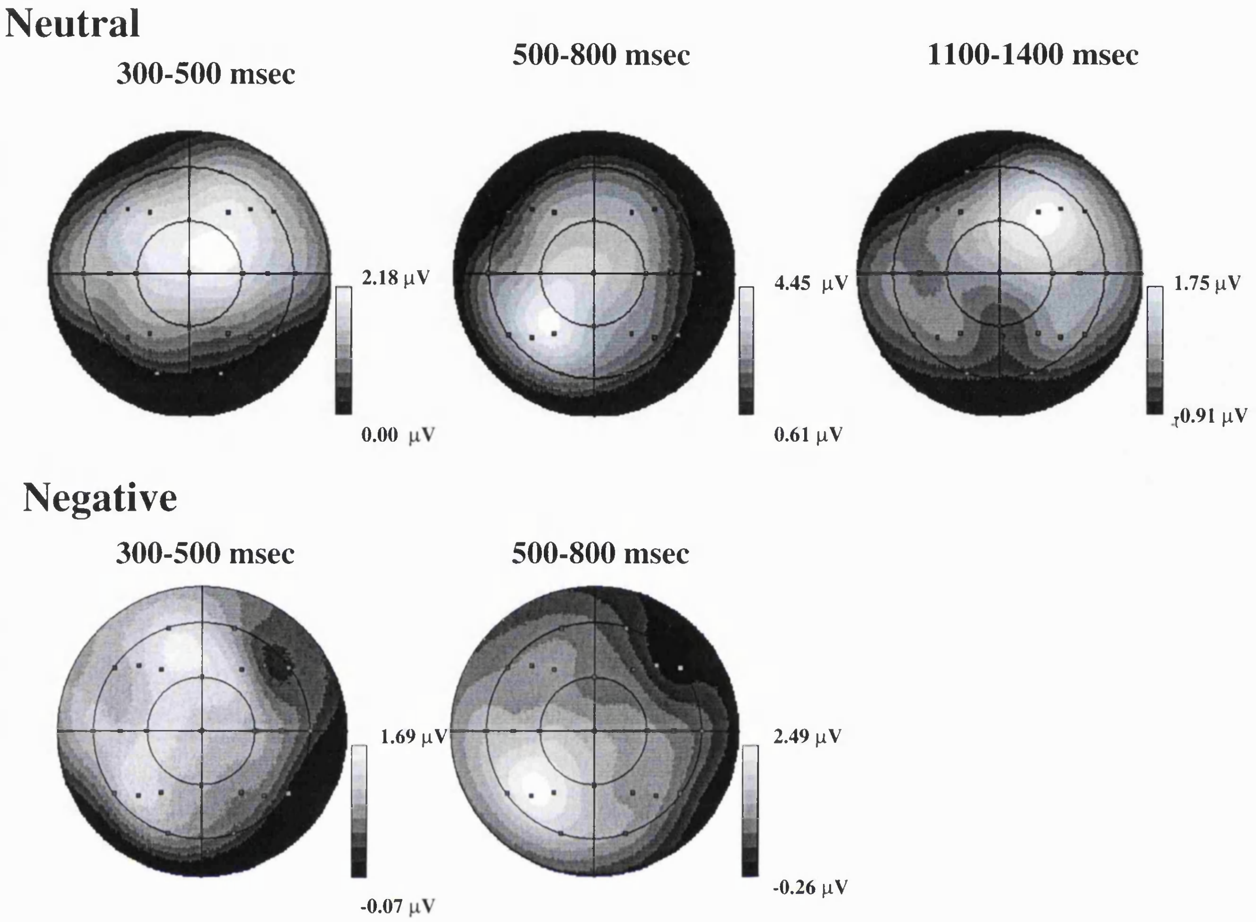


Figure 5.6. Experiment 1: Topographic maps illustrating the distribution of the differences between ERPs to correctly classified old and new neutral words (upper row), and between ERPs to correctly classified old and new negative words (lower row), in successive latency regions.

Unsurprisingly, given their similarity, an ANOVA contrasting these topographies gave rise to a site effect ($F(3.6,53.7) = 7.38$, $p < .001$), but not to a site x condition interaction ($F < 1$).

A third analysis compared the topographies of the old/new effects elicited by neutral and negative items in the 500-800 msec latency region (i.e. the only region post-500 msec in which effects were reliable for the negative words). The scalp distributions of these effects are illustrated in figure 5.6, where it can be seen that both show a strong left posterior focus. ANOVA of these data revealed a reliable site effect ($F(3.9, 58.7) = 4.40$, $P < 0.005$, but no evidence of a site x valence interaction ($F = 1.3$).

The final set of analyses compared the scalp distributions of the old/new effects elicited by the neutral words as a function of latency region, in order to confirm that the effects do indeed reflect the contributions of generator configurations that differ over time. The comparison was conducted across the three latency regions – 300-500, 500-800, and 1100-1400 msec - in which old/new effects appeared to show the most disparate distributions (see figure 5.6). ANOVA revealed a significant site by latency region interaction ($F(4.9, 73.3) = 4.06$, $p < .005$), indicating that the old/new effects for the neutral words do indeed differ with time. As shown in figure 5.6, these distributions initially evolve from a fronto-central to a left parietal maximum, and culminate in a right frontal focus.

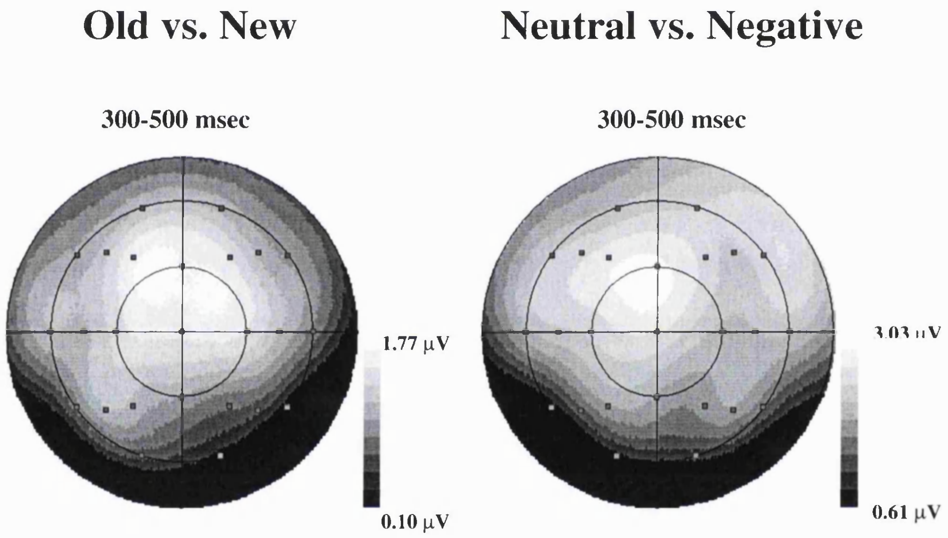


Figure 5.7 Experiment 1: Topographic maps illustrating the distribution of the differences between correctly classified old and new items (left), and between neutral and negative items (right), in the 300 msec – 500 msec epoch.

Summary of ERP Results

Reliable old/new effects were elicited by negative and neutral words in both the 300-500 and 500-800 msec latency regions. In the first of these regions, the effects had a fronto-central scalp distribution, whereas in the later region their topography showed a left parietal maximum. Neither the magnitude nor the scalp topography of the old/new effects differed according to valence in the 300-500 msec region. In the 500-800 msec region, the scalp topography of the old/new effects elicited by the two classes of word was again equivalent, but the magnitude of the effects was greater for the neutral items. This difference was largely due to the enhanced positivity of the ERPs to new negative items, rather than an attenuation of the waveforms elicited by old negative words. From 800 msec onwards, old/new effects were reliable for the neutral items only, and evolved with time from a left posterior to a right frontal focus.

Discussion

Performance Data

Recognition memory was poorer for negative than for neutral items. Crucially, this difference in recognition accuracy was entirely due to a marked difference in the rate of false alarms elicited by the two classes of word (34% vs. 14% for negative and neutral items respectively). These findings are broadly consistent with previous research investigating recognition memory for emotionally valenced words (e.g. Leiphart et al., 1993; Danion et al., 1995) and are well accounted for by the 'semantic cohesiveness' hypothesis outlined in the introduction. Specifically, it is proposed that the excessive false alarm rate for negative words reflects the same mechanisms that give rise to false recollection effects in studies investigating recognition memory for semantic associates of emotionally neutral study items (Robinson and Roediger, 1997).

The RT data add support to the foregoing hypothesis. Participants were some 100 msec quicker to respond correctly to new neutral words than to new negative words. By contrast, false alarm responses to negative words were 125 msec faster than those to neutral words. This pattern of results presumably reflects the propensity of new negative items to elicit information which is either difficult (in the case of correct rejections) or impossible (in the case of false alarms) to discriminate from that associated with a veridical memory of the study episode.

ERP Effects

Between 300 and 500 msec post-stimulus ERPs were modulated by both the valence and the study status of the test items. Crucially, however, these two factors did not interact with respect to either the magnitude of their effects, or their scalp topographies. To the extent that Rugg et al., (1998b) are correct in their proposal that frontally distributed old/new effects in this latency range reflect familiarity-driven recognition rather than episodic retrieval (recollection), these findings suggest that valence has little effect on familiarity. This conclusion adds weight to the proposal (see below) that valence influences recognition memory primarily through its effects on recollection.

Valence exerted a marked effect on ERPs between 300 and 500 msec. Specifically, neutral items elicited a fronto-centrally distributed negative-going deflection, peaking around 400 msec, that was approximately $3\mu V$ greater than the deflection elicited by negative words. One possibility is that this effect reflects the modulation of one or more of the generators of the 'N400', an ERP component well known for its sensitivity to semantic relatedness and association (Kutas and Hillyard, 1980; Rugg, 1985; Bentin, McCarthy and Wood, 1985; Holcomb, 1988). According to this hypothesis, the high level of inter-item association between members of the negatively valenced word set meant that these items tended to prime one another semantically, leading to an attenuation of N400 in a fashion similar to that seen in studies of semantic priming (e.g. Rugg, 1985; Holcomb, 1988). To the extent that this account is correct, it underscores the differences that exist with respect to semantic 'cohesiveness' between otherwise unselected sets of emotionally negative and neutral words.

As is evident from figure 5.7, the scalp topographies of the old/new and valence effects in the 300-500 msec latency range were remarkably similar. While this finding does not rule out the possibility that there exist brain regions, undetectable by the ERP method, which respond differentially to the two variables, it suggests that valence and study status modulate a common generator population. According to this suggestion, therefore, these generators are sensitive both to 'semantic' (valence) and 'episodic' (old vs. new) factors. A discussion of possible reasons for this observation can be found in Rugg et al. (2000).

Left parietal old/new effect

Neutral words elicited a prominent left parietally distributed old/new effect which extended from approximately 500 to 1200 msec post-stimulus. In the early part of the same latency range, negative words also elicited a reliable left parietal effect. While this latter effect was topographically indistinguishable from that elicited by the neutral items, it was both smaller in magnitude and considerably more short-lived. Crucially, the smaller magnitude of the left parietal effect elicited by negative items was carried (wholly, in the 500-800 msec latency range, and partially, in the later time region) by the greater positivity of the ERPs elicited by new negative words relative to those elicited by new neutral words. For the reasons outlined in the introduction, this pattern of results is interpreted as a reflection of the capacity of new negative items to elicit spurious or 'illusory' episodic memories. Presumably, the fact that this effect was observed in the ERPs elicited by items which were correctly (albeit relatively slowly) classified as new means that the information 'retrieved' on these trials was sufficiently distinct from that elicited by genuinely old words to permit a false alarm to be avoided. Had there been sufficient trials to allow ERPs with adequate signal-to-noise ratio to be formed for false alarm trials, it is assumed that false alarms to negative items would have elicited a left parietal effect as large as or larger than that elicited by correctly rejections (see Düzel et al., 1997; Johnson and Rye, 1998). Indeed, this prediction necessarily follows from the interpretation given above for the effects of emotionality on the left parietal effect, and a failure to obtain the finding would call that interpretation into question.

Right frontal old/new effect

A final old/new effect elicited by the neutral words took the form of a late-onsetting, sustained right frontal positive shift. No such effect was observed in the ERPs to the negative words. Instead, the ERPs elicited by both old and new negative items in this latency range over the right frontal scalp were only slightly smaller in amplitude than those elicited by the old neutral items (see figure 5.4).

'Right frontal' effects similar to the one observed here have been described in several previous studies (for review see Rugg and Allan, 2000). The effect has been interpreted functionally as a reflection of 'post-retrieval' operations carried out on the products of memory retrieval, which are brought into play when retrieved information must be 'monitored' with respect to its relevance to current behavioural goals (Koriat and Goldsmith, 1996a). It has been further proposed (Wilding and Rugg, 1996) that the right frontal old/new effect reflects differential neural activity in the same regions of the right prefrontal cortex that are frequently activated in functional neuroimaging studies of memory (e.g. Fletcher et al., 1997; Buckner and Koutstaal, 1998) and which are hypothesised by some authors to be the neural substrate of memory monitoring operations (e.g. Rugg et al., 1998a; Henson et al., 1999a).

Although not predicted, the findings regarding the right frontal effect in the present study can be accounted for fairly comfortably within the framework outlined above. Unlike in 'standard' tests of yes/no recognition memory (when right frontal old/new effects tend to small or non-existent (e.g. Allan, Wilding and Rugg, 1998) the mere retrieval of episodic information was not a reliable guide as to whether a test item was old or new. Rather, as in tests of source memory, it was necessary for participants to evaluate the content of the 'retrieved' information in order to ascertain the likelihood that it represented a veridical episode from the study phase (a similar argument was advanced by Schacter, Reiman et al. (1996b) to account for their observation of right prefrontal activation during the processing of associative lures in a PET study of false recollection). Thus, post-retrieval monitoring operations were engaged whenever a test item elicited episodic information from memory. The only class of items in the present experiment for which such operations were not necessary, therefore, were the new, neutral items. Hence, neutral items, but not negative ones, elicited a right frontal effect.

To summarise, ERP old/new effects found differed according to the emotional valence of the words that elicited them. These differences involved modulations of a common set of memory-related effects, which, along with the behavioural findings, could be understood on the assumption that negatively valenced words share higher levels of inter-item associations than do words of neutral valence (the semantic cohesion hypothesis of Phelps et al., 1998). There was no evidence that recognition memory for the two different word classes engaged qualitatively distinct neural systems. With the caveat that accompanies any conclusion based on a null result, the findings suggest that emotionally negative words engage memory retrieval operations that are neither functionally nor neurally distinct from those that support the retrieval of emotionally neutral words.

CHAPTER 6

Experiment 2: Recognition Memory for Emotionally Negative and Neutral Words: The Effect of Blocking Items at Test

Chapter Summary

Scalp recorded ERPs were used to investigate the neural activity elicited by emotionally negative and emotionally neutral words during the performance of a recognition memory task, however, in contrast to experiment 1, items were blocked at test according to valence. Consistent with the findings from experiment 1 the principal difference behaviourally between the two word classes was that the false alarm rate for negative items was approximately double that for the neutral words. Similarly, the amplitude of the N400 component was attenuated for negative relative to neutral items and, the parietally-based ‘recollection-related’ old/new effect was smaller in magnitude for such items. These findings provide further support for the proposal that emotionally valenced words influence recognition memory in a manner similar to lures in the Deese paradigm. In light of the results from the previous experiment, the ERP data also provide evidence that the arrangement of items at test (blocked versus mixed) affects the type of processing participants engage in when distinguishing between old and new emotional items. In contrast to the findings from the first experiment, the early frontal effect associated with familiarity-driven recollection was no longer evident in the ERPs to the negative items. In addition, old/new differences for negative items were more apparent later in the recording epoch at right frontal sites. These findings suggest that when negative words are blocked at test, participants are less able to make recognition judgements on the basis of familiarity and compensate with post-retrieval processing tailored to distinguish features that differ between the old and new words. The experiment highlights methodological issues relating to the use of emotionally and neutrally valenced stimuli to allow cross-condition comparisons in investigations of emotional episodic memory. In effect, non-emotional factors such as semantic cohesiveness may interact

with aspects of the experiment, such as arrangement of test items, thus influencing memory.

Introduction

The discussion of the findings of the previous experiment was predicated on theories of true and false memory. Specifically, it was suggested that emotionally negative words influence recognition through their high levels of semantic cohesion and as such promote false recollection as in the Deese paradigm. An explanation of the Deese Effect is proposed in the Source Monitoring Framework (SMF) (Johnson, Hashtroudi and Lindsay, 1993). By this account, individuals make memory decisions based upon a range of psychological attributes such as perceptual details or related memories that may be called to mind at test. Falsely recognised associative lures in the Deese paradigm are thus proposed to result from participants mistakenly attributing psychological experience from one source (prior thought or present feature familiarity) to another source (prior perceptual experience) (Johnson et al., 1997).

Although the similarity of information at study and test may lead to difficulty in distinguishing between new and old items, evidence suggests that false memories do differ from true memories in terms of cognitive processing. For example, findings suggest that memories for falsely recognised lures tend to have less auditory details and less remembered feelings than do memories for presented words (Norman and Schacter, 1997; Mather, Henkel and Johnson, 1997). In addition, neuroimaging evidence suggests that, under certain experimental conditions, false memories do in fact differ from true memories in terms of both cognitive processes and accompanying brain activation (e.g. Schacter et al., 1996b; Cabeza et al., in submission).

In a review of neuroimaging studies it was noted that differences between true and false recognition are most apparent when true and false targets are tested in separate blocks (Schacter and Curran, 2000). Under these circumstances, functional imaging studies have revealed differences in brain activity in temporal cortices (Schacter et al., 1996b; Garrett, Flowers et al., 2000) and an ERP study revealed pronounced waveforms differences over left temporal parietal and frontal sites (Johnson et al., 1997). By contrast, when true and false targets are randomly mixed, differences in brain activity are minimal (Johnson et al., 1997; Düzel et al., 1997; Schacter et al., 1997).

Johnson et al., (1997) proposed that such differences in activity between test format associated with true and false recognition occur because when old and lure test items are mixed, participants are able to make old/new judgements relying in part on familiarity-based recognition to discriminate between items. They can also recruit such familiarity-driven processes, when distinguishing between old and new non-lure items which are blocked. By contrast, in a block of similar items, familiarity will not vary much between successive items thus forcing participants instead to evaluate memories for specific differentiating information (for example, perceptual-contextual detail) in order to make old/new judgements. Thus when categorising lures under blocked conditions, frontal cortex activity associated with extensive post-retrieval processes is elicited (Johnson et al., 1997; see also Rugg and Wilding, 2000).[1]

The foregoing analyses raises a number of issues that are assessed in the current experiment by employing a modification of the recognition paradigm in experiment 1 such that negative and neutral words are blocked at test. First, if Johnson et al., (1997) are correct in their assertion that the blocking of semantically-related items impairs familiarity-driven recognition, then in the current study familiarity-related ERP effects should be small or non-existent for negative items. By contrast, neutral words should elicit a familiarity-related ERP effect comparable with that found in the previous experiment when test items were mixed.

Effects which are independent of either familiarity-driven processing or post-retrieval strategic processing adopted by the participants should be less affected by the test format and differences in the strategic processing adopted by the participant. The same attenuation of the N400 component for negative items is predicted since the high-level of inter-item association between negatively valenced word sets should still entail that these items prime one another semantically (see discussion of experiment 1, also Kutas and Hillyard, 1983; Holcomb, 1988). Similarly, when items were randomly mixed, the reduced left parietal effect for such items was proposed to reflect the capacity of new negative items to elicit spurious or 'illusory' episodic memory,

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[1] In addition, enhanced parietal lobe differences associated with contrasts between true and false targets under blocked conditions have been linked been linked with phonological processing rather than retrieval processing (Schacter, Reiman et al., 1996, Johnson et al., 1997).

and as such should remain attenuated for the negative items relative to the neutral items when items are blocked.

The third issue regards the proposal that under blocked condition, lure items associate with extensive evaluation processing relative to when such items are inter-mixed (Johnson et al., 1997). The implication of this proposal for the ERP results following a change in the arrangement of items at test from mixed to blocked in the current study is not immediately obvious. The results of the previous experiment suggested that, even when words are mixed, participants had difficulty in discriminating between old and new negative words and both types of item elicited extensive retrieval-related processing (as reflected by elevated positivity in the ERPs over right frontal sites). Hence, even if such retrieval-related evaluation processing is increased under blocked relative to mixed conditions, it is unclear how this would be reflected in the ERPs to old and new negative words since both kinds of words 'already' elicit post-retrieval processing as reflected by a sustained right frontal positivity in their ERPs.

A direct prediction can however be made with regard to the right frontal effect found for the neutral items in the previous experiment. In that experiment it was suggested that the right frontal effect for neutral items in experiment 1 was a consequence of inter-mixing the neutral and negative items at test, hence when items are blocked at test no right frontal effect should be elicited.

Finally, addressing a more general issue, this study emphasises the importance of considering how brain activity associated with emotional and non-emotional memory may be critically affected by the arrangement of items at test not only through 'emotional' factors such as habituation (see Chapter 4), but also through 'non-emotional' factors such as 'semantic cohesion'.

Method

Procedure

The experiment took the form of two study-test cycles, one session with negative words blocked at test and the other with neutral words blocked at test. As the primary aim of the experiment was to assess the effect of the arrangement of the test items on retrieval processing, most other aspects of the experiment (such as randomly intermixing negative and neutral items at study) were unchanged from the previous experiment. However, as a result of the changed design of the experiment it was necessary to inform participants prior to the study phase that their memory would be tested. An interval of around of around 5 minutes separated each study and test phase, and approximately 10 minutes separated the two study-test sessions; participants were instructed to relax during these times.

Participants

In total 19 young male and female right-handed participants were employed in the study. 3 participants' data were discarded prior to data analysis due to excessive electro-oculographic artefact leading to a failure to provide more than 16 artefact-free trials for one or more of the ERP categories. The 16 participants whose data were analysed consisted of 9 females and 7 males. Each participant gave informed consent prior to participation in the study and all were remunerated at the rate of five pounds per hour.

Experimental Material

The critical stimuli consisted of the same 224 negative and neutral words used in experiment 1. As a result of changing the experiment design from mixed to blocked, an additional 68 neutral and 68 negative filler words were used (again selected from The Balanced Affective Word Project – Siegle, 1998). Of these filler words, 56 neutral and 56 negative words were needed to pad out study lists such that each contained an equal number of neutral and negative words, whilst not violating the constraint that a critical word must only appear in one of the two (negative, neutral) blocks.

Four study lists were created. Two study lists each contained a set of 56 critical neutral words and 56 negative filler words. One study list contained 56 critical negative words and 56 neutral filler words. Due to an error, one study list contained 55 (instead of the intended 56) critical negative words and 56 neutral filler words. The words in the study lists were randomly ordered. A neutral buffer word was added to the beginning and end of the study lists containing the negative critical words. A negative buffer word was added to the beginning and end of the study lists containing the neutral critical words. Four test lists were created, two of which contained the entire set of 112 critical negative words (different randomly determined orders in each list), the other two containing the entire set of 112 critical neutral stimuli (again different randomly determined orders in each list). A negative or neutral buffer word (consistent with type of test list) was added to the beginning of each list.

The combination of study and test lists used was counterbalanced across participants, thus ensuring there was no correlation between either word type and old/new status for block type (negative, neutral) and session (first, second).

Results

Behavioural Data

The mean rating assigned to the critical negative words was -1.52, (across participant s.d. $= 0.31$) whereas the mean rating for the critical neutral words was 0.44, (across participant s.d. $= 0.34$). These means, which are comparable to those obtained in Experiment 1, differed reliably ($t15 = 14.87$, $p < 0.001$). For every participant, the mean rating given for the critical negative words was significantly lower than that given for the neutral words (minimum $t109 = 9.98$, $p < 0.001$).

Hit and correct rejection rates for the neutral and negative items, along with the discrimination (Pr) and bias (Br) indices (Snodgrass and Corwin, 1988) are shown in table 6.1. Pr for neutral words was significantly greater than that for negative words ($t(15)=4.85$, $p<0.001$). Additional t-tests revealed that the hit rates were significantly greater for the neutral items ($t15 = 2.82$, $p = 0.01$) whereas the false alarm rates were significantly greater for the negative items ($t15 = 5.62$, $p < 0.001$). The bias indices did not differ significantly neither from each other nor from 0.5.

Table 6.1 Experiment 2: Accuracy data.
Columns 1 and 2: Mean proportion (standard deviation in brackets) of hits and correct rejections to each word type. Column 3 and 4: Discrimination Index (Pr) and bias indices (Br).

WORD TYPE	HIT	CR	Pr	Br
NEUTRAL	0.84 (0.12)	0.87 (0.08)	0.72	0.48
NEGATIVE	0.76 (0.11)	0.72 (0.10)	0.51	0.52

RT data are shown in 7.2. ANOVA of the RTs for hits and correct rejections revealed main effects of response category and valence [($F(1,15) = 21.41$, $p < 0.001$), and (F(1,15) = 28.11, $p < 0.001$) respectively] but no interaction between these factors (F = 0.003). RTs were faster for the hits (relative to the correct rejections) and for the negative (relative to the neutral) items. A further t-test revealed that RTs to false alarms did not differ.

Table 6.2 Experiment 2: Reaction time data (msec)
Mean reaction times (standard deviations in brackets) for hits, correct rejections and false alarms to each word type.

WORD TYPE	HIT	CR	FALSE ALARM
NEUTRAL	951 (235)	1060 (250)	1188 (260)
NEGATIVE	1033 (236)	1141 (288)	1183 (302)

ERP data

The mean number of trials (range in brackets) contributing to the average ERPs for the neutral hits, neutral correct rejections, negative hits and negative correct rejections were 39 (24-47), 40 (24-48), 36 (24-48), 34 (26-43) respectively. The proportion of trials lost because of artefact was 16%, 19%, 15% and 16%. The proportions are similar to those obtained in the previous experiment. There was no evidence that physiological arousal during viewing of emotional items resulted in more emotional trials being rejected than neutral trials.

Grand average waveforms from selected lateral and midline sites are shown overlaid according to response category and valence in figures 6.1 and 6.2 respectively. The earliest ERP effects associated with response category and valence appear from around 200msec post-stimulus when the ERPs to negative hits are more positive going than those to negative correct rejections over right anterior sites. From around 300msec post-stimulus onset, ERPs to negative words are more positive-going than those to the neutral words and ERPs to the old words become more positive going than those to the new words. From approximately 500 msec post-stimulus, old/new effects for the negative words demonstrate a left posterior maximum. By contrast, although old/new effects for the neutral items demonstrate a posteriorly distributed maximum, they do not demonstrate any hemispheric laterality. From around 800 msec the old/new effects for negative words begin to exhibit a right frontal maximum which extends to the end of the recording epoch.

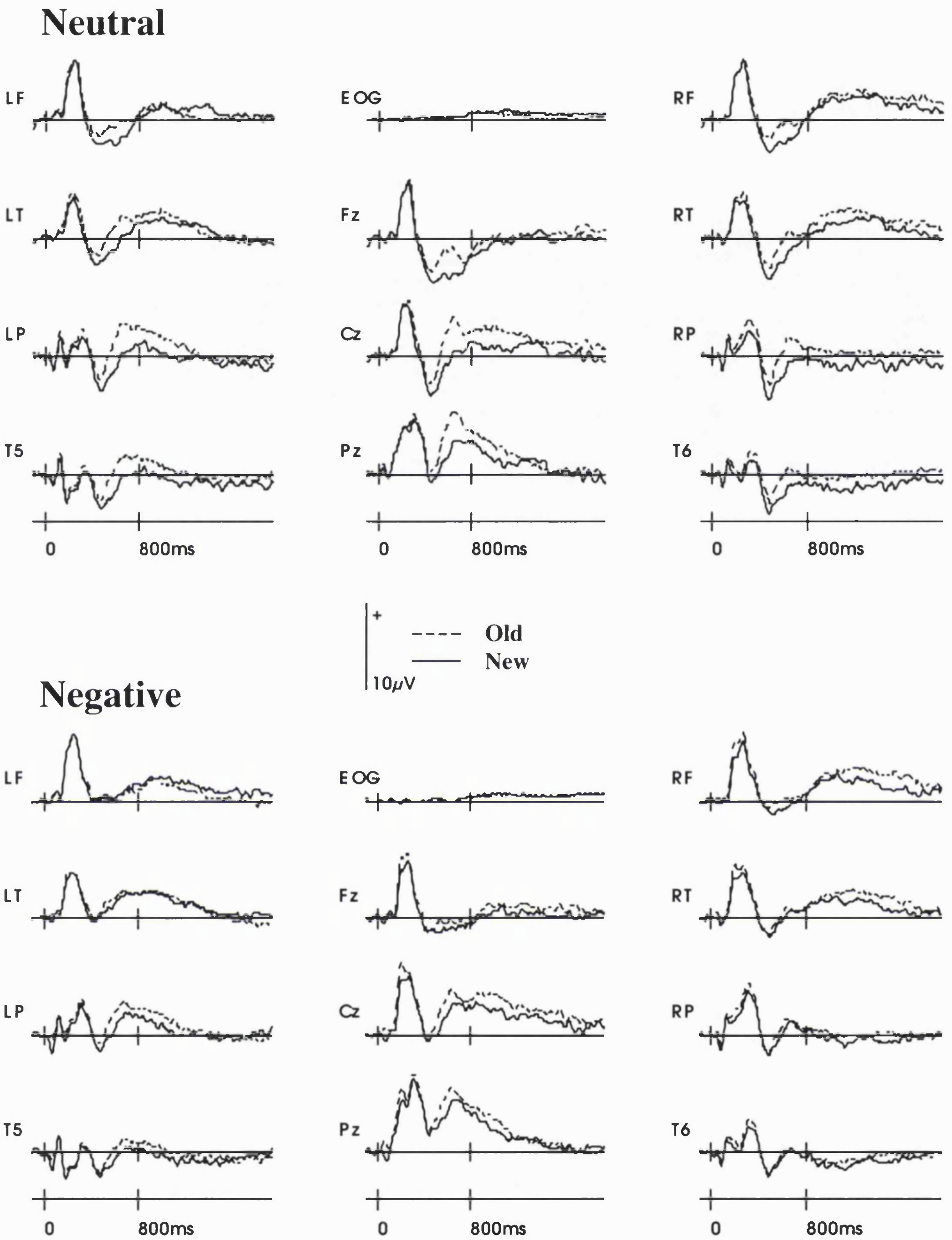
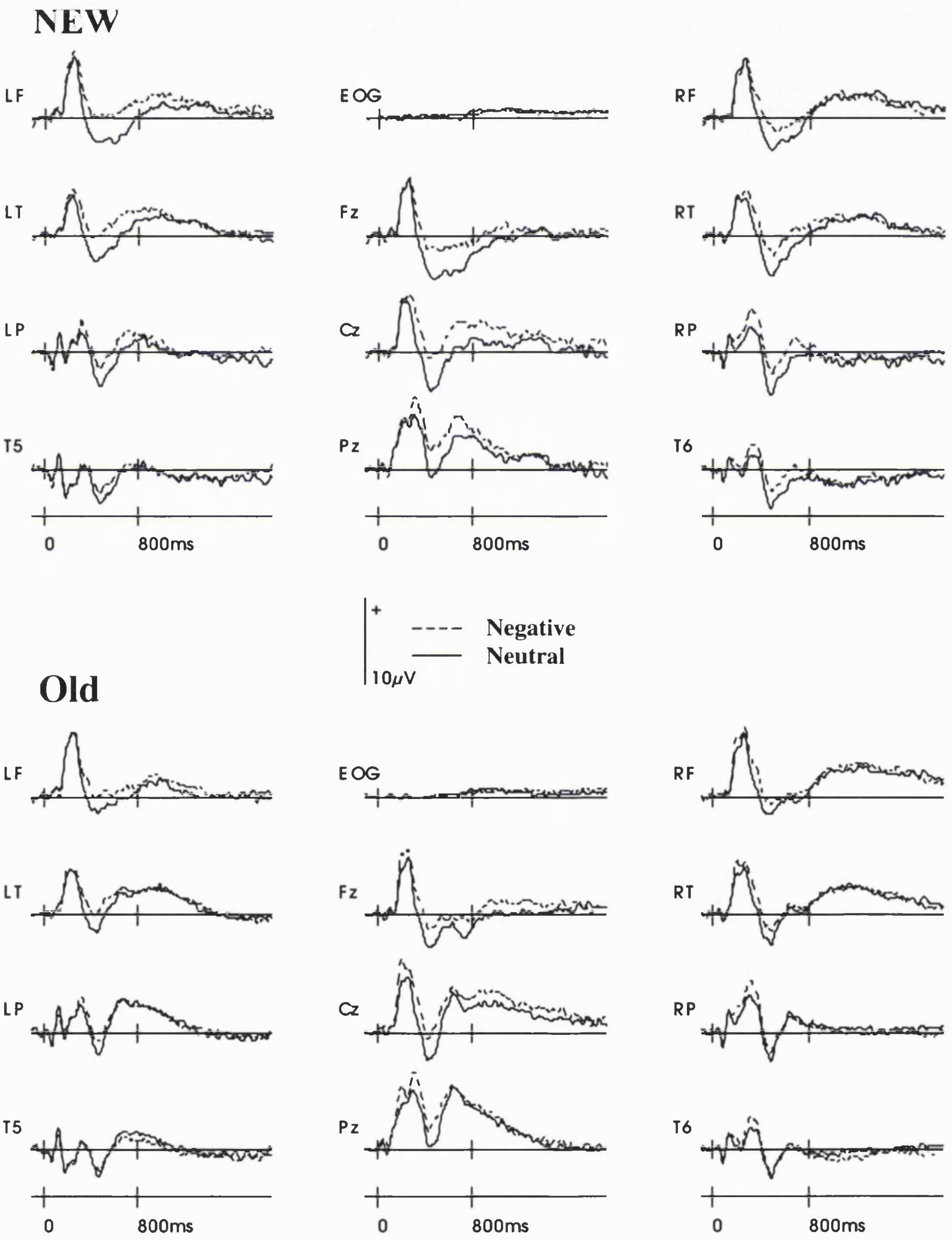


Figure 6.1. Experiment 2: Top: Grand average ERP waveforms elicited by correctly classified old and new neutral words. Bottom: Grand average ERP waveforms elicited by correctly classified old and new negative words.
Electrode locations are described in the text. Gain for the EOG channel is x5 lower than for the EEG.

ERPs were quantified by measuring (with respect to the mean of the pre-stimulus baseline) the mean amplitudes in the same the 4 consecutive time regions (300- 500, 500-800, 800-1100, 1100-1400) used in the previous experiment over the same subset of lateral anterior/posterior sites. Since visual inspection of the waveforms suggested that these epochs might not contain all ERP effects in this experiment, an additional earlier epoch (100-300 msec) was incorporated into the analysis. The strategy employed to analyse amplitude and topographic differences between the old/new effects during each time epoch was the same as in the previous experiment.

Figure 6.2. Experiment 2: Top: Grand average ERP waveforms elicited by correctly classified neutral and negative new words. Bottom: Grand average ERP waveforms elicited by correctly classified neutral and negative old words



Mean amplitude analysis

Results of the ANOVAs conducted on data from lateral anterior/posterior sites are reported in table 6.3. These ANOVAs were followed up by additional subsidiary ANOVAs as reported below.

In the first latency region, 100–300 msec, ANOVA contrasting valence and response category at lateral anterior/posterior sites revealed a main effect of response category reflecting the greater positivity of hits. The response category effect interacted with a number of the sites factors and the factor of valence (Table 6.3). To elucidate the nature of the two interactions involving the response category and valence factors, separate ANOVAs were conducted on the data for the neutral and negative items. There were no significant interactions involving the factor of response category in the ANOVA of the data for the neutral items. ANOVA of the data for the negative items revealed interactions between response category and hemisphere ($F(1,15) = 7.03$, $p < 0.025$, response category and site, ($F(1.1,16.3) = 7.50$, $p = 0.013$) and response category, location and hemisphere ($F(1.8,27.1) = 6.24$, $p = 0.007$). Figure 6.3 shows that the negative old/new effects were largest over the right hemisphere and that the asymmetry on the size of the effects was most pronounced at anterior sites.

Analysis of data from the 300-500msec latency range revealed effects of response category and valence, the former effect reflecting the increase in the positivity of ERPs elicited by hits. The effect of valence reflects the increase in positivity of ERPs elicited by negative items relative to neutral items (figure 6.2, 6.3). Additionally the ANOVA also revealed a significant main effect of response category which, as with the previous epoch, reflects an increase in the positivity of the waveforms associated with the old items compared with the new. Although both the valence and response category factors interacted with a number of site factors (see table 6.3), they did not interact with each other (maximum $F = 1.57$).

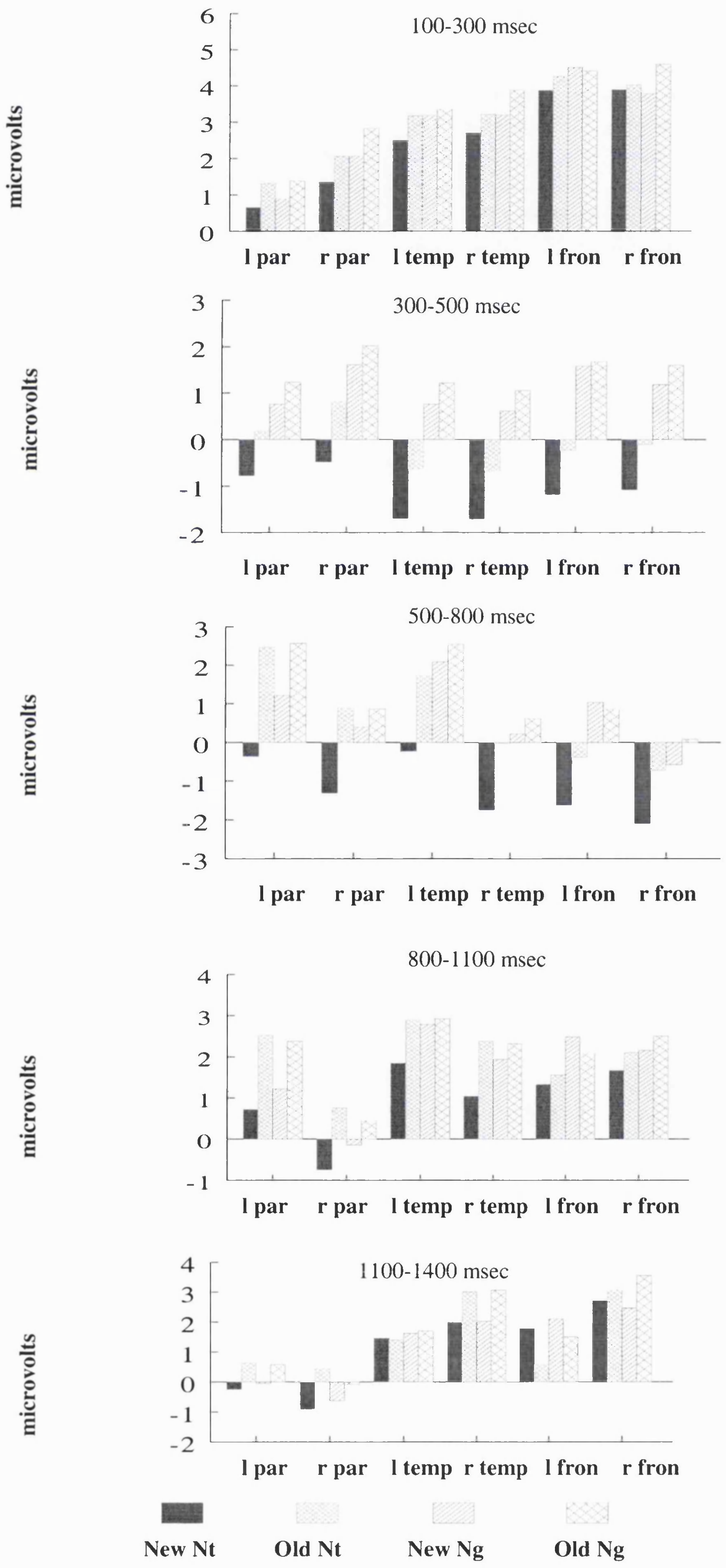
As with the previous experiment, analysis were conducted on F3, Fz and F4 in order to investigate the to investigate the putative familiarity effect. The waveforms from these sites are shown in figure 6.4. Although there was a significant effect of valence, ($F(1,15) = 18.42$, $p = 0.001$), there was no effect of response category or any significant interaction between the response category and valence factors.

Table 6.3 Experiment 2: Mean amplitude analyses, significant effects summary
Table summarising the results of ANOVAs at lateral anterior and posterior sites during the 4 latency intervals shown. Only the significant effects involving the condition factors (word type, response category) are reported. ON = old/new (response category), NE = neutral/negative (valence), CH = frontal/anterior/temporal location, HM = hemisphere (left, right), ST = electrode site (Inferior, Mid-lateral, Superior).
Significant F values of interactions involving the factors of valence and response category are shown in bold.

	100-300msec	300-500msec	500-800msec	800-1100msec	1100-1400msec	1400-1944msec
NE	-	F(1,15)=22.87,p<0.001	F(1,15)=12.84,p<0.005	-	-	-
ON	F(1,15)=9.03, p<0.01	F(1,15)=6.45, p<0.023	F(1,15)=22.84,p<0.001	-	-	-
NExST	-	F(1.1,16.0)=12.85, p<0.005	F(1.1,15.9)=7.72,p=0.01	F1.1,15.8)=4.43,p=0.05	-	-
ONxCH	F(1.5, 22.5) = 4.42,p<0.05	-	F(1.1,17.0)=6.70,p=0.025	F(1.4,20.9)=8.53,p<0.005	F(1.3, 19.5)=5.27, p= 0.025	
ONxHM	-	-	-	-	F(1,15)=8.36,p= 0.01	F(1,15)=14.52, p<0.005
ONxST	F(1.1,17.2)=5.12,p<0.05	-	F(1.1,16.2)=24.8,p<0.001	F(1.0,15.7)=9.91,p<0.01	-	-
NExCHxHM	F(1.2,18.7)=5.9,p<0.05	F(1.3,19.2)=4.29,p<0.05	F(1.3,20.2)=5.35,p<0.025	-	-	-
NExCHxST	-	F(1.9,28.4)=9.25,p=0.001	F(1.6,24.0)=4.72,p=0.025	F(1.9,28.0)=3.55,p=0.05	-	-
NExHMxST	-	F(1.3,20.2)=3.81,p=0.05	F(1.3,19.7)=4.74,p<0.05	F(1.7,26.0)=5.14,p<0.025	-	-
ONxCHxHM	-	-	F(1.3,20.0)=6.15,p<0.025	-	F(2.0,29.8)= 6.4,p=0.005	-
ONxCHxST	-	-	F(2.8,42.1)=3.88,p<0.025	F(2.3,33.9)=3.84,p<0.05	F(2.1, 31.9)=5.60,p<0.01	F(1.7,25)=19.76, p<0.001
NExONxCHxHM	**F(2.0,29.9)=5.75,p<0.01)**	-	-	-	-	-
NExFPxHMxST	-	-	-	-	-	-
NExONxFPxHMxST	**F(3.1,46.3)=4.78,p<0.005**	-	-	-	-	-

Figure 6.3. Experiment 2: Differences in mean amplitude for old negative minus new negative, and old neutral minus new neutral, for the 100-300, 300-500, 500-800 msec, 800-1100 msec, and 1100-1400msec, latency regions.

Amplitude measures are averaged over the electrode site indicated and the sites immediately adjacent to it.



Separate ANOVAs showed that the effect of valence was significant for both the old and new items [($F(1,15) = 8.21$, $p = 0.012$ and ($F(1,15) = 15.14$, $p = 0.001$) respectively]. The response category effect was reliable for the neutral items ($F(1,15) = 5.54$, $p < 0.05$) but not for the negative items.

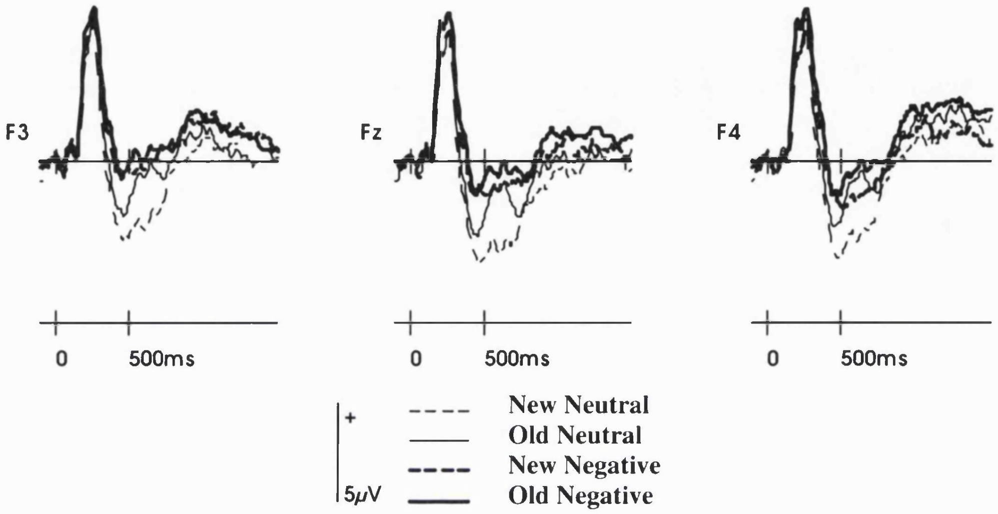


Figure 6.4. Experiment 2: Grand average waveforms for all word types (neutral; negative; old; new) from a subset of frontal electrode sites (F3, Fz, F4).

The ANOVA on data from lateral anterior/posterior sites during the 500-800msec region revealed main effects of valence and response category, along with a number of interactions (Table 6.3) involving either (but not both) of these factors. As can be seen from figure 6.3, it appeared as if both neutral and negative old/new effects were associated with a posterior maximum, and that additionally the neutral old/new effects over these sites were larger than the negative old/new effects. However, the old/new effects for the neutral items did not appear as lateralised as those for the negative items. This impression was verified by the separate ANOVAs conducted on the data for neutral and negative items. The ANOVA for the neutral items revealed a main effect of response category ($F1,15) = 22.18$, $p < 0.001$), an interaction between response category and location that approached significance at $p = 0.065$, ($F1.1,6.8 = 3.78$) and an interaction between response category and site ($F(1.1,15.9) = 12.94$, $p < 0.005$). There was no three way interaction between response category, location and hemisphere ($F < 1$). An ANOVA conducted at the parietal sites only (T5,LP,P3,P4,RP,P6) gave no indication of any asymmetry in the size of the old/new effects ($F = 1.0$). By contrast, the ANOVA for the negative items revealed a interaction between response category and site ($F(1.0,15.6) = 7.94$, $p = 0.01$) and the typical three way interaction between response category, location and hemisphere ($F(1.2,17.8) = 8.41$, $p < 0.01$).

The above results confirm that old/new effects for the negative items are focused over left posterior sites. Additionally, the negative old/new distributions showed an inferior to midline site gradient. However, the old/new effects for the neutral items, whilst showing a tendency to be largest over posterior sites, and in addition showing the same inferior to midline site gradient as the negative items, did not show any hemispheric laterality.

This lack of laterality over posterior sites in the old/new data associated with the neutral items meant that, whereas in experiment 1 difference waveforms at 'left parietal sites' were used as signatures of the level of episodic retrieval for neutral and negative items, it was inappropriate to conduct such an analyses in this experiment. Instead, analyses on the mean amplitudes of the waveforms differences were conducted over the entire subset of posterior sites and were factored by response category, valence, hemisphere and site. An ANOVA revealed a main effect of valence ($F(1,15) = 4.50$, $p= 0.05$), a main effect of response category ($F(1,15) = 31.22$, $p < 0.001$) and also a marginally significant interaction between response category, valence and site ($F(1,15) = 4.30$, $p = 0.056$).

Table 6.3 shows that the ANOVA of data from the 800-1100msec epoch revealed various interactions involving either the response category factor or the valence factor, but, as with the preceding epoch, no interactions involving both of these factors. ANOVAs were again conducted testing for the presence of the left parietal effect in each of the conditions separately. The ANOVA for the neutral items revealed an interaction between response category and location that approached significance at 0.061 ($F(1.2,18.4 = 3.77$), also revealed was an interaction between response category and site ($F(1.0,15.5) = 5.23$, $p<0.05$). This again reflects the tendency of the neutral old/new to be distributed over the posterior sites around the midline. Again there was no sign of any laterality in the distribution of the neutral old/new effects ($F < 1$). The ANOVA for the negative items in this epoch revealed an interaction between response category and site ($F(1.1,15.9)=7.11$,$p < 0.05$)

indicating, that whilst negative old/new differences in this epoch were still centred around midline sites, they no longer showed a left posterior maximum.

ANOVA of the 1100-1400 msec epoch revealed a number of interactions involving the response category factor (Table 6.3). Figure 6.3 shows that old/new effects in this epoch for negative items had a distribution over right frontal scalp sites whereas the old/new effects to the neutral item show a reverse polarity over left frontal sites. There were however no interactions involving both the valence and response category factors. As with the previous experiment, analyses were directed to frontal sites alone. Although this ANOVA revealed interactions between response category and hemisphere ($F(1,15) = 21.44$, $P< 0.002$) and between response category and site ($F(1.2,17.9) = 6.36$, $p < 0.025$), there were no interactions involving both the response category and the valence factors.

ANOVA on the data for the neutral words over lateral anterior/posterior sites revealed interactions between response category and location ($F(1.2,18.6)=6.4$, $p< 0.025$) and between response category and hemisphere ($F(1,15)=5.58$,$p\ 0.032$). ANOVA confined to the data from frontal sites alone for these items revealed an interaction between response category and hemisphere ($F(1,15) = 10.69$, $p = 0.005$). These effects occurred because the waveforms in this latency regions were more negative going to old neutral items than new neutral items over left frontal sites, but there is a tendency for this pattern to reverse over frontal sites. ANOVA on the data for negative words from lateral anterior/posterior sites revealed a three way interaction between response category, location and hemisphere ($F(1.7,25.2)= 6.60$, $p < 0.01$) and an interaction between response category and hemisphere at frontal sites ($F(1,15)=9.43$,$p<0.01$). The results reflect the old/new effects for negative items being focused over right frontal sites.

Analysis on data from the right frontal sites alone (F4, RF, F8) revealed no effect involving the factor of response category for the neutral items. By contrast, for the negative items there was an interaction between response category and site ($F(1.3,18.8) = 5.22$, $p < 0.05$) which reflects larger old/new effects at sites F4 and RF than at site F8.

Topographic analysis

Analyses consistent with the previous experiment were performed which included contrasting the neutral and negative old/new effects with each other and also examining how the scalp distribution of the old new effects differ across epochs.

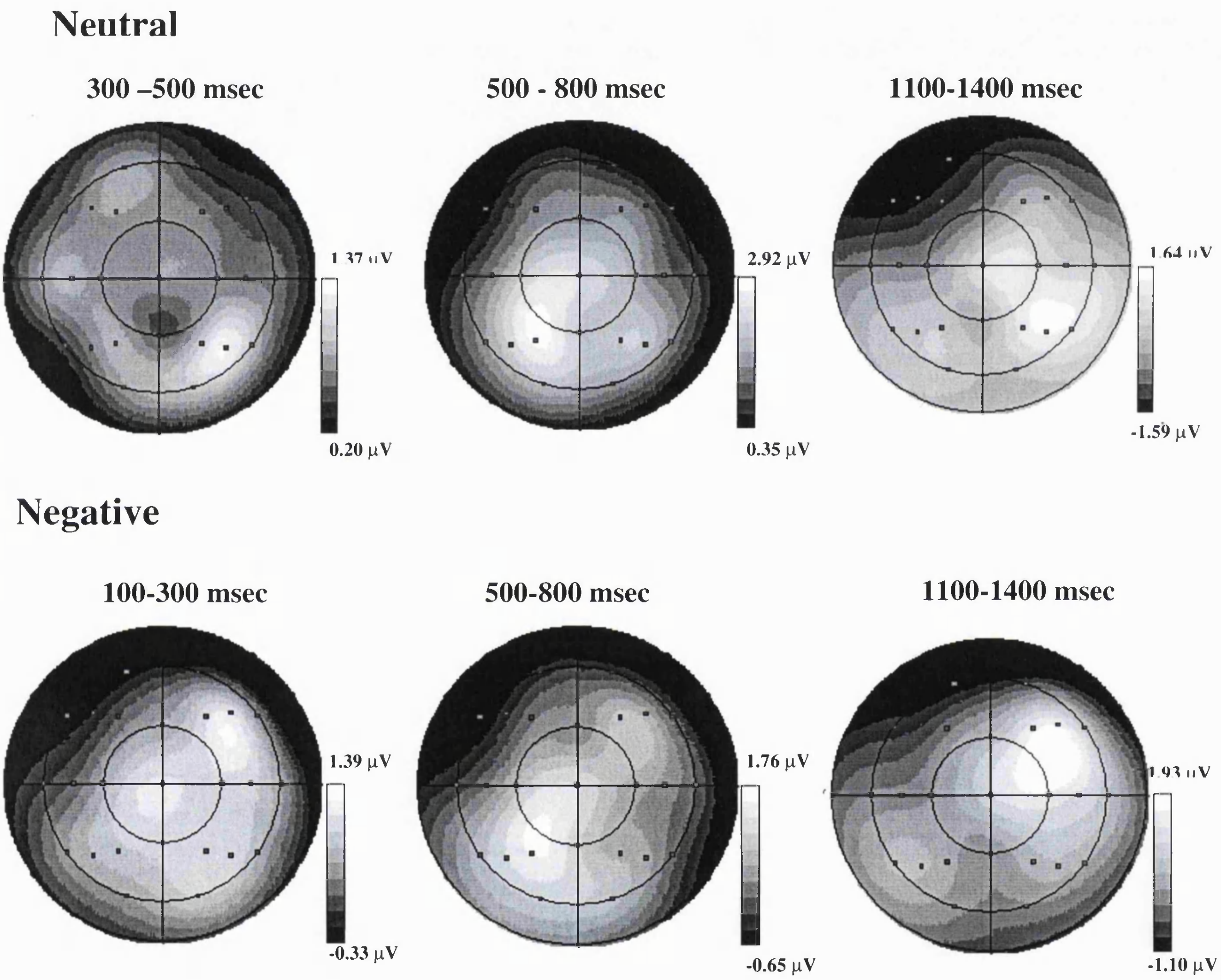


Figure 6.5 Experiment 2: Topographic maps illustrating the distribution of the differences between ERPs to correctly classified old and new neutral words (upper row), and between ERPs to correctly classified old and new negative words (lower row), in successive latency regions.

A first set of analyses contrasted the scalp distributions of the old/new effects for negative and neutral words between 500-800 msec, and separately, the 1100-1400 msec epoch. The topographies of the effects are illustrated in figure 6.5. ANOVA on data from the 500-800 msec region (factors of electrode site and valence) revealed a main effect of site $(F(4.3,64.5) = 5.85, p < 0.001)$ but no evidence of any site by valence interaction (F < 1). Similarly, for the 1100-1400 msec region, ANOVA revealed an effect of site (F(4.2,62.4) = 4.39, p < 0.005) but no site by valence interaction (F = 0.75).

A second analysis tested the scalp distribution of the neutral old/new effect (Figure 6.5), and the valence effects (collapsed across old and new, figure 6.6), in 300-500 msec. The analysis revealed no main effect of site (F < 1) and no site x condition interaction (F < 1).

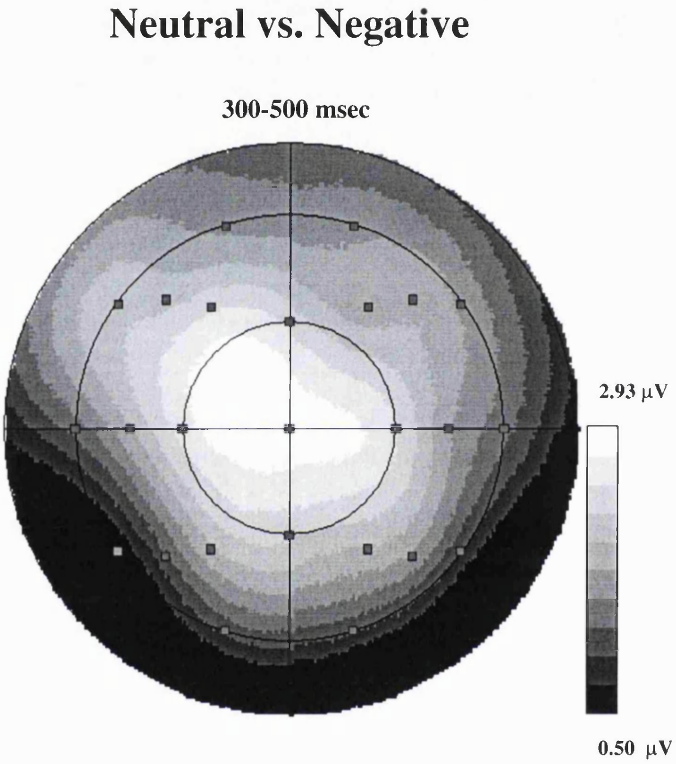


Figure 6.6. Experiment 2: Topographic map illustrating the distribution of the differences between correctly classified neutral and negative items, in the 300 msec – 500 msec epoch.

A third set of analysis contrasted the topographies of the foregoing old/new effects as a function of latency region to confirm that the effects do reflect the contributions of generator configurations that differ over time. The comparison [factored by valence, latency region (500-800, 1100-1400) and site] revealed a significant latency region by site interaction (F(2.9, 42.8) = 4.44, p < 0.01) indicating that the old/new effects do differ with time. As shown in figure 6.5 the distributions evolve from the posterior maximum to the anteriorly distributed effect. There was no interaction between latency region, valence and site (F < 1).

Discussion

Performance Data

Participants were able to discriminate between old and new words at a level well above chance in both the neutral and negative conditions. As with the previous experiment there was a reduction in recognition accuracy for negative words carried by an elevated false alarm rate. Although the discrimination indices (PR) for both types of word are comparable with those obtained in experiment 1, by contrast, bias indices differed between the two experiments. Whereas in experiment 1 participants applied a fairly liberal criterion when distinguishing between old and new negative items, indicating that they were more willing to reply 'yes' to such items, in this experiment they displayed no such bias. This finding is consistent with the proposal that participants alter their retrieval strategies according to the arrangement of the items at test (Johnson et al., 1997).

ERP Effects

The findings from the present experiment resemble those from experiment 1 in that the ERP old/new effects reflected the modulation of a number of components including the N400, early frontal effect, left parietal and right frontal old/new effects. As predicted there was a marked reduction in amplitude of the N400 component for the negative words relative to the neutral words indicating that negative words were priming one another semantically.

The first effect in the data reflected an increase in the waveforms for negative old items relative to the three other classes of items over right frontal sites in the first epoch (100-300 msec). This pattern reflects the modulation of the P2 and P3 components by the negative old words. Although not predicted from the findings of the previous experiment, this modulation of P2 and P3 is unsurprising in light of the results of previous ERP studies of emotion, (e.g. see Schapkin et al., 2000). As discussed in Chapter 4, early increased positivity in ERP waveforms to emotional stimuli relative to neutral stimuli have been noted before and it is suggested that modulation of the P2 component indexes early sensory processing exclusive to the detection of emotional stimuli (Schapkin et al., 2000) whereas the subsequent modulation of the P3 component is suggested to index task-relevant processing of emotional stimuli following detection (for example target effects, oddball effects) (Carretie et al., 1997; Schapkin et al., 2000, but see Naumann et al., 1992).

However, it is of interest to note that in this experiment, emotional valence per se did not appear to modulate the size of the P2 or P3, rather it was the retrieval of old emotional items which modulated the processing indexed by these effects. With regard to the functional significance of the P2 this interaction between valence and old/new status may reflect the sensitivity of activity in low level avoidance/approach systems to experience (cf. Halgren and Marinkovich, 1995). With regard to the P3 such an interaction probably reflect 'targetness' to emotional old items relative to the other classes of item (cf. Carretie et al., 1997).

Between 300 and 500 msec, only the neutral words elicited old/new effects over the frontal sites held by Rugg and colleagues to be the sites where old/new effects indexing recollection are maximal (Rugg et al., 1998b). The finding that negative items no longer elicited frontally distributed old/new effects under blocked conditions is consistent with the proposal that in these circumstances participants are less able to distinguish between semantically-related items on the basis of familiarity (Johnson et al., 1997). It is proposed that the sustained level of high familiarity elicited by successive negative items de-sensitised (habituated) familiarity-driven processes forcing participants to rely instead on processing associated with episodic retrieval. No such de-sensitisation of familiarity during recognition of negative lures occurred when the design was mixed since the level of familiarity continuously varied between successive (negative and neutral) items.

As predicted, parietally based old/new effects over the 500-800 msec period were smaller for the negative items relative to those for neutral items. However, although the scalp distributions of the negative and neutral old/new effects in this epoch were qualitatively indistinguishable, the parietally distributed old/new effect for the neutral items did not show the typical amplitude maximum over left parietal scalp sites, rather the parietally based old/new effect associated with episodic retrieval of neutral information in the present study had a bilateral distribution. While this is unusual, bilaterally distributed parietal old/new effects in episodic retrieval have been observed before (e.g. Schloerscheidt, 1998; Heron, 2000), although the functional significance of this bilaterality has not yet been defined. Nethertheless, consistent with the previous experiment, the smaller magnitude of the parietal effect elicited by negative items was carried at least in part by the greater positivity of the ERPs elicited by new negative words relative to those elicited by new neutral words. For reasons outlined in the preceding chapter, the most likely interpretation of this pattern of results is that it reflects the capacity of new negative items to elicit spurious or 'illusory' episodic memories.

An important difference between this experiment and the previous experiment is that when old and new negative words were blocked at test, episodic retrieval of such words elicited a right frontal effect. Whilst this finding was not predicted a priori, it can be accounted for, albeit with more than a degree of speculation, by the source-monitoring framework outlined in the introduction. By this account when semantically-related items are blocked at test familiarity based recognition memory is impaired, thus participants are forced to strategically evaluate different features of old and new items and employ appropriate post-retrieval monitoring and evaluation operations in order to make old/new decisions (Johnson et al., 1997). Hence the differences in the waveforms over the right frontal sites reflect these post-retrieval processing.

It is important however to note that since negative words in this experiment still tended to elicit spurious recollection (as indicated by the increased positivity in the negative correct rejection waveforms over parietal sites and the elevated false alarm for negative words), such items are still probably receiving post-retrieval processing (as outlined in the discussion of experiment 1). Critically, it is proposed that the right frontal effect elicited by negative words reflects differences in post-retrieval processing applied to the old and new words, rather than all-or-none differences in post-retrieval processing between the two conditions. Thus, a speculative interpretation of the finding of a right frontal effect for negative items is that, whereas in the previous experiment when encountering a negative item at test participants applied a 'generic' form of post-retrieval processing, in the current experiment old and new negative words received post-retrieval processing specific to information held in mind. For example, old items may well have received more retrieval-processing evaluating perceptual-contextual detail relative to new items (Norman and Schacter, 1997; Mather et al., 1997).

However, such an interpretation highlights an issue which has been raised previously concerning the functional significance of right frontal effect in ERP data, namely that functional interpretations of the right frontal effect 'over-fit' data, that is they can be applied to a variety of circumstances and patterns of experimental results (cf. Rugg and Wilding, 1996 vs. Rugg et al., 2000). As described in Chapter 3, this over-inclusivity has been accounted for by the suggestion that the right frontal effect reflects activity in disparate, functionally heterogeneous, regions of the prefrontal cortex, and therefore may index a number of kinds of post-retrieval processing.

Turning now to the later (post-800 msec) old/new effects associated with neutral items. It is less clear that this effect should be identified with a right frontal effect. Instead of taking the form of a positive-going effect distributed over the right hemisphere, the frontal old/new effect associated with episodic retrieval of neutral information in the present study involved a greater negativity over left frontal sites. Thus, while the direction of the asymmetry of the effect (right more positive than left) is the same as the right frontal effect found both in the previous experiment for neutral items and in the current experiment for negative words, the magnitude and polarity of the effect over each hemisphere is not.

A similar pattern of old/new effect has been reported previously by Rugg et al. (1998c) to attend recognition of neutral words accompanied by correct source memory. In that study the pattern appeared to be a consequence of a right frontal old/new effect summating with another component - a late negative (parietally-based) shift that also associated with the recollected items. On this assumption, and an accompanying analyses indicating that the scalp distribution of the old/new effect was statistically equivalent with a right frontal old/new effect elicited under a comparable task, the authors concluded that the pattern of old/new effect described for such recollected items was indeed reflective of a right frontal effect.

In the current experiment, whether the old/new effects for neutral words reflect a right frontal effect is more ambiguous. In statistical terms, the answer is affirmative since the scalp distribution associated with neutral and negative words were equivalent. However, examination of the magnitude and the polarity of the ERP old/new effects associated with the neutral words indicates that, unlike with Rugg, Schloerscheidt and Mark (1998), this may not be the case. In the first instance there is no evidence that the left frontal negativity is receiving any contribution from other components over the surrounding sites. Indeed on inspection of the waveforms it can be seen that the negativity appears localised to the left frontal scalp site. In addition the small reverse polarity at right frontal sites appears to receive most of its contribution from a positive slow wave that is present for the neutral items over the posterior sites, quite probably reflecting the continuation of the earlier onsetting parietal effect through to the end of the recording epoch.

By this analysis, the pattern of effects for neutral words in the final epoch could be interpreted as consisting primarily of a robust parietally based old/new effect being sustained to the end of the epoch, and as such indexing high levels of episodic retrieval rather than post-retrieval processing. This interpretation is consistent with the prediction outlined in the introduction that for simple recognition of neutral items, the mere retrieval of episodic information would be a reliable guide as to whether a test item was old or new. (By this account the lack of qualitative differences between the scalp distributions of neutral and negative items reflects a type 2 error.) However, it is not possible to rule out the alternative possibility that the parietally based effect is simply disguising the right frontal effect for the neutral items, hence the results are indeterminate with regard to whether neutral items associate with a right frontal effect or not.

Finally, the present results have important implications for interpreting the outcomes of neuroimaging studies which necessitate the blocking of stimuli – the typical example being PET. Whilst general issues regarding experimental design (blocked versus mixed) and memory have been discussed on numerous occasions, the findings of this experiment contribute further to the issue providing evidence that brain activity associated with emotional memory is differentially affected by the arrangement of items at test in more ways than previously documented. To date, concerns regarding experimental design and emotional memory have focused on the notion that patterns of brain connectivity are dynamic and change over time in relation to particular events – for example habituation to emotional stimuli or the extinction of a CER (Büchel et al., 1999). This study instead provides evidence that, 'retrieval orientation', that is the processing applied to a retrieval cue (see Rugg and Wilding, 2000), is affected by both stimulus type (emotional versus non-emotional) and the manner in which retrieval cues are presented.

Interim Summary: Experiments 1 and 2

Experiments 1 and 2 provide evidence that the recognition of emotional relative to neutral words modulates a common set of retrieval processes. Differential retrieval effects are driven primarily by negatively valenced words sharing higher levels of inter-item associations relative to neutral words, rather than the influence of 'specialised' emotional neural circuitry. In addition, such effects of valence influence recognition memory primarily through episodic retrieval (spurious or real) as opposed to familiarity. The two experiments serve to highlight three important methodological issues regarding the use of emotional stimuli in studies of memory retrieval. First neutral and emotional stimuli differ on more dimensions than just emotionality. As shown, emotion influences memory primarily through mechanisms of semantic-cohesion, but it is also probable that other 'non-emotional' factors may differentially influence retrieval processing for emotional and neutral stimuli. For example, in the case of words, differences are also likely with respect to imagability and concreteness (Campos et al., 1999). Second, as a result of the differential influence of semantic-cohesion on retrieval processing according to valence type, test format critically affects the type of processing that is applied to the retrieval cue. Although the effect of test format has been considered previously with respect to emotional memory (Büchel et al., 1999; Büchel and Dolan, 2000), discussion has focused on issues relating to habituation and extinction as opposed to 'retrieval orientation'. The third issue, necessarily following from the second, is that when emotional stimuli are employed as both study and test items, the emotional attributes of the retrieval cues are confounded with the emotional attributes of the information to be retrieved. Because of this, it may be difficult or impossible to distinguish between neural activity associated with accessing emotional vs. non-emotional memories, and activity associated with the representation and further processing of these memories.

CHAPTER 7

Experiment 3: Electrophysiological correlates of the incidental retrieval of emotional and non-emotional context

Chapter Summary

Scalp recorded ERPs were used to investigate the neural activity elicited by the incidental retrieval of emotional and non-emotional contextual information. In contrast to the previous experiments, the paradigm employed did not confound the emotional valence of the retrieval cues with the valence of the 'to-be-retrieved' information. Participants studied neutral words presented in negatively or neutrally toned sentences. At test, participants made old/new recognition judgements to these words. Left parietal old/new ERP effects were larger and more sustained when elicited by words that had been studied in negative sentences, and a right frontal old/new effect was elicited by these words exclusively. The findings indicate that incidental retrieval of emotional context gives rise to greater activation in neural systems supporting conscious recollection than does retrieval of non-emotional context.

Introduction

The first two experiments addressed the effects of valence on episodic memory and highlighted one of the few circumstances in which episodic retrieval is impaired for events with emotional content, (i.e. when episodic memory is assessed by recognition memory for emotional and non-emotional words). When other types of retrieval tasks are employed however the findings generally indicate that memory is enhanced for events with emotional content (for review see Christianson, 1992). For example, relative to emotionally neutral stimuli, free recall is greater for pictures, words and stories with emotionally negative or positive content (Danion et al., 1995; Phelps et al., 1997; 1998). Similarly, recognition memory for pictures with emotional content is better than that for emotionally neutral items (Hamann et al., 1999).

It is unclear whether the mechanisms underlying the retrieval of information with emotional content are the same as those mediating retrieval of emotionally neutral information. One possibility is that a common neural network is responsible for retrieval of both emotional and neutral information. By this scenario, the effects of emotion upon memory act at the time of encoding or consolidation (for review see Cahill and McGaugh, 1998). Evidence that emotion influences memory consolidation in humans comes from a study of memory for 'taboo' words (LaBar and Phelps, 1998; see also Phelps et al., 1998). These authors found that differences in recall rates for taboo and control items grew with time, with only the latter class of items demonstrating significant forgetting over a one hour study-test interval.

It has been suggested, however, that in addition to its effects at encoding and during consolidation, emotion modulates retrieval processing through the engagement of emotion-sensitive structures such as the amygdala (Dolan et al., 2000; LeDoux, 2000). The question of whether emotion influences retrieval processing has been the subject of studies employing functional neuroimaging methods to investigate the neural correlates of emotional and non-emotional memory retrieval. The results from these studies are inconclusive. Using PET, Taylor et al. (1998) found that relative to recognition memory for neutrally-toned pictures, recognition judgements on emotionally negative pictures was associated with enhanced activation in occipital cortex (lingual gyrus). Taylor et al. (1998) concluded that while retrieval of emotional information did not recruit the same emotion-sensitive structures (e.g. amygdala) involved at the time of encoding, it was associated with enhanced processing in sensory regions. By contrast, in another PET study (Dolan et al., 2000) found that recognition memory for emotional relative to neutral pictures was associated with activation in the amygdala, leading these authors to conclude that emotional memory retrieval did indeed recruit regions specialised for the processing of emotion.

This question of whether the mechanisms underlying the retrieval of information with emotional content are the same as those mediating retrieval of emotionally neutral information was also addressed indirectly in the previous ERP experiments (1 and 2). There it was concluded that there was no evidence that recognition of emotionally negative vs. emotionally neutral words associated with distinct patterns of retrieval-related activity. Importantly, the two experiments highlighted two principle methodological limitations in studies investigating emotional memory using an approach whereby participants either recall or recognise previously presented emotional and non-emotional stimuli (words or pictures).

First, neutral and emotional items may differ on more dimensions than just ‘emotionality’. In the case of words, for example, differences are also likely with respect to imagability and concreteness (Campos et al., 1999). Perhaps most importantly, emotional items are more likely to be ‘semantically cohesive’, that is, to share strong inter-item associations with one another (Phelps et al., 1998). Therefore, the effects of emotional stimuli on memory (and the neural correlates of these effects) may, at least to some extent, be a by-product of their high levels of semantic cohesion. Consistent with this proposal Phelps and LaBar (1997) (cited in Phelps et al., 1998) found that, when inter-item associations were controlled, the recall advantage normally found for emotional words over neutral words was eliminated.

Second, when emotional stimuli are employed as both study and test items, the emotional attributes of the retrieval cues are confounded with the emotional attributes of the information to be retrieved. Because of this, it may be difficult or impossible to distinguish between neural activity associated with accessing emotional vs. non-emotional memories, and activity associated with the representation and further processing of these memories (see Rugg and Wilding, 2000 for a general discussion of these and related issues).

The foregoing problems are well illustrated by the first two experiments in this thesis. Behavioural measures revealed that recognition memory was markedly lower for the negative words, an effect that was carried entirely by the differential false alarm rates for the two classes of word. This finding (for similar results see Leiphart et al., 1993) was attributed to the high levels of semantic association between the negative words, which, it was argued, led to a 'false recollection' effect for unstudied items analogous to the effect found for 'related lures' in experimental studies of false memory (Roediger and McDermott, 1995).

The ERP data from the previous experiments also differed according to the emotional status of the eliciting words. The left parietal old/new effect was greatly reduced in amplitude for negative relative to neutral words. Echoing the behavioural findings, the effects of emotion were carried almost entirely by the ERPs elicited by correctly classified new items, the waveforms elicited by the two classes of recognised words barely differing from one another. It was proposed that, as a result of high levels of semantic relatedness between studied and unstudied negative words, the latter items tended to give rise to 'false' recollections (evidenced by a left parietal effect) which, if not monitored accurately (evidenced by the right frontal effect), translated into false alarms.

For present purposes, the key point from the first two experiments is that, despite the marked differences exhibited between the memory effects elicited by emotional and non-emotional stimuli, the confounding of the nature of the test items with the nature of the information to be retrieved meant that these differences could not be attributed to emotion-specific differences in retrieval processing. In the present study, ERPs were employed again to investigate the retrieval of emotional and non-emotional memories, but here an experimental design was employed which removed the confound noted above. This was achieved by contrasting the neural activity elicited by only one kind of retrieval cue (emotionally neutral words) according to the emotional valence of the study context in which the words had been encoded. With such a procedure, any differences between ERPs elicited at retrieval by the two classes of studied words can confidently be attributed to the consequences of retrieving emotional vs. non-emotional memories. At issue is the question of whether such differences will be quantitative, as was the case in the previous two experiments, or qualitative.[1] The presence of qualitative differences, which would be indicated by an effect of emotion on the scalp distribution of the memory effects elicited by studied words (Kutas and Dale, 1997), would provide support for the view that the retrieval of emotional and non-emotional memories engages neural systems that are at least partially distinct.

Methods

Participants

All participants were right handed, had English as their first language and were aged between 18 and 30. 23 participants were employed. Each gave informed consent prior to participation in the study and was paid £5 per hour. Seven participants' data were rejected; in 3 cases because of excessive electro-oculographic artefact, in 2 cases because of inadequate behavioural performance, and in another 2 cases because of technical failure. The 16 participants whose data were analysed consisted of 10 females and 6 males.

Experimental materials

260 emotionally neutral words were used as critical stimuli (see below for details of how normative ratings were acquired). The words varied in length between 4 and 10 letters and in frequency between 30 and 100 per million (Francis and Kucera, 1972). For each word, one neutral and one negative sentences was constructed. For example, for the critical word 'gas', the sentences 'She put the pan on the stove and turned on the gas', and 'She put her head in the oven and lit the gas', were generated as 'neutral' and 'negative' sentences respectively. Critical words never featured in sentences other than their designated negative and neutral sentences. Sentences were of equal length (neutral; mean = 9.38, s.d. = 1.70, negative; = mean = 9.12, s.d. = 1.88) and were formed so as to be roughly equivalent in the nature and range of grammatical constructions employed.

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[1] Where ERP and behavioural findings elicited by the emotional context manipulation (this study) are compared with effects elicited by the alternative emotional item manipulations, comparisons are made with the effects obtained in experiment 1 (but not experiment 2) since in experiment 1 the data were obtained using a recognition memory task most similar to that employed here, i.e. negative and neutral items mixed at test

Word norms and selection

Normative emotional valence ratings were collected for 320 ostensibly neutral words. In order to obtain the norms for these words they were randomly intermixed with 35 emotionally positive words and 35 emotionally negative words (taken from Siegle, 1998). Ten participants were given the resulting list of 390 words and asked to rate each word on a Likert scale (ranging from –3 to +3) according to how emotionally 'neutral', 'negative' or 'positive' they felt it to be. The average ratings given to the negative, neutral and positive words were –1.8, 0.4 and 1.6 respectively. Of the 320 neutral words forming the initial pool, 21 were dropped because they received ratings of ± 1, another 35 were dropped because of difficulties in constructing a negative or a neutral sentence for the word, and 24 were used as filler items. The remaining 260 words were employed as the critical stimuli.

Generation of study and test lists

Four study lists were created, each containing a set of 65 negative and 65 neutral sentences. The sentences in the study lists were randomly ordered and a neutral filler sentence was added to the beginning and end of each list. Two test lists were created. Each list comprised all 260 critical words (different randomly determined orders in each list) with a filler word added to the beginning of each test list. The combination of 4 study lists and 2 test lists resulted in 8 possible study-test list combinations. Each combination was employed with two participants. Study and test lists were assigned such that, across the experiment, each critical word appeared 8 times as a new item, 4 times as an old item encoded in an emotionally negative sentence, and 4 times as an old item encoded in a neutral sentence.

Procedure

Before the electrode cap was applied, participants were informed that the experiment would involve the presentation of emotionally negative sentences. They were further informed that parts of the experiment would involve a memory task. An example of the study phase was then given. This consisted of the presentation of 3 neutral and 3 negative practice sentences.

Study Phase

Participants were presented with the study materials on a computer monitor (white text on a dark screen). Each study trial consisted of two stages. First, participants were presented with a sentence and required to give it an affective rating. The critical word from the sentence was then presented alone on the monitor with the requirement to read it aloud and remember it in the context of the sentence of which it had been part. Sentences were presented approximately every 10 - 15 seconds.

Test Phase

Each trial began with the presentation of a fixation character for 1000 msec, which was removed 104 msec before the onset of the test word. The word was displayed for 300 msec, following which the monitor was blanked for 2700 msec. Participants were required to judge whether or not each test word had been presented in the study phase. No mention was made of the different types of sentences employed at study. Responses were made by button press using one or other index finger. The mapping of fingers to response type was counterbalanced across participants. Participants were instructed to relax, to keep body movements to a minimum, and to blink only when the fixation character was in view. Responses faster than 300 msec or slower than 2500 msec were treated as errors.

ERP Recording

EEG was recorded from 25 tin electrodes embedded in an elasticated cap and from an electrode placed on the right mastoid process. All channels were referenced to a left mastoid electrode, and re-referenced off-line to represent recordings with respect to linked mastoids. EOG was recorded bipolarly from electrodes placed above the supraorbital ridge of the right eye and on the outer canthus of the left eye. EEG electrodes were located according to the International 10-20 system (Jasper, 1958). They were located over the midline (Fz, Cz, Pz), and at the following additional locations: left and right frontal [FP1/FP2, F3/F4, LF/RF (75% of the distance from Fz to F7/8), and F7/F8], central/anterior temporal [C3/C4, LT/RT (75% of the distance from Cz to T3/4), and T3/T4], parietal/posterior temporal [P3/P4, LP/RP (75% of the distance from Pz to T5/6), T5/T6], and occipital (O1,O2). Data were sampled at a rate of 8 msec per point and digitised with 12 bit resolution. The duration of the recording epoch was 2048 msec including the 104 msec pre-stimulus baseline.

All channels were amplified with a bandpass of .032-35Hz (3dB points). Trials on which base-to-peak EOG activity exceeded ±98 microvolts were rejected, as were trials on which A/D saturation occurred, or on which baseline drift across the recording epoch (i.e. amplitude of the first point relative to the amplitude of the last point of the epoch) exceeded ±55 microvolts in any EEG channel.

ERPs were formed for 3 response categories: correctly rejected new words (correct rejections); correctly recognised old words previously presented in a neutral sentence (neutral hits); and correctly recognised old words previously presented in an old negative sentence (negative hits). The waveforms were smoothed with a 5 point binomally weighted filter. There were insufficient trials to form ERPs to error trials.

Results

Behavioural Data

The mean rating assigned to the negative sentences was -1.90, (sd = 0.42) whereas the mean rating for the neutral sentences was 0.51, (sd = 0.34). These means differed reliably ($t_{15} = 13.80$, $p < 0.001$). For every participant, the mean rating given for the negative sentences was significantly lower than that for the neutral sentences (minimum t64 = 8.4).

Correct rejection and hit rates for words, and their associated reaction times, are shown in table 7.1. A one-way ANOVA on the accuracy scores revealed a main effect of condition (F(1.4, 21.5)=5.90, p<0.05). Tukey HSD tests revealed that participants made a higher proportion of correct responses to new words than to either type of old word. The mean proportions of neutral and negative hits did not differ reliably. Reaction times (RTs) for the three classes of word did not differ significantly. When tested separately the mean reaction times for the neutral and negative hits did not differ significantly.

Table 7.1 Experiment 3: Behavioural data
Mean proportions (standard deviation in brackets) of correct rejections, neutral hits and negative hits along with associated reaction times.

	CR	Neutral Hit	Negative Hit
Proportion	0.80 (0.08)	0.70 (0.11)	0.71 (0.08)
Reaction time (msec)	1094 (280)	1053 (284)	1027 (276)

ERP Data

The mean number of trials (range in brackets) contributing to the average ERPs for correct rejections, neutral hits and negative hits were 76 (52-104), 33 (22-44) and 36 (23-49) respectively. Grand average waveforms from selected lateral and midline sites are shown overlaid in figure 7.1.

As can be seen from figure 7.1, ERPs began to diverge from around 300msec post-stimulus onset. Both classes of old word exhibit left parietal old new effects, which appear to be greater in size and more extended in time for the negative hits. From around 800 msec a right frontal old/new effect is evident for the negative hits; this effect appears to be absent in the ERPs elicited by the neutral hits.

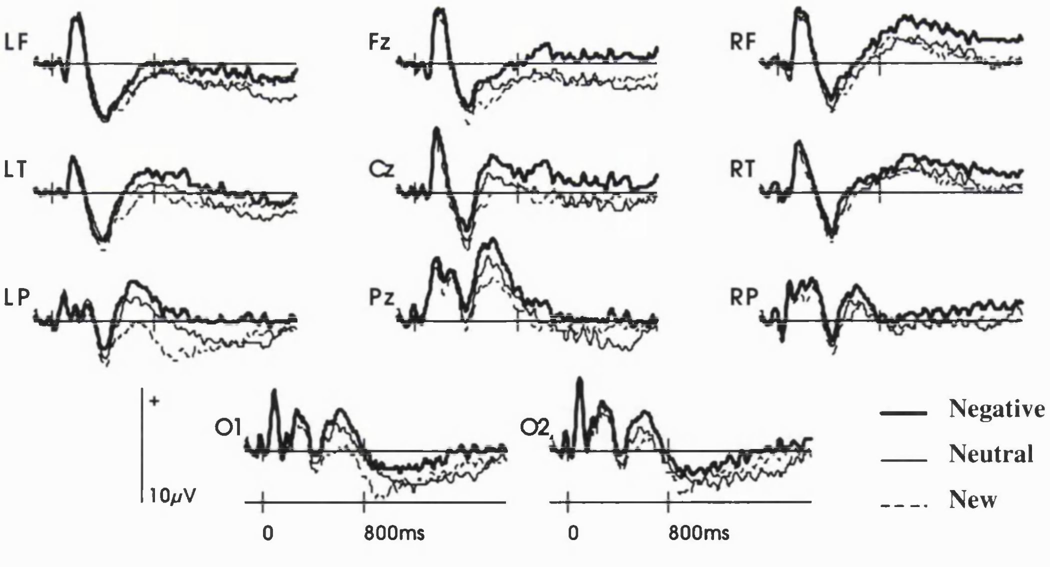

Figure 7.1. Experiment 3: Grand average ERP waveforms
See text for electrode locations.

ERPs were quantified by measuring (with respect to the mean of the pre-stimulus baseline) the mean amplitudes of 3 consecutive latency regions (500-800 msec, 800-1100 msec, 1100-1900 msec). These intervals correspond to latency regions selected for analysis in experiments 1 and 2 of this thesis and also previous studies of episodic memory (e.g. Wilding and Rugg, 1996; Schloerscheidt and Rugg, 1997; Donaldson and Rugg, 1999). Two sets of analyses were performed. The first set investigated differences in the amplitude of the ERPs to the three classes of items (negative, neutral, new). These analyses took the form of ANOVAs on data from 18 lateral electrode sites, the outcomes of which are shown in table 7.2. In addition to these multi-site ANOVAs, separate ANOVAs were also conducted on data from the left parietal and right frontal sites respectively; these analyses were performed to permit a direct comparison with the findings of experiment 1.

The second set of analyses tested for differences in the scalp distributions of the old/new effects as a function of the emotional status of the old word (negative vs. neutral) and latency. In all ANOVAs degrees of freedom were corrected for non-sphericity with the Greenhouse-Geisser procedure (Keselman and Rogan, 1980) and F ratios are reported with corrected degrees of freedom. Data employed in the topographic analyses were rescaled to eliminate the confounding effects of between-condition and between-epoch differences in amplitude (McCarthy and Wood, 1985).

Mean Amplitude Analyses

ANOVAs were conducted for each latency region on the data from lateral frontal (F7/8,LF/RF, F3/4), temporal/central (T3/4, LT/RT, C3/4), and parietal (T5/6, LP/RP, P3/4) electrode sites, employing the factors of condition (negative, neutral, new), hemisphere, location (frontal, temporal/central, parietal) and site (inferior, middle, superior). The outcomes of these ANOVAs are shown in table 7.2. They were followed up by subsidiary ANOVAs, contrasting separately the waveforms to each class of hit (negative, neutral) with the new waveforms, and where appropriate, with each other.

Table 7.2 Experiment 3: Mean amplitude analyses, significant effects summary
Outcome of ANOVAs of mean amplitudes of the latency intervals. Only significant effects involving the condition factor (correct rejection vs. neutral hits vs. negative hits) are reported. CC = condition, CH = location (anterior, centrotemporal, parietal), HM = hemisphere, ST = electrode site (inferior, middle, superior).

	500-800msec	**800-1100msec**	**1100-1944msec**
CC	F(2,29.6)=5.90, p<0.01	F(1.8,27.2)=4.28, p<0.05	F(1.9,29.2)=6.15, p<0.01
CCxCH	F(2.3,33.9)=3.07, p=0.05	-	-
CCxST	F(1.8,26.8)=9.07, p=0.001	F(1.6,23.9)=4.76, p<0.05	-
CCxCHxHM	F(2.6,38.5)=6.62, p<0.005	F(1.9,28.3)=4.19, p<0.05	F(3.1,45.8)= 3.09, p<0.05
CCxCHxHMxST	F(4.4,65.5)=3.33, p=0.01	F(4.5,68.1)=3.13, p<0.05	-

Analysis of the data from the 500–800 msec region revealed a main effect of condition, and also a number of interactions between the condition and site factors. As can be seen from figures 7.1 and 7.2, old/new effects in this latency range exhibited a left parietal maximum in both the negative and the neutral condition. ANOVA contrasting the ERPs to the neutral hits and correct rejections revealed interactions between response category (i.e. hits vs. correct rejections) and site (F(1.1,16.4) = 5.49, p = 0.05), response category, location, and hemisphere (F(1.8, 27.2) = 7.27, p < 0.005), as well as a four way interaction between response category, location, hemisphere and site (F(3.0,44.9) = 5.97, p < 0.005). These interactions reflect the fact that the neutral old/new effect was largest at left parietal scalp sites, and showed a tendency to increase in size towards the midline. The same contrast for the negative condition revealed a main effect of response category (F(1,15) = 12.98, p < 0.005) and interactions between response category and location (F(1.4, 21.7) = 8.16, p < 0.005), response category and site (F(1.2,18.2) = 24.26, p < 0.001) and between response category, location and hemisphere (F(1.6,24.4) = 9.74, p = 0.001). As can be seen from figure 7.2, these interactions reflect a tendency for negative old/new effects to be greatest at left parietal scalp sites. Analysis contrasting the two types of hit revealed no significant effects involving the factor of context.

ANOVA on the data from the left parietal site alone revealed a main effect of condition (F(1.9, 28.3) = 15.03, p < 0.001). Old/new effects were reliable for both the neutral (F(1,15) = 9.27, p < 0.01) and the negative conditions (F(1,15) = 28.06, p < 0.001). An ANOVA contrasting the waveforms to neutral and negative hits revealed a main effect (F(1, 15) = 5.96, p < 0.05), ERPs to the negative hits showing greater positivity than those to the neutral hits.

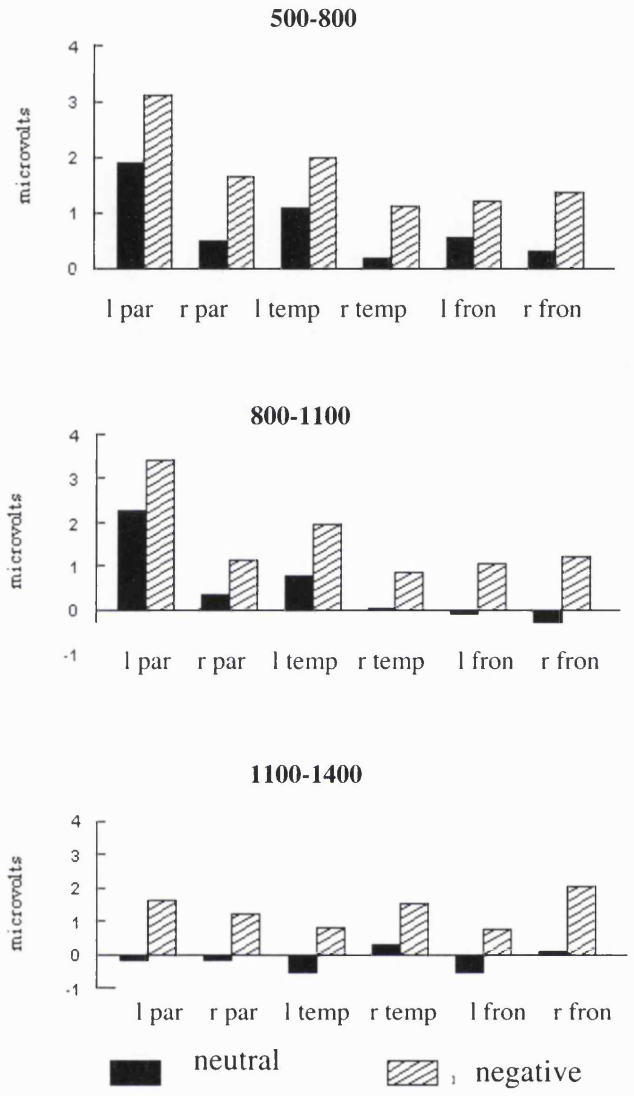

Figure 7.2. Experiment 3: Mean old/new effects for the 500-800 msec, 800-1100 msec, and 1100-1944 msec epochs.
l post, r post, l temp, r temp, l ant, and r ant refer to left and right posterior, temporal/central, and anterior electrodes respectively.

ANOVA on data from the 800-1100msec region revealed a main effect of condition, and interactions between condition, location and hemisphere, and between condition, location, hemisphere and site (see table 7.2). ANOVA of the data for the neutral old/new effects revealed interactions between response category and location

$(F(1.1,17.1) = 4.14, p = 0.05)$, and between response category, location, hemisphere and site $(F(3.0, 45.2) = 5.34, p < 0.005)$, indicating that the old/new effects were largest at left parietal scalp sites. The contrast between negative hits and correct rejections gave rise to a main effect of response category $(F(1,15) = 7.39, p < 0.05)$, an interaction between response category and site $(F(1.2,17.4) = 9.36, p = 0.005)$, and a three way interaction between response category, location and hemisphere $(F(1.4,20.3) = 5.25, p < 0.025)$. These effects reflect the fact that the negative old/new effects in this latency range maintain their left parietal maximum (see figure 7.2). ANOVA contrasting the data from the 800-1100 msec latency region for the two classes of hits revealed a main effect of context $(F(1,15) = 5.75, p < 0.05)$, and a marginally significant interaction between context, location and hemisphere $(F(1.5, 22.6) = 3.58, p < 0.06)$. As illustrated in figure 7.2, these effects reflect the relatively greater positivity in the ERPs to the negative hits, an effect which is most pronounced at left parietal and right frontal sites.

ANOVA of the 800-1100 msec data from the left parietal site revealed a significant condition effect $(F(1.3, 19.1) = 12.23, p = 0.001)$. Old/new effects were reliable for both for the neutral $(F(1,15) = 7.73, p < 0.05)$ and negative hits $(F(1,15) = 17.61, p = 0.001)$. Analysis contrasting the data for the neutral and negative hits revealed a significant effect of context $(F(1,15) = 9.30, p < 0.01)$, reflecting the greater positivity of the waveforms to the negative hits.

As shown in table 7.2, ANOVA of the 1100-1900msec latency regions revealed a main effect of condition, and a three-way interaction between the condition and site factors. Figure 7.2 shows that old/new effects in this latency region were present over the left posterior and right hemisphere scalp sites, but were confined to the negative words. In keeping with this impression, the ANOVA contrasting the neutral hits with the correct rejections gave rise to no significant effects involving response category. ANOVA of the negative old/new effect revealed a main effect of response category $(F(1,15) = 9.18, p < 0.01)$, and a three way interaction between response category, hemisphere and location $(F(1.8, 27.7) = 5.10, p = 0.01)$. As can be seen in figures 7.2 and 7.4, these effects reflect predominantly the presence of a right frontal old/new effect for the negative items in this latency region. ANOVA contrasting the data for neutral and negative hits revealed a main effect of context $(F(1,15) = 9.14, p < 0.01)$, reflecting the relatively greater positivity of the ERPs to negative hits.

ANOVA of the 1100-1900 msec data from the right frontal site alone revealed a main effect of condition ($F(1.9, 28.5) = 5.01$, $p = 0.01$). Old/new effects were reliable in the negative condition ($F(1,15) = 8.83$, $p = 0.01$) but not in the neutral condition ($F < 1$). An ANOVA contrasting the waveforms to neutral and negative hits revealed a main effect of context ($F(1, 15) = 5.51$, $p < 0.05$), reflecting the more positive ERPs for the negative hits.

Topographic Analyses

The first set of topographic analyses contrasted the scalp distribution of the old/new effects elicited by neutral and negative hits for both the 500-800 msec and, separately, the 800-1100 msec latency regions. The scalp distributions of these effects are illustrated in figure 7.3. For both latency regions, ANOVAs revealed effects of site [$F(3.3, 50.2) = 3.79$, $p = 0.01$, and $F(3.6, 54.5) = 3.42$, $p < 0.025$, for the 500-800 and 800-1100 msec regions respectively] but no evidence of an interaction between site and context (both $Fs < 1$). As can be seen in figure 7.3, the old/new effects elicited by the neutral and negative items in these latency regions show prominent left parietal maxima.

A second set of analyses contrasted the scalp distributions of the old/new effects elicited by the negative words as a function of latency region. The contrast was conducted across the two latency regions – 500-800 msec and 1100-1944 msec - in which the old/new effects appeared to show the most disparate distributions (see figure 7.3). The ANOVA revealed a significant site by latency region interaction ($F(3.3, 50.2) = 3.07$, $p < 0.05$) indicating that the scalp distribution of these old/new effects differed with time. As is shown in figure 7.4, the distributions evolved from a left parietal to a right frontal maximum.

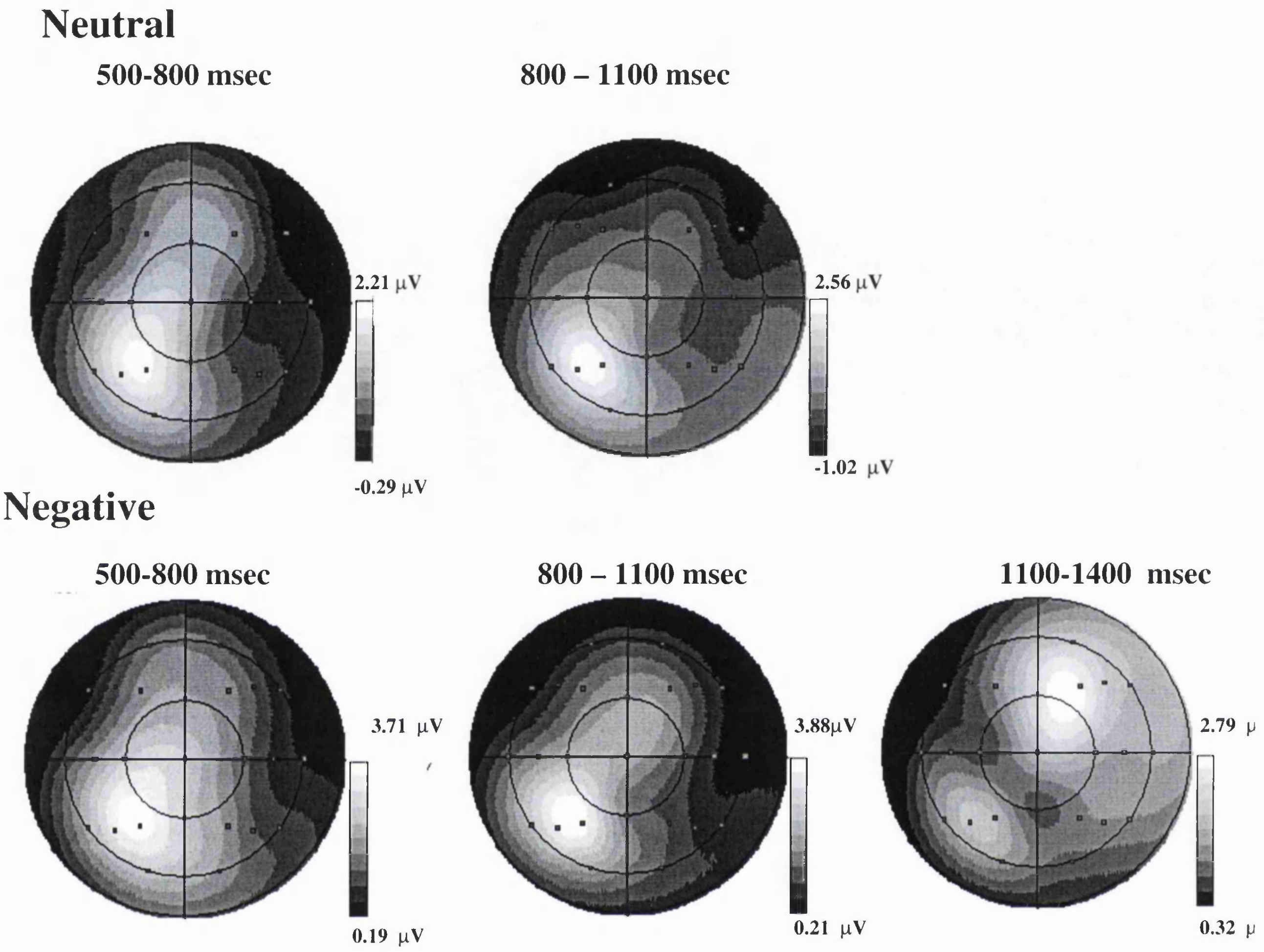

Figure 7.3. Experiment 3: Topographic maps illustrating the scalp distributions of the old/new effects for the latency intervals indicated.

Summary

Old/new effects were elicited by negative hits from around 500 msec post-stimulus until the end of the recording epoch. These effects evolved with time from a left-parietal to a right frontal focus. Old/new effects were present for the neutral items in the first two latency regions analysed only, were smaller in magnitude than the effects elicited by the negative items, and were restricted to the left posterior scalp.

Discussion

Performance Data

Items encoded in the neutral and negative contexts were recognised with equivalent levels of accuracy, and with comparable RTs. These findings, which stand in contrast to when emotional and non-emotional words were employed as stimuli, suggest that when inter-item associations between emotional and non-emotional test items are controlled the effects of emotion on recognition memory are, at best, subtle.

The present findings are inconsistent with previous reports that emotionally toned contexts enhance memory (as indexed by free recall) for pre-experimentally neutral stimuli (Phelps et al., 1997; Phelps et al., 1998). However, as noted in the Introduction, there is evidence that emotionality effects grow with time, and may emerge out of differential forgetting rates (LaBar and Phelps, 1998). It is possible therefore that effects of the present emotionality manipulation would have been more evident had the study-test interval been longer. It is also possible of course that recognition memory is not sufficiently sensitive to detect differences in memory arising from the contextual manipulation employed here, perhaps because participants could base their recognition judgements on item 'familiarity' as well as on the products of episodic retrieval (Mandler, 1980; Jacoby and Kelley, 1992), and that some other task, such as free recall, would have revealed such differences. On a more positive note, the failure to find context effects on recognition accuracy or RT means that it is unlikely that the differences that were observed between the ERPs to negative and neutral hits are a simple consequence of differences between conditions in such variables as the speed or confidence of recognition judgements.

ERP Effects

As when emotional and non-emotional words were used as stimuli, and in line with numerous earlier reports (for review see Chapter 3), words correctly judged old elicited ERPs that were more-positive going than those elicited by correctly rejected new items. This effect could be dissociated into two topographically and temporally distinct components, corresponding to the left parietal and the right frontal effects described in earlier studies (see Introduction). In contrast to when emotional and non-emotional words were used as stimuli, the left parietal old/new effect in the present experiment was smaller for the neutral items than the negative items. Furthermore, whereas in experiment 1 the right frontal effect was present only in the ERPs to the neutral items, in the present experiment it was present exclusively in the ERPs to the negative items.

The smaller ERP effects for negative words were accounted for by the assumption that emotionally negative words shared higher levels of inter-tem associations than did the emotionally neutral words, and that these associations caused unstudied negative words to elicit 'false' or spurious recollection, which was manifested both as an elevated false alarm rate, and enhanced ERP positivity for correctly rejected new words. The present results support this interpretation, in that they demonstrate that such effects are not present when the semantic cohesion of the retrieval cues for emotionally negative and emotionally neutral memories are controlled. More important, though, the present findings demonstrate that, even in the absence of a detectable effect on memory performance, the neural correlates of the incidental retrieval of emotional and non-emotional contexts differ reliably.

The finding that the left parietal old/new effect was greater for retrieval of negative context than for neutral context is reminiscent of previous studies in which the effect was found to covary with variables influencing either the probability of episodic retrieval or the amount of information retrieved (Smith, 1993; Rugg et al., 1995; Wilding et al., 1995; Wilding and Rugg, 1996; Düzel et al., 1997; Donaldson and Rugg, 1998). In light of these findings, one plausible interpretation of the present result is that recognition of items encoded in the negative contexts was associated with the retrieval of more information about the encoding episode than was recognition of the words encoded in the neutral contexts. This could have come about either because emotional content is inherently 'richer' or more 'salient' information wise, or because of the facilitatory effects of emotional arousal in memory encoding.

Either of the foregoing interpretations is predicated on the assumption that the averaged ERPs elicited by the negative and neutral hits are representative of the situation at the single trial level. An alternative possibility however is that the left parietal old/new effect is, in fact, an 'all or none' phenomenon, and that the differences in the size of this effect in the average ERPs for negative and neutral hits reflect differences in the proportion of trials on which the effect was elicited, rather than differences in its magnitude. In other words, the differing magnitudes of the left parietal effects in the ERPs to negative and neutral hits are a consequence of the effect being elicited more frequently by negative hits. By this account the seemingly graded nature of the left parietal effect elicited by the two word classes is an artefact of across-trial averaging.

The two accounts given above of the differential left parietal effects observed in the present study are not mutually exclusive (cf. Donaldson and Rugg, 1998). Importantly, an implication of both accounts is that episodic retrieval is facilitated when a test item is subjected to prior study in an emotionally negative as opposed to an emotionally neutral context. Thus, in contrast to when emotional words were used as stimuli, the present ERP results are consistent with previous research suggesting that emotion facilitates episodic memory (see Introduction). As described in Chapter 3, the locus of the differential activity reflected by the left parietal effect would probably be found in the medial temporal/posterior cortical regions subserving the initial retrieval of episodic information, (Nyberg et al., 1996; Rugg et al., 1997a).

The second old/new effect observed in the present experiment, elicited solely during retrieval of negative context, took the form of a late-onsetting, sustained right frontal positive shift. As noted a number of times already, this effect is held to reflect processes that operate on the products of memory retrieval. More specifically, the effect has been interpreted as reflecting 'post-retrieval' operations which are brought into play when retrieved information must be represented, maintained and monitored with respect to its relevance to current behavioural goals (Rugg and Wilding, 2000).

At first sight, the present findings indicate that, unlike the left parietal effect, the right frontal effect was elicited solely by the negative hits. Thus the effect may reflect cognitive operations which were engaged exclusively by retrieval of the emotionally negative contexts. Before accepting this conclusion, however, it is necessary to consider the possibility that the failure to detect a right frontal effect for neutral hits is merely a consequence of the fact that these items failed to elicit episodic retrieval on a higher proportion of trials than did the negative hits.

As already noted, other things being equal, a reduction in the proportion of trials on which the studied items were recollected will be reflected in a corresponding reduction in the size of the neural correlates of recollection in averaged ERPs. As discussed above, this could explain the finding of a smaller left parietal effect for neutral hits relative to negative hits. However, relative to the effect elicited by the negative hits, the right frontal effect for neutral hits was attenuated to a greater extent than that observed for the left parietal effect; had it been attenuated to the same extent (i.e. to approximately 40% of its size for the negative hits) its mean magnitude at the right frontal site in the 1100-1900 msec latency region would have around 1.17μV. The observed magnitude, by contrast, was 0.18 μV.

The presence of a right frontal effect in the ERPs to the negative hits alone suggests that recollection of emotionally negative, but not emotionally neutral, contexts triggered cognitive operations supporting post-retrieval processing. Thus, it would appear that the retrieval of emotional information, even when incidental to task requirements, is sufficient to engage what are held to be resource demanding evaluation and monitoring operations supported by the right prefrontal cortex (Rugg et al., 1996; Shallice and Burgess, 1996; Henson et al., 1999b; McDermott et al., 2000; Henson et al., 2000). It would be of considerable interest to know whether the engagement of these operations was voluntary or involuntary.

An important aim of the present experiment was to assess whether the neural correlates of the retrieval of emotionally negative information differed qualitatively or quantitatively from the correlates of the retrieval of emotionally neutral information. Despite the differences discussed above between the ERP old/new effects elicited by negative and neutral hits, the findings provide no evidence that the effects elicited by the negative hits reflected neural activity uniquely sensitive to emotional information. Rather, the differences took the form of modulations of two memory effects which have both been reported in previous studies that employed non-emotional experimental items (Rugg and Allan, 2000). Thus, as when emotional words are employed as stimuli, the present results do not support the proposal that retrieval of emotional information recruits emotion-sensitive neural systems additional to those engaged during the retrieval of emotionally neutral memories.

As has been noted already, the effects of emotion discussed above were a consequence of incidental retrieval of context. The question arises whether similar effects would be observed when retrieval of study context was an explicit task requirement, as would be the case for example in a test of source memory for the study items. With this task, contextual information must both be intentionally retrieved and subjected to post-retrieval evaluation. If the differential old/new effects observed in the present experiment reflect some inherent property of emotional memories, larger old/new effects for items encoded in emotional contexts might be expected regardless of task demands. If, however, the differential old/new effects reflect some ‘second order’ property of emotional memories, such as their capacity to capture attention and processing resources, the differences observed between the ERPs to negative and neutral hits when emotional context is irrelevant to the task should be attenuated when retrieval of study context is made task relevant.

CHAPTER 8

Experiment 4: Electrophysiological correlates of the intentional retrieval of emotional and non-emotional context

Chapter Summary

This experiment addressed the effects of emotional vs. non-emotional study contexts on ERP old/new effects in a task where there was, in contrast to experiment 3, an explicit requirement for contextual retrieval. Participants studied words presented in negatively or neutrally toned sentences. At test, participants made old/new recognition judgements to these words and for words judged old also indicated whether the words had been studied in a neutral or a negative context. The left parietal and right frontal effects elicited by old words correctly assigned to their study context were equivalent in size regardless of the nature of the context, and a third ERP old/new effect, maximal over posterior scalp regions, was elicited exclusively by words from negative contexts. The findings indicate that when contextual retrieval is intentional recollection of emotional and non-emotional information are associated with equivalent engagement of neural systems supporting conscious recollection. The findings are also consistent with the existence of additional neural circuitry that is activated selectively during retrieval of emotionally toned episodic information.

Introduction

The aim of this experiment was to assess the effects of emotional vs. non-emotional study contexts on ERP old/new effects in a task where there was an explicit requirement for contextual retrieval. This aim was achieved by modifying the yes/no recognition procedure employed in experiment 3 to include a subsequent judgement of the context in which each recognised test word had been presented. This task was very similar to, and based upon, the source memory procedure introduced by Wilding and Rugg (1996)

The present experiment also provides an opportunity to reassess the question of whether neural correlates of the retrieval of emotionally negative and neutral memories differ qualitatively. For two reasons, this question can be addressed with more power than was the case in experiment 3. First, the experimental task permits ERPs to be formed only for those recognised items for which there is behavioural evidence of successful contextual retrieval; in experiment 3, by contrast, the ERPs elicited by old items would have included an unknown number of trials on which recognition was not accompanied by episodic retrieval [and was instead based exclusively on familiarity; (Mandler, 1980; Jacoby and Kelley, 1992)]. Second, a more extensive recording montage was employed in the present experiment, permitting a more comprehensive sampling of the scalp distribution of the ERP old/new effects.

Methods

In most respects, the experimental procedure was identical to that employed in experiment 3. In the present experiment however, two study-test blocks were employed in order to ensure adequate levels source memory. An interval of around 5 minutes separated the two blocks.

Participants

25 participants were employed in the study. They were drawn from the same population as those employed in experiment 3, and received the same level of payment. Nine participants' data were rejected; 1 because of uncorrectable EOG artefact, 2 because of inadequate behavioural performance, and 6 because of technical

failures. The 16 participants whose data were analysed consisted of 7 females and 9 males.

Experimental Items

The critical words and sentences were the same as those employed in the previous experiment.

List Creation

Each of the 4 study lists created for experiment 3 was divided into two. The first set of 65 sentences of each study list formed the study items for the first study-test block, and the second set of 65 sentences were used as study items for the second block. Neutral filler sentences were added to the beginning and end of each study list. Test lists were created such that each study list could be followed by a test list containing the 65 old words from the sentences in the study block and 65 previously unseen words. Filler words were added to the beginning and end of each test list. In total, eight test lists were created, each with a different randomised order. As in experiment 3, study/test list combinations were rotated across participants to ensure that each critical word appeared in all three conditions in a balanced fashion.

Study Phase

The study procedure was identical to that in experiment 3.

Test Phase

The test phases began approximately five minutes after the end of their corresponding study phases. Each trial began with the presentation of a fixation character which was removed 104 msec before the onset of the test item. The test item was then displayed for a period of 500 msec, following which the monitor was blanked. Participants made an old/new response as quickly and as accurately as possible. One second after this first response a question mark character was displayed for 2000 msec to cue the second, source, response. The requirement was to judge in which of the two encoding contexts the word had been presented at study, responding ‘negative’ or ‘neutral’ as appropriate. This decision was signalled with the same two keys employed for the initial old/new decision. The hands required for the first and second decisions were counterbalanced across participants such that there was no correlation between the old/new and negative/neutral judgements. As in experiment 3, participants were instructed to respond as quickly and as accurately as possible, to relax, and to keep body movements to a minimum. As is described below, an EOG correction procedure was employed to remove blink artefacts from ERPs. Therefore participants were not instructed to refrain from blinking during any part of a trial. They were however instructed to maintain fixation on the fixation character between trials.

ERP Recording

The recording system and montage differed from that used in experiment 3. EEG was recorded from 31 silver/silver chloride electrodes. Twenty-nine of these were embedded in an elasticated cap, and one was placed on each mastoid process. The 29 site montage was based upon 'Montage 10' of the Easy Cap Electrode system (http://www.easycap.de/easycap; see figure 8.1). All channels were referenced to Fz, and re-referenced off-line to represent recordings with respect to linked mastoids. Horizontal EOG was recorded from electrodes on the outer canthus of each eye, and vertical EOG was recorded from electrodes placed above and below the right eye.

With the exception of 3 participants who blinked very infrequently, an EOG correction procedure was applied to minimise the number of trials rejected due to blink artefact. The procedure was similar to methods employed in previous studies (e.g. Rugg et al., 1997b) and used linear regression to estimate and correct the contribution of blink artefact to the scalp EEG.

In all participants, trials on which horizontal or non-blink vertical movements were made were rejected. For the three participants whose proportion of blink trials was too low to permit correction, trials containing blink artefact were rejected as in experiment 3. In all participants trials were rejected if A/D saturation occurred, or baseline drift across the recording epoch exceeded ±55 microvolts. EEG and EOG recording parameters were identical to experiment 3.

ERPs were formed for 3 response conditions: correctly rejected new words (correct rejections), and old words recognised and assigned to their correct encoding context ('negative source hits' and 'neutral source hits').

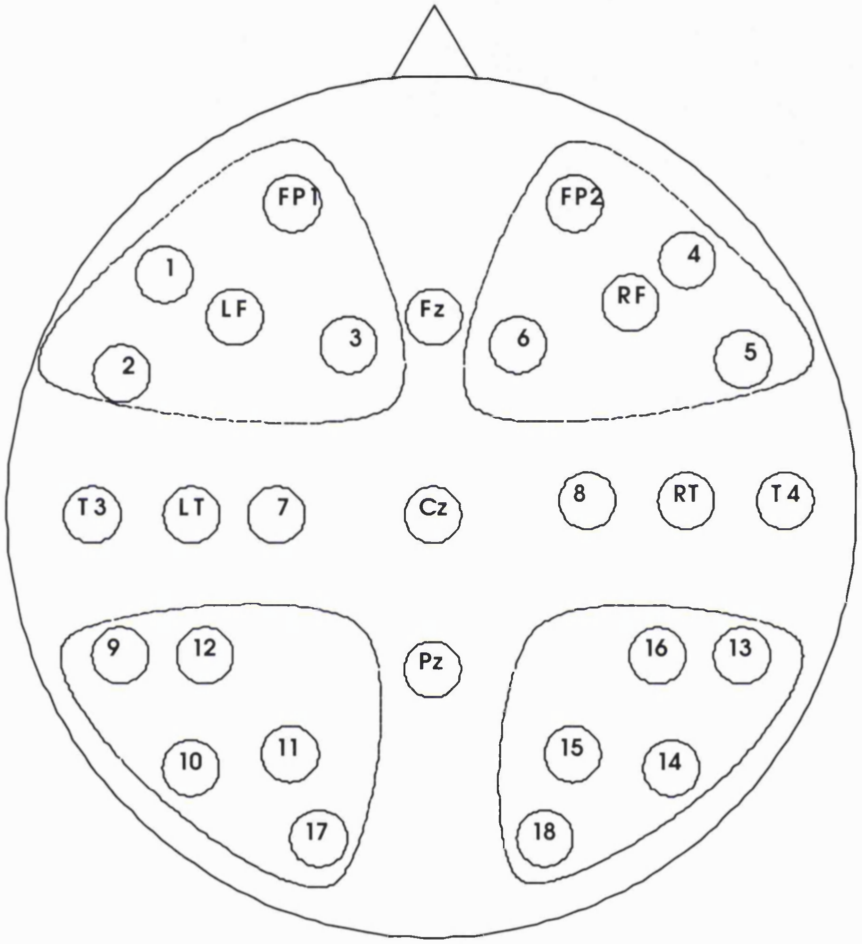

Figure 8.1. Electrode montage employed in experiment 4.
Sites overlapping those employed in experiment 3 are labelled accordingly. Electrodes used in the analyses of anterior and posterior regions (see text) are enclosed within broken lines.

Results

Behavioural Data

The mean rating assigned to the negative sentences was -1.88 (sd = 0.26), whereas the mean rating for the neutral sentences was 0.39 (sd = 0.31). These means, which are comparable to those obtained in experiment 3, differed reliably ($t_{15} = 20.54$, $p < 0.001$). For every participant, the mean rating given for the negative sentences was significantly lower than that for the neutral sentences (minimum t64 = 11.1).

Hit rates for the initial recognition decision are shown in table 8.1, along with correct rejection rates. A one-way ANOVA on these data revealed a main effect (F(1.3,19.2) = 8.29, $p < 0.01$). *Post hoc* analyses (Tukey HSD) revealed that participants were more accurate at correctly detecting new words than they were at detecting either type of old word. A separate planned t-test revealed that the 4.0% difference in hit rate in favour of the negative items was significant ($t_{15}= 2.38$, $p< 0.05$).

Table 8.1 Experiment 4: Behavioural data
Mean proportions (standard deviation in brackets) of correct rejections, neutral hits, negative hits, neutral source hits and negative source hits and their associated reaction times. Proportion of source hits is conditionalised on proportion of hits.

	CR	Neutral Hit	Negative Hit	Neutral Source	Negative Source
Proportion	0.88 (0.11)	0.74 (0.09)	0.78 (0.09)	0.84 (0.09)	0.70 (0.14)
Reaction time (msec)	1308 (228)	1245 (223)	1246 (211)	1212 (202)	1207 (205)

The probability of a correct source judgement for correctly recognised words was 0.77, which was significantly above the chance level of 0.5 ($t_{15} = 13.48$, $p < 0.001$). The proportion of neutral hits receiving a correct source judgement was 0.84, whereas that for negative hits was 0.70. These proportions differed significantly ($t_{15} = 3.19$, $p < 0.01$). To assess whether participants were biased to respond in favour of one or other of the sources in the absence of veridical memory, source judgements were also analysed for false alarms. The probability of a neutral judgement to a new word incorrectly judged old was 0.70. This value differed significantly from 0.5 ($t_{15} = 3.82$, $p < 0.005$), indicating a response bias in favour of the neutral context.

RTs for correct old judgements, both independent of and contingent on source accuracy, are shown in table 8.1 along with the RTs to correct rejections. ANOVA of the RTs for correct rejections, neutral hits and negative hits was not significant. An additional ANOVA of RTs to old items, factored by response accuracy (correct vs. incorrect source) and context (negative vs. neutral), also revealed no significant effects.

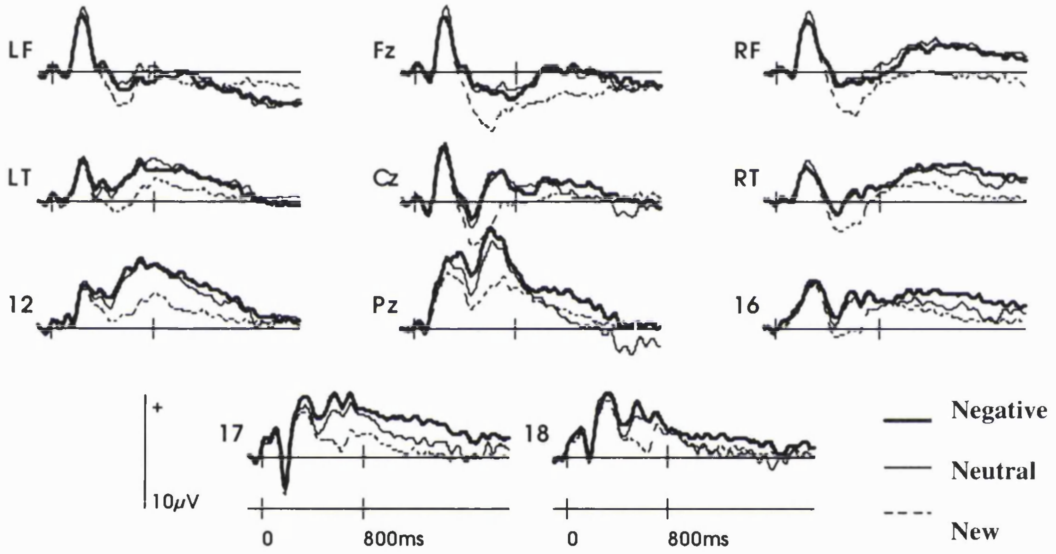

Figure 8.2. Experiment 4: Grand average ERP waveforms.
See figure 8.1 for electrode locations.

ERP Data

The mean number of trials (range in brackets) contributing to the ERPs for correct rejections, neutral source hits and negative source hits were 82 (54-118), 32 (18-41) and 29 (18-48) respectively. The proportion of trials lost because of artefact was 27%, 20% and 20% respectively. Grand average waveforms are shown in figure 8.2 for a range of sites. The ERPs begin to diverge from around 400msec post-stimulus, the ERPs to old words becoming more positive-going than those to new words. Initially, these differences are maximal over left parietal sites but shift with time to become greatest over the right frontal scalp. Unlike in experiment 3, the ERPs to the negative and neutral items appear to contain left parietal and right frontal effects of equivalent size. Also in contrast to the findings from experiment 3, there is evidence, from approximately 400 msec onwards, of an additional bilateral posterior positivity in the waveforms elicited by the negative source hits. This effect is shown in greater detail in figure 8. 3.

The ERPs were quantified by measuring the mean amplitudes of the same three latency regions (500-800 msec, 800-1100 msec, 1100-1900 msec) as were measured in experiment 3. As in that experiment, separate analyses were conducted to assess between-condition differences in amplitude and scalp topography.

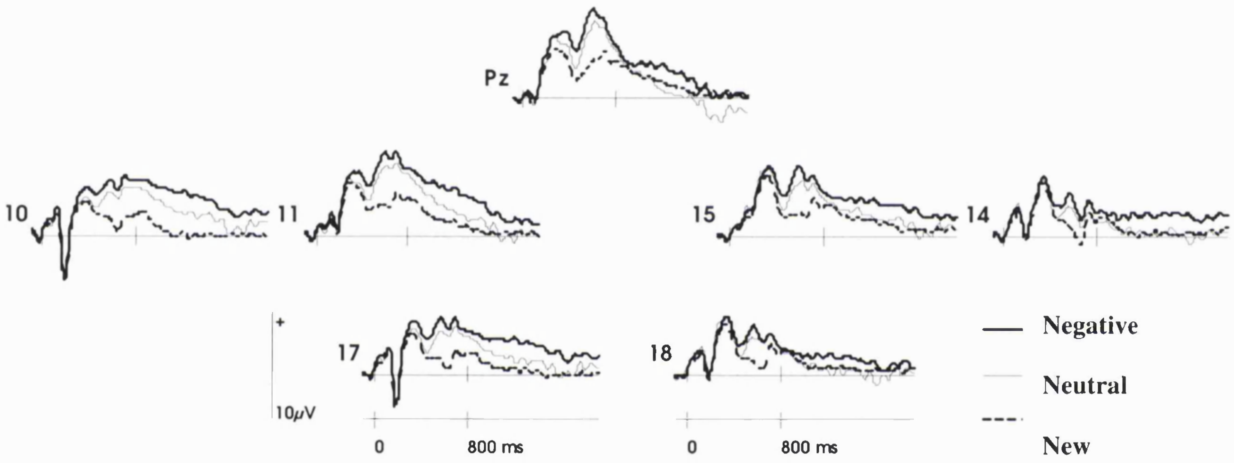

Figure 8.3. Experiment 4: Grand average waveforms from the posterior-most sites
See figure 8.1 for electrode locations.

Analyses of mean amplitudes

Twenty sites, 10 anterior and 10 posterior, were selected for the analysis of mean amplitudes (see figure 8.1). Unlike in experiment 3, separate ANOVAs were conducted on the data from anterior and posterior sites, employing the factors of condition, hemisphere and site. This procedure was adopted because of the arbitrariness that would have accompanied any attempt to 'match' anterior and posterior electrodes on a site factor. The results of these ANOVAs are shown in table 8.2.

Table 8.2 Experiment 4: Mean amplitude analyses, significant effects summary
Outcome of ANOVAs of mean amplitudes in the latency regions analysed from anterior and posterior sets of electrodes in experiment 4. Only significant effects involving the condition factor (3 levels: correct rejection, neutral source hits , negative source hits) are reported. CC = condition, HM = hemisphere, ST = electrode site (inferior, middle, superior).

		500-800msec	800-1100msec	1100-1944msec
Anterior	**CC**	-	-	-
	CCxHM	-	-	F(2.0,29.7)=14.34,p<0.001
	CCxST	F(3.0,45.3)=7.90,p<0.01	F(3.6,54.5)=4.86,p<0.005	-
	CCxSTxHM	-	-	-
Posterior	**CC**	F(1.8,26.7)=18.03,p<0.001	F(2.0,29.3)=5.92,p<0.01	F(1.9,27.9)=6.30,p<0.01
	CCxHM	F(1.9,27.9)=6.62,p=0.005	F(1.6,24.4)=10.44,p=0.001	
	CCxST	F(4.0,60.1)=5.18,p=0.001	F(4.5,67.1)=2.94,p<0.05	F(4.8,72.2)=2.93,p=0.02

For the 500–800 msec latency region, ANOVA of the data from anterior sites revealed an interaction between condition and site. Follow-up analyses contrasting the neutral source hits with the correct rejections revealed a main effect of response category (F(1,15) = 10.89, p = 0.005) and an interaction between response category and site (F(1.8, 27.7) = 14.42, p < 0.001). Analysis contrasting the negative source hits with the correct rejections revealed an interaction between response category and site (F(1.7, 24.8) = 10.35, p < 0.001). In both cases, these results reflect larger old/new effects nearer to the midline (sites 3 and 6 in figure 8.1). ANOVA contrasting the data from the two hit conditions was not significant.

ANOVA of the 500–800 msec data from posterior sites revealed a main effect of condition and interactions between condition and hemisphere, and between condition and site. ANOVA contrasting the neutral source hits with correct rejections revealed a main effect of response category (F(1,15) = 23.7, p= 0.001), and interactions between response category and hemisphere (F(1,15) = 7.04, p < 0.05) and response category and site (F(2.5, 37.4) = 3.34 p < 0.05). The analogous ANOVA for the negative source hits also gave rise to an effect of response category (F(1,15) = 24.06, p < 0.001) as well as the same two interactions response category and hemisphere F(1,15) = 11.37, p < 0.005; response category and site: F(2.5, 36.9) = 7.97, p < 0.001]. These results reflect similar patterns of 'left parietal' old/new effects for both neutral and negative items. ANOVA of the ERPs to the two classes of old item revealed an interaction between item type and site (F(2.2, 32.4) = 3.7, p < 0.05). This effect reflects the greater positivity in the ERPs to the negative source hits at sites 10,11 and 17 and their right hemisphere counterparts.

For the sake of comparability with experiment 3, analyses were also conducted on sites which could be factored by location (frontal, temporal/central, parietal), hemisphere and site (inferior, middle, superior). ANOVAs for both neutral and negative items revealed response category x location x hemisphere interactions (F(1.5,23.0) = 10.94, p = 0.001) and (F(1.3, 20) = 13.33, p = 0.001) respectively. These interactions are indicative of the left parietal old/new effects in the data. As there was no directly comparable ‘left parietal’ site in this experiment, the three closest sites were used to address more specifically the size of the left parietal effect in each condition. These sites formed a triangular montage encompassing the co-ordinates of the ‘left parietal’ scalp site. Old/new effects were reliable in both the neutral condition (F(1,15) = 34.46, p < 0.001) and the negative condition (F(1,15) = 35.26, p < 0.001) at this site. However, in contrast to experiment 3, analysis specifically contrasting the waveforms to neutral and negative source hits at this site revealed no effect of context (F < 1).

ANOVA of the data from 800-1100 msec region for anterior sites revealed an interaction between condition and site. ANOVA of the neutral old/new effects old/new effects revealed interactions between response category and site (F(2,30.5) = 5.13, p = 0.01) and between response category, hemisphere and site (F(2.5, 37.9) = 3.4, p < 0.05). The effects reflect a tendency for the old/new effects to be largest at the sites nearest to the midline, and to be somewhat larger over the right hemisphere. ANOVA of the negative old/new effects revealed an interaction between response category and site (F(1.9, 28.5) = 7.61, p < 0.001), again reflecting larger effects at the sites nearest the midline. The contrast between the two types of old item revealed no significant effects.

ANOVA of the data from the 800–1100 msec region for posterior sites revealed a main effect of condition, and interactions between condition and hemisphere, and condition and site. ANOVA of neutral old/new effects gave rise to an interaction between response category and hemisphere (F(1,15) = 10.71, p = 0.005), reflecting the tendency for the effects to be larger over the left hemisphere. ANOVA of the negative effects revealed an effect of response category (F(1,15) =10.59, p = 0.005), as well as interactions between response category and site (F(2.4, 35.4) = 3.13, p < 0.05), and response category and hemisphere (F(1,15) = 15.02, p = 0.001), again reflecting the left-sided lateralisation of the effects. ANOVA contrasting the two classes of old item revealed an interaction between item type and site ($F(2.5, 37.6) = 4.22$, $p < 0.025$). As for the preceding latency region, this effect reflected greater positivity of the ERPs elicited by the negative source hits at the most posterior sites within the selection.

For the 1100–1944 msec latency region, ANOVA conducted on the anterior sites revealed an interaction between condition and hemisphere. The ANOVAs of the neutral and negative old/new effects both gave rise to an interaction between response category and hemisphere neutral: $F(1,15) = 19.22$, $p < 0.001$; negative: $F(1,15) = 21.59$, $p < 0.001$]. In both cases, the interactions reflected the fact that old/new effects were lateralised to the right hemisphere. ANOVA contrasting the two items types directly revealed no significant effects.

As with experiment 3, an ANOVA was conducted on the data from the right frontal site alone. Old/new effects were reliable in both the neutral ($F(1,15) = 19.09$, $p < 0.001$) and negative conditions ($F(1,15) = 5.65$, $p < 0.05$). Analysis specifically contrasting the waveforms to neutral and negative source hits at this site revealed no effect of context ($F < 1$).

For the posterior sites, ANOVA of the data from the 1100-1944 region revealed a main effect of condition, and an interaction between condition and site. ANOVA revealed that the old/new effect for neutral items was not reliable. ANOVA of the negative effect revealed a main effect of response category ($F(1,15) = 9.63$, $p < 0.01$), reflecting the greater positivity of the ERPs to the negative source hits. ANOVA of the data for the two classes of old item revealed an interaction between context and site ($F(3.1,45.9) = 4.45$, $p < 0.01$), once again reflecting the posterior maximum of the bilateral positivity elicited by the negative source hits.

Topographic Analyses

The topographic analyses compared the scalp distributions of the old/new effects observed in each latency region. An initial ANOVA employed the factors of site (all 29 sites), latency region, and context (negative vs. neutral). The ANOVA revealed an interaction between all three of these factors ($F(6.4, 96.6) = 2.44$, $p < 0.05$), indicating that the scalp distribution of the old/new effects differed according to both context and time.

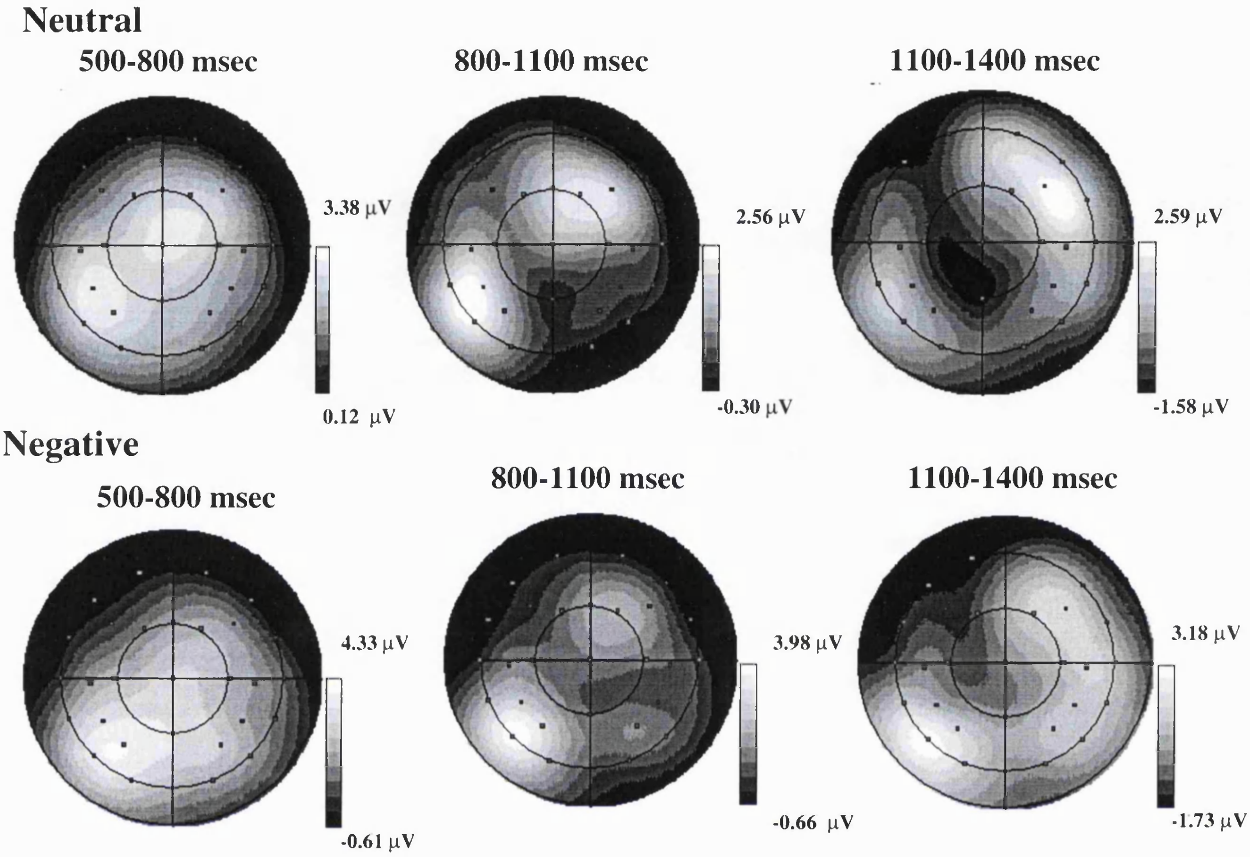

Figure 8.4 Experiment 4: Topographic maps illustrating the scalp distributions of the old/new effects for the latency intervals indicated.

To elucidate the above interaction, the scalp distributions of the old/new effects were contrasted within each epoch separately. For the 500-800 and the 800-1100 msec latency regions, ANOVA revealed a reliable effects of site $F(4.2, 62.6) = 8.61$, $p < 0.001$, and $F(4.7, 71.0) = 3.91$, $p < 0.005$ respectively] but no evidence of a site by context interaction (maximum $F = 1.85$). As can be seen from figure 8.4, the old/new effects in these regions exhibit similar distributions, with maxima over the left parietal scalp. For the 1100-1944 msec latency region, ANOVA again revealed a significant site effect ($F(3.8, 56.5) = 4.1$, $p < 0.01$), but also gave rise to a site by context interaction ($F(6.9, 103.3) = 2.96$, $p < 0.01$). The interaction reflects the more posterior distribution of the old/new effects elicited by the negative source hits.

Summary

Reliable old/new effects were elicited by negative and neutral source hits in each of the three latency regions analysed. Two of these effects – corresponding to the left parietal and right frontal effects observed in experiment 3 – were of equivalent magnitude. A third effect appeared to be elicited specifically by the negative items; this took the form of a long lasting, bilateral, posterior positivity which was sufficiently large in the last of the latency regions analysed to cause a reliable difference between the scalp distributions associated with the two classes of old/new effect.

Discussion

Performance Data

In contrast to experiment 3, participants were slightly but significantly more accurate in recognising words from the negative contexts. This finding is consistent with previous results (e.g. Phelps et al., 1997) and suggests that, the findings from experiment 3 notwithstanding, the effects of emotional vs. non-emotional encoding contexts on subsequent memory for single words can be detected with recognition memory as well as free recall.

Seemingly in contradiction to the findings for recognition memory, the probability of a successful source judgement was higher for words encoded in the neutral rather than the negative contexts. At first sight this result suggests that neutral contexts were encoded more effectively than were their negative counterparts. The analysis of the source judgements assigned to false alarms indicates however that this was not the case; some 70% of these judgements were made in favour of the neutral source. Thus, in the absence of source-specifying information, there was a strong response bias to respond 'neutral'. It seems highly probable that this bias was responsible for the disparate rates of correct source judgements made to recognised old words. Indeed, it has been reported that, in situations of uncertainty, binary source attributions are more likely to be made in favour of the less memorable source (Hoffman, 1997). Thus, it is possible that the response bias observed in the present experiment reflects better memory for the negative encoding contexts. On the assumption that the bias shown for false alarms is a good estimate of that operating for recognition hits, the probability of recollection of negative and neutral contexts can in fact be estimated. The probabilities are 0.57 and 0.47 for negative and neutral contexts respectively.

ERP Effects

The findings from the present experiment resemble those from experiment 3 in that the ERP old/new effects reflected the modulation of two components, one maximal over left parietal scalp, and the other showing a right frontal maximum. In striking contrast to the findings from experiment 3, however, there were no differences in the magnitude of either of these old/new effects according to the context in which the test items had been encoded. In a further departure from the findings of the previous experiment, a third ERP effect, with a bilateral posterior distribution, differentiated the ERPs elicited by the two classes of old item.

Unlike in experiment 3, the present experiment enabled ERPs to old words to be formed, in the main, from trials on which the encoding context of the test item was recollected. Thus, there was less opportunity than in the previous experiment for the ERPs elicited by the two classes of old item to be differentially diluted by trials on which recognition occurred without retrieval of context. (On the basis of the estimates of source recollection given in the foregoing paragraph, ERPs to negative hits would have included only about 5 additional recollected trials than ERPs to neutral hits.) This may have contributed to the failure to find emotion-related differences in the magnitude of the left parietal and right frontal effects in the present experiment.

A second, and arguably more important, difference between the previous and present experiments is that the retrieval of context was incidental in the former experiment and intentional in the latter. Indeed, the primary aim of the present experiment was to clarify the findings from experiment 3, which were ambiguous with respect to whether they reflected some inherent property of emotional memories, or instead some ‘second order’ effect. With respect to both the left parietal and right frontal old/new effects, the results from the present study are clear: when encoding context is task relevant, and hence the content of retrieved information must be attended and subjected to post-retrieval evaluation, the effects do not differ according to whether that information derives from an emotionally negative or an emotionally neutral context. Therefore the findings from experiment 3 do not reflect some property of emotional memories that necessarily leads to a potentiation of left parietal and right frontal ERP old/new effects. Rather, when the content of retrieved memories is task-irrelevant, emotional content is more likely to capture attention and trigger further processing than is non-emotional content.

A further aim of the present experiment was to address the question whether any aspect of ERP memory effects might differ qualitatively according to whether the encoding contexts of the old test items were emotionally negative or neutral. The experiment revealed the presence of a long duration positivity elicited by the items from negative encoding contexts. The presence of this positive shift led to a significant difference in the scalp topographies of the negative and neutral old/new effects in the latter part of the recording epoch, indicative of a qualitative difference in the effects elicited by the two classes of old item. The failure to observe the effect in experiment 3 could have arisen for a number of reasons. For example, contextual retrieval was incidental rather intentional; there was less comprehensive electrode coverage of the posterior scalp; and the effects might have been diluted by the inclusion of trials on which there was no contextual retrieval.

To my knowledge, this posterior positivity has not previously been reported in ERP studies of memory retrieval. To the extent that the amplitudes of the left parietal and right frontal effects index the amount of information retrieved in response to the two classes of test item, it is unlikely that the positivity merely reflects a tendency for negative contexts to contain more information. The effect may, therefore, represent a neural correlate of memory retrieval that is relatively specific for emotional content. The precise nature of this content (for example, whether valence is a crucial variable) is unclear. Equally unclear are the cognitive operations reflected by the effect, and its intracerebral origins. With respect to this last issue, one speculative possibility arises out of the hypothesis that the retrosplenial cortex acts as an interface between episodic memory and emotional processing (Maddock, 1999). According to this hypothesis, the retrosplenial area should be differentially activated by the retrieval of emotional relative to non-emotional information. Alternatively, the additional old/new effect elicited by the items from the negative contexts might reflect activation of the occipital regions reported by Taylor et al. (1998) as activated during emotional memory retrieval. It will be of interest to determine, in studies specifically directed to this question, whether the scalp distribution of the emotion-related positivity is more consistent with generators located in retrosplenial or ventral occipital regions.

Interim Summary: Experiments 3 and 4

The first general point to make concerns the experimental procedure adopted in these studies. By employing a single type of test item (emotionally neutral words), it was possible unequivocally to attribute differences in the neural activity elicited by the items to their encoding context; specifically, in the present case, to whether the context had a negative or a neutral affective valence. The findings represent, to my knowledge, the first demonstration in a neuroimaging study that it is possible to distinguish the neural correlates of the retrieval of emotional vs. non-emotional memories without confounding the nature of the memory with the nature of the retrieval cue. This confound is not unique to Experiments 1 and 2 and (with the exception of Phelps and colleagues, 1997; 1998 who employed a similar paradigm previously in their clinical study of emotional memory) is virtually endemic to the field of emotional memory as a whole.

It is important to note, however, that no attempt was made to determine the extent to which these findings reflected differences between the emotional valence of the contexts as opposed to their capacities to evoke emotional 'arousal' (Heilman and Gilmore, 1998). In addition, no strong claims are made regarding the locus of the effects of emotionality. It is possible that such effects have their origin in either encoding, for example reflecting greater attentional engagement of negative sentences, or at retrieval.

A further point to note is that although critical items were counterbalanced between contexts, 'item effects' may have involved uncontrolled sources of variance in the context sentences. This possibility is unlikely since the sentences were created with this factor in mind and thus inspected for systematic differences between negative and neutral sentences in variables such as length, word frequency etc. However, although inspection revealed no obvious systematic differences, the possibility that some extraneous variable from the encoding contexts was confounded with the emotionality manipulation cannot be ruled. The full stimulus set is provided in the appendix for inspection by the reader.

Summarising the results, in both experiments, differences between ERPs elicited by new items, and items previously encoded in emotionally negative or neutral contexts, took the form of the modulation of two well studied effects – the left parietal and right frontal ERP old/new effects. Thus, one conclusion from these experiments is that both the incidental and intentional retrieval of emotional contextual information engages much of the same neural circuitry that supports the retrieval of non-emotional information. A second conclusion, arising from a comparison of the findings from the two experiments, is that emotional information does not necessarily lead to enhanced activity in this retrieval network; rather, when greater retrieval effects are observed for emotional information, this may be because such information is more likely to be retrieved, and, once retrieved, more likely than non-emotional information to receive post-retrieval processing.

The findings from experiment 4 indicated that the retrieval of emotional information was associated with a seemingly specific memory effect. To the extent that the effect turns out to be emotionally-specific, this finding supports the proposal that retrieval of emotional memories is associated with activity in neural circuits additional to those engaged during the retrieval of emotionally neutral information (Dolan et al., 2000; LeDoux, 2000).

Chapter 9

Functional Neuroimaging

This chapter has been included to introduce magnetic resonance imaging (MRI) and its development as a tool for imaging brain activity. Also provided in this chapter is a general introduction to Statistical Parametric Mapping – the method employed to analyse data from the fMRI experiment conducted. Specific aspects of the design and analysis of the fMRI experiment are discussed in the methods section of the following (experiment) chapter.

Background

The basis of Nuclear MRI is that the physical and chemical construction of a substance can be determined by monitoring changes that occur when nuclei are placed in a magnetic field. Although NMRI was applied initially to chemical spectroscopy, it has since been developed for use in neuroimaging wherein the term nuclear was dropped because of negative connotations. MRI allows 3-D reconstructions of the brain by imaging grey and white matter across one of the three planes; sagittal, coronal and transverse. In addition, methods can be applied that enable changes in the intensity of MR signals to be coupled with changes in activation in the human brain.

In brief, the construction of brain images through MR techniques is based upon changes in the absorption and emission of energy, this being determined by the properties and environment of hydrogen atoms present in water molecules in the brain. Under normal circumstances (equilibrium), the moments of hydrogen atoms are orientated in random directions producing a net magnetic field of zero. If a constant magnetic field is applied to the protons, then a proportion of the protons will align with the direction of the applied field (defined as the z axis). In addition, their spinning begins to precess around the z-axis at a rate particular to hydrogen atoms and proportional to the strength of the field applied (the Lamar frequency). If radio pulses are then applied to the hydrogen atoms at the Lamar frequency, then radiofrequency (RF) energy is absorbed by the protons (resonance). When the radio pulse is subsequently removed, the RF energy is re-emitted and the rate at which the protons loose their extra energy (signal relaxation) can be measured. Since grey and white matter contain varying amounts of hydrogen, imaging of the brain can be performed by converting the strength of the (NMR) signal at brain tissue voxels to colour shades in corresponding image pixels (T1-imaging). [For a fuller discussion of the physics and historical development behind MRI the reader is referred to Andreasen (1989); Turner and Friston (1997); Turner, Schmitt and Stehling (1998); Cohen (1998); Hornak, (2000).]

Key to functional imaging (T2-imaging) methodology, NMR signals are affected by the environment of the atoms. As determined by Pauling and Coryell (1936), the level of oxygen carried within the haemoglobin in the tissue has a remarkable effect on the magnetic properties of the haemoglobin, and hence the NMR signal from protons in neighbouring water molecules. Critical to functional imaging, in resting cortex the concentration of deoxygenated heamoglobin is greater than when the cortex is in an active state, thus Ogawa, Lee, Nayak and Glynn (1990) were subsequently able to demonstrate that by monitoring the magnetic properties of the haemoglobin, associated changes in the amount of oxygen could be matched to specific locations within the brain (see also Turner, Le Bihan, Moonen, Despres and Frank, 1991). Thus, techniques were developed that enabled measurements of 'Blood Oxygenation Level Dependency' (BOLD) signals to be used as indices of cortical activity contingent on functional processes (see Raichle, 1998; Turner, Howseman, Rees, Josephs and Friston, 1998; Kwong, 1998; Bandettini and Wong, 1998 for overviews).

Spatial resolution of fMRI is primarily dependent upon factors such as the speed of signal acquisition, the required signal to noise ratio and the strength of the magnetic field applied. Typically, the spatial resolution of fMRI is about 3mm (superior to ERP spatial resolution; see Chapter 2, figure 2.1). In addition, it has advantages over other haemodynamic neuroimaging methods (specifically PET) since it does not employ ionising radiation and is non-invasive. (To date, it is not associated with any known biological risk as long as safety procedures are followed). The main constraint upon temporal resolution in fMRI is brain physiology since blood flow changes slowly relative to variations in neural activity. Other methodological issues in fMRI relate to signal to noise ratios, especially problems with signal voids in certain brain regions due to susceptibility artefact and generalised problems relating to image artefacts such as image distortion, (for reviews see Nadeau and Crosson, 1995; Howseman, Josephs, Rees and Friston, 1997; Segebarth, 2000; Josephs, 2000). Also problematic in fMRI data are movement-related effects since movement in earlier scans can affect the signal in subsequent scans, or, if the motion is stimulus-related differences in signals may be accumulated over the scanning session (see Hajnal, Myers et al., 1994).

Functional Imaging Data Analysis and Interpretation

Theoretical Considerations

Early psychological theories of the anatomical organisation of the brain were based either upon the idea that distributed brain regions integrate to produce functional connectivity or alternatively, that brain regions are segregated by the function that they subserve. Nowadays, it is recognised that the two scenarios are not mutually exclusive and it is generally accepted that the anatomical basis of a function may involve a number of spatially segregated brain regions, each subserving an 'aspect' of the function (functional segregation), the union of which (through functional integration) constitutes the function (Frith, 1997).

Two main approaches have been developed for analyses and interpretation of functional neuroimaging data. One approach, addressing functional integration, is to employ multivariate statistics to estimate distributed signal changes (corresponding to distributed physiological changes) within the brain (for more information on these analyses see Friston, Frith, Fletcher, Liddle and Frackowiak, 1996; Büchel and Friston, 1997). The second approach addresses functional segregation and employs univariate statistics to estimate regionally specific responses in terms of an associated function (Friston, 1997). This second approach is adopted in the following fMRI study and is thus discussed below. There are of course other statistical methods for analysing functional imaging data and for fuller reviews of all of the methods the reader is referred to Petersson, Nichols, Poline and Holmes (1999a) and Petersson, Nichols, Poline and Holmes, (1999b).

Statistical Parametric Mapping

Statistical parametric mapping (SPM) was developed by Friston and colleagues to characterise the physiology of brain function in terms of the significance of regionally specific responses (Friston, Holmes et al., 1995b). In brief, once the BOLD signal has been obtained, SPM analysis (of each and every voxel) can be partitioned into three stages; pre-processing, estimation and inference. Pre-processing involves the removal of head movement effects in the data, normalising the data into standard stereotaxic space, and also spatially and temporally smoothing the data (Ashburner and Friston, 1997a; Ashburner and Friston, 1997b). Estimation of the parameters of a model of the data involves the use of a design matrix to estimate the statistical parameters that pertain to the data set (Holmes and Friston, 1997; Holmes, Poline and Friston, 1997). In the third 'inference' stage, whether contributions of factors specified in the design matrix are bigger than chance is estimated and p-values assigned (Friston, Holmes, Poline, Price and Frith, 1996; Worsley, 1997; Poline, Holmes, Worsley and Friston, 1997; Poline, Holmes, Worsley and Friston, 1997).

Pre-processing

Voxel-based analyses require that data are in the same anatomical space. Since participants never stay perfectly still, movement-related effects must be corrected (as far as possible) in the data. Whilst correcting for movement is essential in SPM this step is also beneficial to statistical analysis since it reduces residual variance in the data making the statistical tests more powerful. The general procedure adopted in realigning data to estimate head movements for each scan relative to a reference scan and to resample data using these estimates (Friston, Ashburner et al., 1995a). Six movement parameters (translation and rotation - each defined in the x, y and z direction) are estimated that describe the rigid body transformation between each scan and the reference such that the sum of squares difference is minimised.

To implement voxel-based analysis of imaging data across different participants, the data from different participants must derive from homologous parts of the brain. This is achieved by normalisation – the transformation of fMRI data so that all participant's brains map onto the same space (some idealised or standard brain). There are three advantages to normalising data. First, it allows data to be reported in a known stereotaxic space (SPM uses co-ordinates close to the Talairach stereotaxic atlas). Second, as with realignment, it reduces residual variance in the data and hence makes the statistical tests more powerful. Third, if a Random Effects model is implemented (see below), it allows results to be generalised to the population. The disadvantages of normalisation are that individual variation in brain morphology is ignored.

SPM normalises an image by warping it to the template image and minimising the sum of squared differences resulting in a spatially normalised image and a deformation field (Friston et al., 1995a; Ashburner and Friston, 1997b; Ashburner and

Friston, 1999). If all images of a particular participant have been rigidly registered together (realigned to the same space) then the same deformation field can be applied to all the images requiring normalisation.

In addition, a 'slice-timing' correction routine is incorporated into SPM in order to correct for differences in the acquisition time between slices, i.e. to make the data on each slice correspond to the same point in time. Without this correction the data from different slices reflect brain activity at different time points. The correction works by shifting the signal on each slice using sinc interpolation in time (effectively this is replacing each scan with an average of itself and its neighbours). This correction results in data values consistent with each slice having been acquired at the beginning of the TR.

Finally, SPM implements 3-D smoothing by convolving the data with a Gaussian kernel defined in terms of full width half maximum. There are two main reasons for smoothing the data in the following study. First, smoothing increases the signal to noise ratio since neurophysiological effects of interest generally have a lower spatial frequency to noise. A second reason for smoothing is that it facilitates inter-participant averaging by ensuring that haemodynamic changes from participant to participant can be assessed on a spatial scale at which homologies in functional anatomy are typically expressed.

Estimation

SPM incorporates parametric statistics (the general linear model - GLM) whereby the time series is modelled as a linear sum of basis functions with unknown weights and an error term (which is assumed to be normally distributed) (Holmes and Friston, 1997). The experiment parameters (design, factors, predictions) are embodied in a mathematical 'design matrix' in which questions of interest to be tested are formulated. SPM partitions the design matrix according to whether the effects are of interest (e.g. event-related activation) or not (e.g. session effects). In the experiment in this thesis the effects of interest reflect factor levels (conditions), alternatively they could instead reflect a continuous function (e.g. a covariate such as time) or some combination of continuous and discrete variables. The contribution of each effect modelled within the design matrix to the observed fMRI time series is estimated using the method of least squares (i.e. estimation of the unknown weights). These estimated weights reflect the mean activity associated with a particular condition. Differences in the weights for different conditions can then be calculated (contrasts) (Friston, Price et al., 1996; Poline et al., 1997).

Inference

There are two ways of implementing the GLM to make inferences about significant effects in contrasts (see Friston, Holmes and Worsley, 1999). In a ‘fixed-effects’ model, inter-participant variance is not taken into account and thus inferences made apply only to the participants studied. However, it is often more useful if the model compares the average activation to variance in data *between* participants (and adjusting the error variance accordingly) enabling inferences about the effects in the general population to be made from the sample of participants (random-effects model). Whereas in a fixed effects model the degrees of freedom are determined by the number of scans, in a random effects model the degrees of freedom are determined by the number of participants used and hence the test is more conservative. Thus, in order to generalise inferences to the population a larger number of participants is required to reliably assess the between-participant variability.

In a random-effects model, the significance of differences in contrasts is assessed by entering the participant-specific contrast images into one sample t-tests. Regionally sensitive effects are then computed for each and every voxel in the contrasts - forming the SPM {t} map, or, if one wishes to make inferences about several effects at the same time, SPM {F}. From these significance values SPM creates maximum intensity projections which can be thought of as X-rays through a statistical parametric map where the t-statistic is thresholded against some specified level.

Event-related fMRI

In the last 5 or so years techniques have been developed that have allowed the development of event-related paradigms in fMRI analogous to those employed in ERP experiments (for reviews see Rosen, Buckner and Dale, 1998; Josephs and Henson, 1999; see also Buckner, Bandettini et al., 1996; Josephs, Turner and Friston, 1997; Friston, Fletcher et al., 1998). As demonstrated by the results of the first two experiments, the implementation of event-related designs is of fundamental importance to studies of emotional memory hence issues regarding blocked and event-related designs have already been discussed at length. However, it is worth emphasising issues relating to event-related designs that have a specific relevance to haemodynamic neuroimaging measures. Whereas PET studies will always be confined by the half-life of the radioactive tracers used (40-60 seconds) and contrasts confounded by a mixture of state- and item- related effects, the temporal resolution of functional imaging is limited only by the time course of the haemodynamic response (to the order of hundreds of milliseconds).

Furthermore, although it used to be thought that a long ISI was appropriate in efMRI studies in order to minimise overlap between successive event-related responses, it has been demonstrated that short ISIs can be employed without a loss of sensitivity (Dale and Buckner, 1997; see also Rosen et al., 1998). Indeed, relatively short inter-stimulus intervals - (<5seconds)- are in fact preferable to long stimulus intervals (Josephs and Henson, 1999). As such fMRI experimental designs identical to those used in typical behavioural and ERP studies allow analysis of closely spaced event-related trials enabling independence from blocked designs and state-effects.

As a consequence of the development of efMRI, studies can now be conducted on experiments in which the nature of the paradigm previously restricted them electrophysiological studies (for example, oddball experiments). This allows the two event-related methods to be employed in investigations of psychological phenomena in a convergent manner (see Rugg, 1998; Rugg, 1999). A frequently adopted strategy in the integration of efMRI and ERP data is to link the two kinds of data through a common theoretical framework whereby findings obtained with one method are used to predict (and interpret) the findings that would be obtained using another technique (Rugg, 1998). That is, predictions using one type of imaging method (i.e. ERP or efMRI) are based on theoretical interpretations of past results from the alternative imaging method where experimental paradigms used in the different studies are either identical or very similar. This 'structured convergence' has proved to 'be more fruitful in integrating electrophysiological and neuroimaging data than have attempts to 'coregister' data sets post-hoc' (see Rugg, 1998) and thus is the approach used in this thesis.

It is important to note however that the controlling of the experimental framework in this manner does not ensure a one-to-one correspondence with respect to the data collected with each method. In line with the points outlined in the chapter 2 regarding the disadvantages and advantages of electrophysiological and neuroimaging data, the preconditions for detecting signals in the two methods differ markedly. For example the effects of spatial insensitivities (e.g. closed fields) in ERP studies on signal detection in structures differ from the effects of spatial insensitivities (e.g. susceptibility artefact) in efMRI. Second, the employment of event-related designs does not resolve the issue of how to identify and characterise state-related changes in brain activity (see Rugg and Henson, in press). Thus under some circumstances, electrophysiological (e.g. Düzel et al., 1999) and functional imaging studies (e.g. Donaldson et al., 2000) that have been designed to allows item- and state- related activity to be assessed concurrently are preferable to those which focus entirely on event-related activity.

Chapter 10

Experiment 5: Neural activity associated with episodic memory for emotional context

Chapter Summary

To address the question of which brain regions subserve retrieval of emotionally-valenced memories, event-related fMRI (efMRI) was used to index neural activity during the incidental retrieval of emotional and non-emotional contextual information. At study, emotionally neutral words were presented in the context of sentences that were either negatively, neutrally or positively valenced. At test, fMRI data were obtained while participants discriminated between studied and unstudied words. Recognition of words presented in emotionally negative relative to emotionally neutral contexts was associated with enhanced activity in right dorsolateral prefrontal cortex, left amygdala and hippocampus, right lingual gyrus and posterior cingulate cortex. Recognition of words from positive relative to neutral contexts was associated with increased activity in bilateral prefrontal and orbitofrontal cortices, and left anterior temporal lobe. These findings suggest that neural activity mediating episodic retrieval of contextual information and its subsequent processing is modulated by emotion in at least three ways. First, there is enhancement of activity in networks supporting episodic retrieval of neutral information. Second, regions known to be activated when emotional information is encountered in the environment are also active when emotional information is retrieved from memory. Third, regions activated during retrieval of emotional episodic information differ according to the valence (positive, negative) of the information retrieved.

Introduction

There are two competing accounts regarding the effects of emotion on episodic memory. In one account emotion acts exclusively during encoding or consolidation (for review see Cahill and McGaugh, 1998). By this account a common neural network supports retrieval of both emotional and non-emotional information (see also Taylor et al., 1996; Maratos, Allan and Rugg, 2000). Alternatively it has been suggested that, in addition to its effects at encoding and during consolidation, emotion modulates retrieval processing through the engagement of emotion-sensitive structures such as the amygdala (Dolan et al., 2000; LeDoux, 2000; Maratos and Rugg, in press).

As illustrated by the preceding chapters, episodic memories can be conceptualised as comprising two components - item (event) and context (the environmental setting in which the event occurred). It is noteworthy that functional imaging studies of emotional memory have focused predominantly upon item information. In one of the first such studies it was reported that activity in occipital-parietal regions was enhanced during visualisation from memory of previously viewed negative images relative to neutral images (Kosslyn et al., 1996). The finding of enhanced activity in sensory regions during emotional memory retrieval was replicated by Taylor et al. (1998), who found greater activity in the lingual gyrus (BA 18) during recognition of previously studied negative images, relative to neutral images, in the absence of the modulation of any other retrieval-related activity. By contrast, in a recent PET study, Dolan et al., (2000) reported that recognition memory for emotional relative to neutral pictures was associated with activation in the anterior temporal pole and the amygdala, leading these authors to conclude that emotional memory retrieval did indeed recruit brain regions specialised for processing the affective significance of stimuli.

The present investigation is instead concerned with the retrieval of emotional context. This study was initiated on the basis of the finding of experiment 3 that incidental retrieval of emotional contextual information is associated with enhanced activity in the same neural systems that support the conscious recollection and subsequent 'post-retrieval' processing of emotionally neutral information. In particular, it was suggested that such additional activity would be found in the medial temporal/posterior cortical regions subserving the initial retrieval of episodic information, (Nyberg et al., 1996; Rugg et al., 1997a) and in right prefrontal regions supporting the subsequent monitoring and evaluation of the retrieved information (e.g. Rugg et al., 1996; Henson et al., 1999b; McDermott et al., 2000; Henson et al., 2000).

The present study employed efMRI to investigate the incidental retrieval of emotional and neutral contexts using the same procedure as employed in experiment 3. By contrasting the neural activity elicited by a single kind of test item (emotionally neutral words) as a function of the emotional valence of study context, any difference in the activity elicited by test items belonging to different classes of context can be attributed unequivocally to their respective encoding contexts.

Method

The experimental procedures were approved by the joint Medical Ethics Committee of the National Hospital for Neurology and Neurosurgery and the Institute of Neurology.

Participants

Thirteen right-handed participants aged between 18 and 30 years were employed in the study after giving informed consent. One participant's data were rejected because of inadequate behavioural performance. The 12 participants whose data were analysed consisted of 7 females and 5 males. All reported good health and no history of neurological illness.

Experimental material

One hundred and twenty words normed for neutral emotional valence (see below) were used as critical stimuli. The words varied in length between 4 and 10 letters and in frequency between 30 and 100 per million (Francis and Kucera, 1982). For each word one negative, one neutral, and one positive sentence were constructed. For example, for the critical word 'corn' the following sentences were generated as negative, neutral and positive sentences respectively: 'The farmer was shredded when he fell into the corn grinder'; 'The farm labourers began harvesting the corn'; and 'The farmer was overjoyed with his bountiful crop of corn'. Critical words never featured in sentences other than their designated neutral, negative or positive sentences. Sentences were of equal length (negative; mean = 9.14, s.d. = 1.77, neutral; mean = 8.85, s.d. = 1.87, positive; mean = 8.50, s.d. = 1.97) and were formed so as to be roughly equivalent in the nature and range of grammatical constructions employed).

Word norms and selection

Normative valence ratings were collected for 320 ostensibly neutral words. The words were randomly intermixed with 35 emotionally negative words and 35 emotionally positive words (taken from Siegle, 1998). Ten participants were given the resulting list of 390 words and asked to rate each word on a Likert scale (ranging from –3 to +3) according to how emotionally 'negative', 'neutral' or positive they felt it to be. The average ratings given to the negative, neutral and positive words were – 1.8, 0.4 and 1.6 respectively. Of the 320 'neutral' words, 21 were dropped because they received ratings outside the range ± 1, another 131 were dropped because of difficulties in constructing a negative, neutral or positive sentence, and 48 words were used as filler items. The remaining 120 words were used as critical stimuli.

Experimental Lists

Eight study lists were created, each containing a set of 15 negative, 15 neutral and 15 positive sentences. The sentences in the study lists were randomly ordered and a neutral filler sentence was added to the beginning and end of each study list. Six test lists were created, each with a different randomised order, such that each study list could be followed by a test list containing the 45 old words from the sentences in the study block and 15 previously unseen words. Two filler words were added to the beginning of each test list.

To accommodate the two study-test sessions, study lists were paired such that across the whole experiment there were four study sets (each set containing a list for session 1 and corresponding list for session 2). Test lists were similarly paired, resulting in 3 test sets. Study and test sets were then combined resulting in 12 possible study-test set combinations, one for each participant.

Study and test lists were assigned to participants such that, across the experiment, each critical word appeared 3 times as a new item and 3 times each in a negative, neutral and positive sentence.

Procedure

Participants were given a description of the study task before entering the scanner. They were informed that the experiment would involve the presentation of emotional sentences and that parts of the experiment would involve a memory task. An example of the study phase was then given which consisted of the presentation of 3 negative, 3 neutral and 3 positive sentences.

The experiment proper began after a 15 minute structural scan. Participants were then administered the study and test lists in the scanner. An interval of 5 minutes separated each of the study and test tasks and also each of the sessions. Functional scans were acquired during each of the two test phases.

Task

Each of the 45 study trials consisted of two stages. A series of 45 sentences, white text on a dark screen, were presented via a mirror mounted on the scanner head coil in direct view of the reclining participant at a viewing distance of approximately 50 cm. First, participants were required to give the sentence an affective rating. The critical word from the sentence was then presented alone with the requirement to read it out aloud and remember it in the context of the sentence of which it had been part. Sentences were presented approximately every 10-15 seconds.

The corresponding recognition memory test consisted of the re-presentation of the critical words from the study sentences along with 15 new items. Each trial began with the presentation of a fixation character for 1000 msec. This was removed 500 msec before the onset of the test word which was displayed for 1000 msec, following which the screen was blanked for 3000 msec. Participants were required to judge whether or not each word had been presented in the study phase. No mention was made of the different types of sentences employed at study. Test stimuli were presented in a white uppercase Helvetica 48 font on a black background. The words were presented using the same display system as for the study phase. Responses were given through a hand-held box by button press with either the right or left thumb. The mapping of thumb to response type was counterbalanced across participants. Participants were instructed to relax and to keep head movement to a minimum. Responses faster than 300 msec were treated as errors.

fMRI Methods

A 2T Siemens VISION system (Siemens, Erlangen, Germany) was used to acquire both T1-weighted anatomical volume images (1 x 1 x 1.5mm voxels, MPRAGE sequence) and T2*- weighted echoplanar (EPI) images (64 x 64, 3 x 3 mm pixels, TE = 40ms) with blood oxygenation level dependent (BOLD) contrast. Each EPI consisted of thirty-two 2 mm thick axial slices (inter-slice gap 1.5 mm), positioned to cover the entire brain with the exception of the vertex and cerebellum. Scanning occurred during the two test sessions. 109 volumes were acquired in each session, the first 5 of which were discarded to allow for T1 equilibration effects. Volumes were acquired continuously with an effective repetition time (TR) of 3.2 s/volume. The SOA was 5.5s, giving an effective sampling rate of 10Hz.

Image Pre-processing

Pre-processing steps were conducted using the Statistical Parametric Mapping toolbox (Wellcome Department of Cognitive Neurology, London, UK; Ashburner, Friston, Holmes and Poline, 1999). For each participant, all volumes were realigned and re-sampled in space using sinc-interpolation. Temporal offsets between successive slices were corrected with sinc-interpolation in time. The data were spatially normalised to a standard EPI template volume (based on the MNI 305 brain average) using non-linear basis functions (Ashburner and Friston, 1999). Finally, the EPI volumes were convolved with an isotropic 8mm (FWHM) Gaussian smoothing kernel to accommodate residual across-participant anatomical differences, and globally scaled to a constant mean signal intensity. The time series for each voxel were high-pass filtered to a maximum of 1/120 Hz.

Data Analysis

Statistical maps of voxels exhibiting differential responses to the different event types were created with SPM 99b (Wellcome Department of Cognitive Neurology, London, UK, Friston et al., 1995b). The volumes acquired during each session were treated as two time series. The analysis consisted of two stages: estimation of the parameters of the HRF for each participant and a subsequent test of the significance of these parameters across participants.

In the first stage, responses to the onset of each event type were modelled with two basis functions; an early HRF ('canonical' HRF: Friston, Josephs, Rees and Turner, 1998) and a delayed HRF, shifted in time relative to the early function by 3.2 seconds (i.e. TR). The use of both an early and late basis function was based on findings (e.g. Schacter et al., 1997) that the haemodynamic response onsets later in some brain regions (e.g. prefrontal cortex) than it does in the sensory regions from which the canonical (early) HRF was derived.[2]

The early and late response functions, when convolved with a sequence of delta functions representing the onset of each event, were used as participant-specific covariates in a GLM. Since the two HRFs were correlated, covariates for the late HRF were orthogonalised with respect to those for the early HRF (Andrade, Paradis, Rouquette and Poline, 1999). This step was taken to ensure that no variance was shared between the two response functions. The parameter estimates for a series of planned contrasts were obtained in each participant's data separately for the early and late covariates. All fMRI contrasts were confined to test trials associated with correct decisions.

The participant-specific contrast images were entered into one sample t-tests (df=11). Regions sensitive to recognition memory regardless of study context were identified as those voxels common to each of the three 'old-new' contrasts (neutral-new; negative-new; positive-new; each thresholded at $p < 0.05$ uncorrected). For the planned contrasts between old words belonging to each type of context a statistical threshold of $t = 4.02$ was employed, corresponding to an uncorrected $p < 0.001$. Only

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[2] Reasons as to why the right prefrontal cortex should exhibit a delayed haemodynamic response relative to other brain regions, especially the left frontal cortex remain unclear. It is possible that the delayed haemodynamic response reflects delayed neural activity in the region. This explanation is fits well with the time course of its electrophysiological counterpart, the right frontal effect, having a delayed onset and prolonged time course relative to other memory-related old/new effects. In addition, delayed neural activity is consistent with the hypothesis that such regions are necessary for post-retrieval operations (e.g., monitoring, source generation, decision making processes) and, as such, dependent on input from other neural populations. A less convincing second hypothesis is that the delayed right prefrontal activity might reflect a delay in the actual haemodynamic response independent of the temporal dynamics of the neural activity somehow peculiar to right prefrontal cortex (see Schacter et al., 1997; Buckner et al., 1998b). Although this could conceivably account for differences in the temporal responses between cortically dissociable regions of the brain (e.g., temporal versus frontal lobes), the explanation appears insufficient to explain such dissociations occurring between left and right prefrontal cortex.

activations involving contiguous clusters of at least 4 voxels were interpreted. The maxima of suprathreshold regions were localised using a combination of the participants' normalised structural images and the stereotaxic atlas of (Talairach and Tournoux, 1988).

Results

Behavioural Data

The mean valence for the negative, neutral and positive sentences were -2.38 (sd = 0.52), 0.21 (0.14) and 1.61 (0.28) respectively. These means differed reliably [(F(1.20,12.80) = 327.82, $p < 0.001$); dfs adjusted by the Greenhouse-Geisser procedure]. A t-test contrasting the absolute differences between negative and neutral ratings (mean = 2.60) and positive and neutral ratings (mean = 1.40) was also significant (t(11) = 64.93, $p < 0.001$), indicating that negative contexts attracted the more extreme ratings.

Hit rates for words from the negative, neutral and positive sentences, along with correct rejection rates and associated reaction times, are shown in table 10.1. ANOVA conducted on the proportion of correct responses (negative hits, neutral hits, positive hits, correct rejections) revealed a main effect of condition (F(2.7, 29.50) = 12.59, $p < 0.001$). Tukey HSD tests revealed that participants made a higher proportion of correct responses to new words than to any type of old word. Planned pairwise comparisons between the three classes of old items (negative, neutral, positive) were not significant, nor were analogous comparisons between reaction times for the these items.

Table 10.1 Experiment 5: Behavioural data
Mean proportions (standard deviation in brackets) of correct rejections, negative, neutral hits and positive hits along with associated reaction times.

	CR	Negative Hit	Neutral Hit	Positive Hit
Proportion	0.85 (0.14)	0.68 (0.14)	0.63 (0.15)	0.69 (0.15)
Reaction time (msec)	1283 (330)	1184 (361)	1198 (330)	1177 (296)

fMRI Data

Old versus New

As illustrated in figure 10.1 and documented in table 10.2, a number of regions were identified that were common to the three possible old vs. new contrasts. Among these regions were left lateral parietal cortex, precuneus, anterior and posterior cingulate, and bilateral prefrontal cortex. These regions correspond closely to those reported in several other recent efMRI studies of recognition memory (e.g. Henson et al., 1999a; Konishi et al., 2000; Henson et al., 2000; Donaldson et al., 2000).

Figure 10.1. Experiment 5: Maximum intensity projections illustrating voxels common to each of the three 'old-new' contrasts (see text)
Early: regions identified by modelling responses with the early HRF. Late: regions identified using the late HRF (see methods).

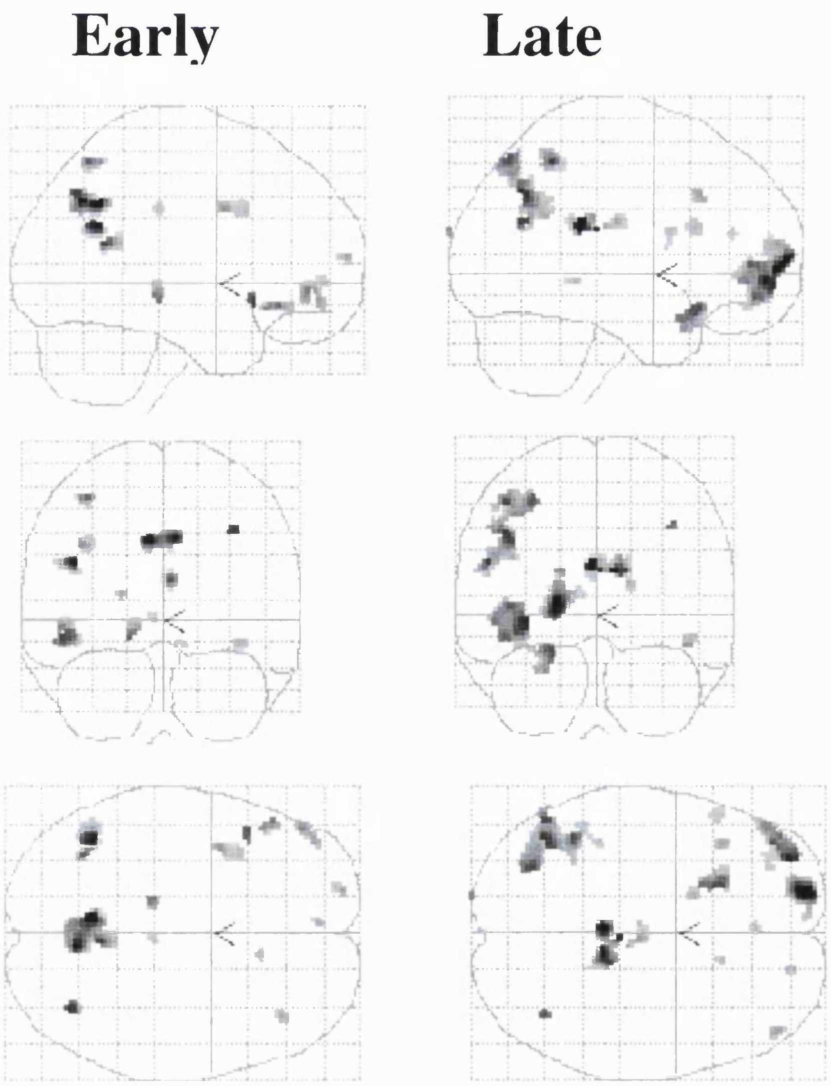

Table 10.2 Experiment 5: fMRI signal increases for old/new contrasts
Maxima within regions showing common signal increases (to 3 old/new contrasts, see text) on the early (a) and late (b) covariates for the old versus new contrast.

Region of activation		**No. of voxels**	**Talairach Co-ordinates**			**BA**
	L/R		**x**	**y**	**z**	
(a) Early						
Superior frontal gyrus	L	7	-20	64	12	10
Medial frontal gyrus	L	5	-4	52	0	10
Medial frontal gyrus	R	4	10	24	-12	11
Middle frontal gyrus	L	33	-48	44	-4	10
Inferior frontal gyrus	R	13	38	34	-10	47
Inferior frontal gyrus	L	19	-52	30	-10	47
Inferior frontal gyrus	L	13	-48	18	-8	47
Precentral gyrus	L	38	-38	4	34	6
Parahippocampal gyrus	L	21	-16	-28	-8	28
Cingulate gyrus	R	6	4	-28	34	31
Posterior Cingulate	R	50	4	-54	18	23
Precuneus	L	180	-6	-58	36	7
Superior temporal gyrus/inferior	L	52	-42	-58	26	39
Superior parietal lobule	L	16	-36	-62	56	7
Inferior parietal lobule	R	15	34	-68	40	7
(b) Late						
Superior frontal gyrus	L	157	-20	64	6	10
Superior frontal gyrus	R	8	16	56	14	10
Middle frontal gyrus	R	255	-34	54	-4	10
Middle frontal gyrus	L	19	46	48	-14	11
Middle frontal gyrus	L	11	-42	22	36	8
Anterior cingulate	L	8	-2	38	20	32
Anterior cingulate	R	4	12	22	22	32
Inferior frontal lobe	L	64	-22	22	-16	47
Inferior frontal lobe	L	25	-52	20	20	45
Inferior frontal gyrus	L	15	-16	8	20	44
Posterior cingulate	R	27	2	-18	24	23
Posterior cingulate	L	108	-2	-36	24	23
Middle temporal gyrus	L	5	-42	-38	-4	21
Inferior parietal	L	61	-44	-50	52	40
Inferior parietal	L	236	-44	-64	38	39
Inferior parietal	R	6	36	-64	40	40
Cuneus	L	4	-16	-100	20	18

Retrieval of negative context

Regions sensitive specifically to retrieval of negative context were identified by contrasts between the responses elicited by old items from negative vs. neutral contexts (Table 10.3).[3] The contrast employing the early HRF revealed several regions with enhanced responses to negative items (Table 10.3a). These regions included right dorsolateral prefrontal cortex, cuneus, and lateral and medial temporal regions including bilateral superior temporal cortex, left anterior temporal cortex, hippocampus, amygdala and primary auditory cortex. The same contrast modelled with the late HRF (Table 10.3b) revealed activation in temporal lobe regions including left superior temporal cortex and left insula, as well as activation in right posterior cingulate, parahippocampal, and extrastriate cortex.

Table 10.3: Experiment 5: fMRI significant effects for negative/neutral contrast
Maxima within regions showing significant ($p < 0.001$ uncorrected) signal increases for early (a) and late (b) covariates for the negative versus neutral contrast.

Region of Activation	L/R	**No. of voxels**	**Talairach coordinates**			**Peak Z**	**BA**
			x	y	z		
(a) Early							
Middle/Inferior frontal gyrus	R	34	44	30	12	3.88	46
Inferior frontal gyrus	R	4	54	24	2	3.68	45
Anterior temporal gyrus	L	17	-30	6	-18	3.81	34
Amygdala	L	4	-26	-8	-24	3.46	34
Anterior temporal gyrus	R	5	-40	-14	-16	3.36	28/34
Hippocampus	L	19	-30	-18	-20	3.89	28
Transverse Temporal gyrus	L	28	-44	-22	12	3.89	41
Middle temporal gyrus	R	10	66	-28	0	3.84	21
Superior temporal gyrus	R	12	64	-42	18	3.43	22
Superior temporal gyrus	L	17	-62	-34	18	3.42	22
Cuneus/Precuneus	L	15	-8	-78	24	3.69	18
(b) Late							
Superior frontal gyrus	L	17	-24	44	30	3.79	9
Middle frontal gyrus	R	8	34	42	36	3.73	9
Inferior frontal gyrus	R	12	50	4	18	3.69	44/6
Insula	L	9	-46	0	-2	3.52	22
Parahippocampal gyrus	R	8	12	-52	-2	3.41	30/19
Superior temporal gyrus	L	12	-50	-56	16	3.5	22/39
Posterior Cingulate gyrus	R	49	4	-54	22	3.83	23/31
Lingual gyrus	R	23	26	-64	0	3.82	18/19

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[3] Old items were contrasted directly against each other rather than against new items (as in the previous experiments) because here the relative frequencies of old and new items in the test lists were unbalanced (3:1). This could potentially result in the new items having something of the quality of task-relevant 'oddball' stimuli and, because such stimuli elicit frontal and parietal activations even in simple tasks which place little or no demand on episodic memory (e.g. Yoshiura et al., 1999; Strange et al., 2000; Stevens et al., 2000; Kirino et al., 2000), any results based on contrasts between old and new items might include effects that are only indirectly related to the memory demands of the task. Hence, results based on contrasts between old and new items would inevitably be difficult to interpret.

A subset of the foregoing regions were also identified in the contrast between responses elicited by items from the negative vs. positive contexts. When modelled with the early HRF enhanced activity was found in the cuneus (44 voxels, xyz = -4,-84,20, $\underline{Z}$ = 4.84) and anterior temporal cortex (6 voxels xyz = -48, 6, 4, $\underline{Z}$ = 3.23). Enhanced activity was also found in the left anterior insula when the threshold was reduced to $p < 0.005$ (81 voxels xyz = -40, 2, 6, $\underline{Z}$ = 2.80). When responses were modelled with the late HRF enhanced activity was found in the left anterior insula (12 voxels, xyz = -44, 10, -4, $\underline{Z}$ = 3.67). Enhanced activity was also found in superior temporal gyrus when the threshold was reduced to $p < 0.005$ (5 voxels, xyz = -56, -50, 12, $\underline{Z}$ = 2.87).

Retrieval of Positive Context

Regions showing a greater response to items from the positive vs. neutral contexts are given in Table 10.4. These regions included right anterior prefrontal cortex, left inferior prefrontal cortex, bilateral orbitofrontal cortex and an anterior medial temporal region (Table 10.4a). Two further regions, right precentral gyrus and left inferior prefrontal cortex, were identified from the contrast performed on parameter estimates derived from the late covariate (Table 10.4b).

Table 10.4 Experiment 5: fMRI significant effects for positive/neutral contrast
Maxima within regions showing significant ($p < 0.001$) signal increases on the early (a) and late (b) covariates for the positive versus neutral contrast.

Region of Activation		**No. of voxels**	**Talairach coordinates**			**Peak $\underline{Z}$**	**BA**
			x	y	z		
(a) Early							
Superior/middle frontal gyrus	R	5	36	58	18	3.43	10
Medial orbitofrontal	R	7	6	48	-18	3.45	11
Medial orbitofrontal	L	13	-4	46	-14	3.51	11
Inferior frontal gyrus	L	9	-48	30	10	3.84	46
Inferior frontal gyrus	R	4	60	8	14	3.27	44
Anterior temporal gyrus	L	6	-36	4	-18	3.83	34
Fusiform gyrus	L	5	-54	-10	-24	3.27	20
Superior temporal gyrus	L	4	-44	-38	16	3.46	22
Middle occipital gyrus	R	7	30	-84	16	3.59	18
Inferior occipital gyrus	R	4	42	-86	-6	3.5	18
(b) Late							
Right precentral gyrus	R	8	50	0	16	4.89	6
Left inferior frontal	L	4	-28	14	14	4.63	44

The contrast between the positive and negative contexts revealed enhanced activity for items from the positive contexts in only one of the foregoing areas, namely the left orbitofrontal cortex (14 voxels xyz = –2, 46, –18, $\underline{Z} = 3.52$). However, the same effect was also observed in the right orbitofrontal cortex when the threshold was reduced to $p < 0.005$ (63 voxels xyz = 2, 36, -24, $\underline{Z} = 3.04$).

Selected regions activated during the retrieval of negative and positive contexts (relative to neutral contexts) are shown in figure 10.2 and 10.3 respectively. Percent signal change associated with contrasts between responses to items from neutral contexts with those from each of the two emotional contexts are shown for selected regions in figure 10.4.

Figure 10.2. Experiment 5: Selected regions identified by the contrast between items from negative vs. neutral contexts (thresholded at $p < .005$ uncorrected), displayed on normalised EPI images averaged across all participants.

Hippocampal, amygdala and right prefrontal cortex were identified in contrasts employing the early HRF, insula and posterior cingulate were identified with the late HRF (see methods).

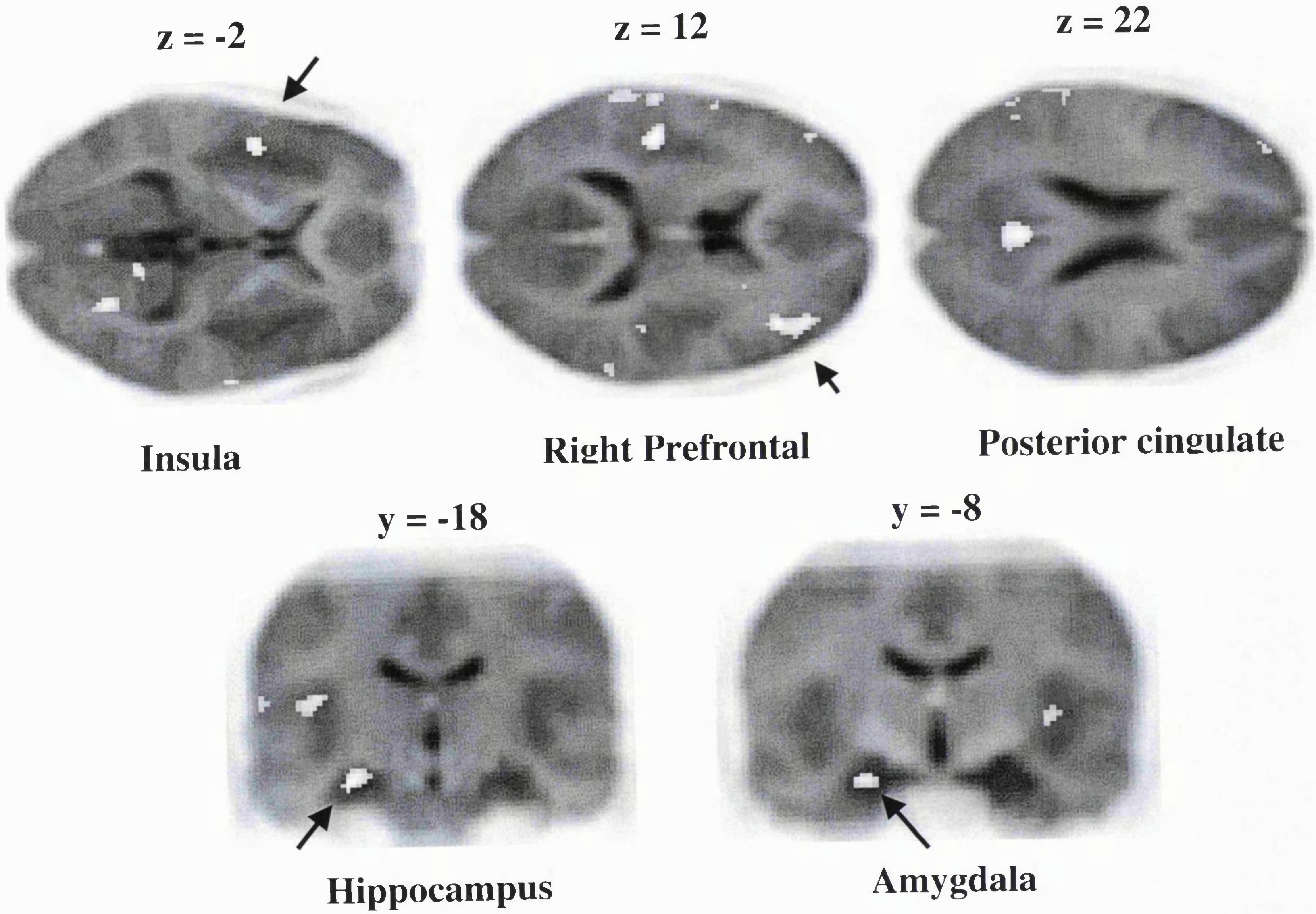


Figure 10.3. Experiment 5: Orbitofrontal regions identified by the contrast between items from positive vs. neutral contexts using the early HRF (thresholded at $p < .005$ uncorrected).
Note that the activated regions are in tissue unaffected by susceptibility artefact.

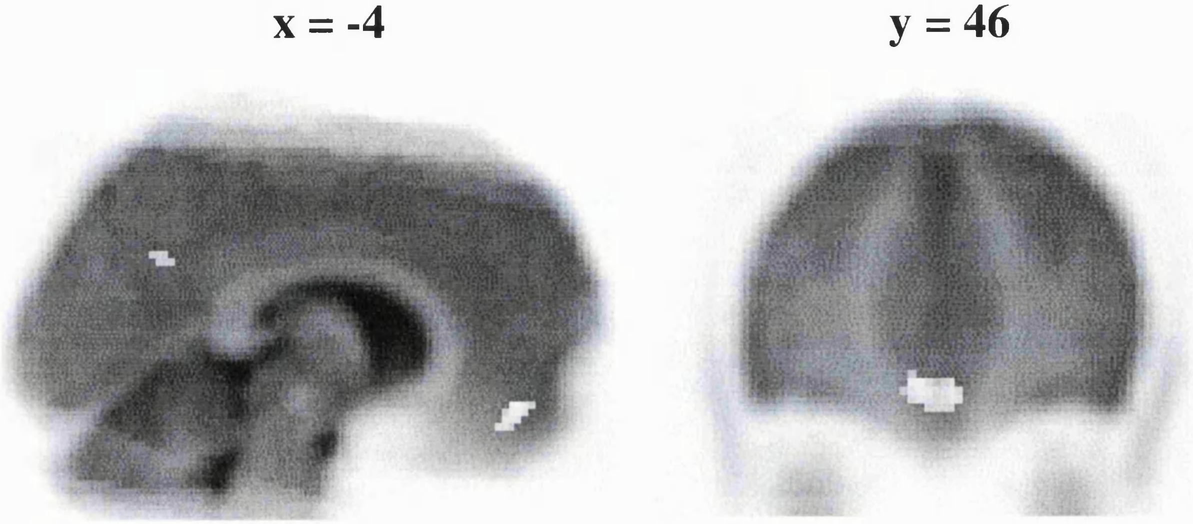
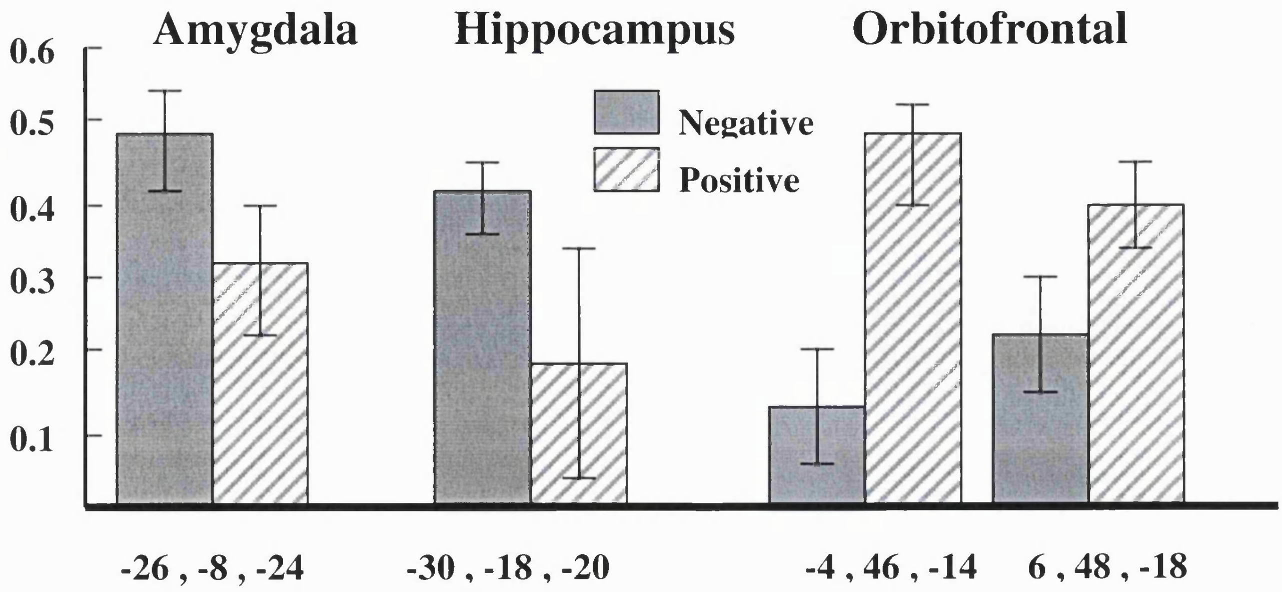


Figure 10.4. Experiment 5: Percent signal change and associated standard errors for positive vs. neutral and negative vs. neutral contrasts at regions indicated.
Contrasts used the early HRF (see methods).



Discussion

Performance Data

Items encoded in the neutral, negative and positive contexts were recognised with equivalent levels of accuracy, and with comparable RTs. These findings, consistent with the results of experiment 3, are inconsistent with previous reports that emotionally valenced contexts enhance memory (as indexed by free recall) for pre-experimentally neutral stimuli (Phelps et al., 1997; Phelps et al., 1998). However, as discussed previously, there is evidence that the effects of emotionality on memory increase with time (LaBar and Phelps, 1998) so it is possible that the effects of the present emotionality manipulation would have become more evident with a longer study-test interval. Also as evidenced from the previous two experiments, straightforward recognition tasks, as opposed to more demanding tasks such as recall/ source tasks, may not be sufficiently sensitive to detect differences in memory arising from the context manipulation. On a more positive note, the failure to find context effects on recognition accuracy or RT makes it unlikely that differences in the BOLD responses elicited by items from the different contexts reflect differences attributable to variables such as speed or confidence of associated recognition judgements.

The finding that negative sentences received more extreme valence ratings than did the positive sentences complicates the interpretation of the fMRI findings. Whereas effects that were larger for the retrieval of positive than negative contexts can be attributed with some confidence to valence-sensitive processes, this is not true for effects in the opposite direction. In this case, it is not possible to distinguish between the possibilities that the fMRI effects reflect processes sensitive specifically to the retrieval of negative memories, as opposed to the retrieval of memories eliciting relatively high levels of emotional 'arousal' (Heilman and Gilmore, 1998).

fMRI Data

The principal aim of this study was to identify neural systems activated by incidental retrieval of contextual emotional information. The findings indicated that retrieval of such information was associated with activation of several regions previously implicated in emotional processing (see LeDoux, 1996), including the amygdala and orbitofrontal cortex. In addition, retrieval of items encoded in an emotional, relative to neutral, context was associated with activation in regions thought to play a more general role in episodic retrieval, notably the prefrontal cortex and hippocampus. Because a single class of retrieval cue (neutral words) was employed to elicit both neutral and emotional memories, these findings cannot be attributed to differential retrieval 'sets' that may be adopted when the emotional valence of the retrieval cue predicts the valence of the stored information (the situation in most studies of emotional memory), or to any other kind of interaction between emotionally valenced cues and the memories they elicit.

Relative to items from neutral contexts, items from the negative contexts elicited enhanced activity in left amygdala. This finding does not however appear to be strongly valence-specific; the direct contrast between items from negative and positive contexts failed to reveal differential amygdala activity and, as can be seen in figure 10.4, items from the positive contexts also tended to elicit activity in this structure ($z = 2.62$, $p < .005$). The finding of amygdala activation during the incidental retrieval of emotional context builds on the recent finding of the engagement of this structure during recognition memory of emotionally items, regardless of their valence (Dolan et al., 2000). These authors proposed that the role of the amygdala in episodic retrieval was to tag retrieved memories with 'representations of their behavioural significance' (Weiskrantz, 1956). The present findings are consistent with this proposal, in as much as it implies that amygdala activation is a consequence, rather than a precursor, of the retrieval of emotionally valenced episodic memories. As noted already, because of the use of a single class of retrieval cue, activity dependent on the encoding context of the cue must have followed, rather than preceded, the retrieval of the contextual information.

The finding of orbitofrontal cortex activation during the retrieval of positive context is consistent with evidence that this region plays a role in emotional processing. For example, previous neuroimaging studies have reported orbitofrontal activation during the recollection of happy and sad life events (Pardo et al., 1993; George et al., 1995), and in the appraisal of reward (Rogers, Owen et al., 1999). In addition, clinical studies have shown that orbitofrontal lesions are associated with abnormal social behaviour hypothesised to result from impairments in decision making (Bechara et al., 2000; also see Damasio, 1999), or in the control and correction of reward- and punishment-related behaviour (Rolls et al., 1994; Rolls, 2000). The present findings add further to the foregoing observations in that they suggest that orbitofrontal cortex is engaged by the retrieval of memories that have been associated with positive (and, presumably, 'rewarding') emotional contexts. Furthermore, the sensitivity of this region for retrieval of emotionally positive contextual information suggests that in some circumstances orbitofrontal cortex is engaged preferentially by emotionally positive, rather than emotionally negative, information (cf. Northoff, Richter et al., 2000).

Other than the amygdala and orbitofrontal cortex, several other regions were identified which previous research has implicated in the processing of emotion, including anterior temporal cortex (Kimbrell et al., 1999; Dolan et al., 2000), posterior cingulate cortex (Fredrikson et al., 1995; Maddock and Buonocore, 1997; Phillips, Bullmore et al., 1998), and anterior insula (Lane et al., 1997; Phillips et al., 1998; Büchel et al., 1999). The finding that retrieval of both negative and positive contextual information is associated with anterior temporal activation accords with Mesulam's (1985) proposal that this region plays a role in imparting affective valence to experience. However, where Dolan et al. (2000) previously revealed anterior temporal cortex activity during retrieval of emotional information the activity was attributed to the tonic emotional 'state' associated with the emotional memory as opposed to a phasic item-related response. This hypothesis is not supported by the findings of the current study which have revealed item-related anterior cortex activity during emotional memory.

With respect to the findings for the posterior cingulate, it is noteworthy that Maddock (1999) proposed that the caudal part of the posterior cingulate cortex [including but not limited to the retrosplenial cortex and encompassing the 'posterior cingulate' regions (BA 23, 31) activated in the present study] acts as an 'interface' between emotion and episodic memory. The present findings are consistent with this proposal. However, posterior cingulate activation has been reported in a number of recent event-related studies of episodic retrieval of emotionally neutral information (Henson et al., 1999a; McDermott et al., 2000; Donaldson et al., 2000). The present findings may therefore reflect enhancement of activity in circuits subserving episodic retrieval in general, rather than systems specialised for the processing of emotion.

Finally, left anterior insula, identified in both the negative vs. neutral and negative vs. positive contrasts, has been linked with the processing of disgust (Phillips et al., 1997; Sprengelmeyer, Rausch, Eysel and Przuntek, 1998), generation of sadness (Reiman et al., 1997; Lane et al., 1997) and emotional learning/fear conditioning (Büchel et al., 1999). The present findings, which are consistent with these observations, may reflect the fact that autonomic activity triggered by retrieval of negative contexts was greater than that triggered by retrieval of positive or neutral information. This suggestion is consistent with the proposal that the insula is involved in representing somatic states (Craig, Chen, Bandy and Reiman, 2000).

The finding of increased activity in regions subserving early perceptual processing (lingual gyrus, primary auditory cortex) during the retrieval of negative information may have been contingent on the output of the aforementioned emotion-sensitive structures, especially (but not exclusively) the amygdala. This is consistent with anatomical reports of inter-connections between emotion-sensitive structures and sensory cortices (Iwai and Yukie, 1987; Armony et al., 1998; LeDoux et al., 1990; Turner and Herkenham, 1991; for reviews see Amaral et al., 1992; Kapp et al., 1992; LeDoux, 2000) and also imaging studies revealing the modulation of sensory processing activity during conditioning (e.g. Morris, Friston and Dolan, 1998) and episodic retrieval of emotional information (e.g. Kosslyn et al., 1996; Taylor et al., 1998). The finding of increased activity in regions subserving early perceptual processing during the retrieval of negative information is also consistent with a previous study which revealed that vivid remembering reactivates sensory-specific cortices (Wheeler, Petersen and Buckner, 2000).

In addition to the findings for regions thought to support emotional processing, retrieval of both positive and negative contexts was associated with enhanced activity in regions implicated more generally in episodic memory retrieval (for reviews see Squire and Knowlton, 1999; Markowitsch, 2000). Most notable among these regions were left and right prefrontal cortex, and left hippocampus. Several proposals have been advanced as to the functional significance of right prefrontal activation during episodic retrieval (Shallice et al., 1994; Kapur et al., 1995; Rugg et al., 1996; Schacter et al., 1997). The present findings are most consistent with the proposal that this region supports 'post-retrieval' processes, specifically, operations involved in the monitoring and evaluation of the products of retrieval (Shallice et al., 1994; Henson et al., 1999b; McDermott et al., 2000) According to this interpretation, retrieval of emotional contexts, either by virtue of the amount or the salience of the retrieved information, engaged these post-retrieval processes to a greater extent than retrieval of emotionally neutral information.

Enhanced left prefrontal activity for old versus new items has been reported in previous event-related studies of recognition memory (Henson et al., 1999a; Donaldson et al., 2000; Konishi et al., 2000; McDermott et al., 2000; for review see Rugg and Henson, in press). In the present study, not only was left prefrontal activity selectively enhanced for retrieval of emotional contexts, but there was evidence of a double dissociation between left frontal regions. These regions are distinct from the more anterior region identified in the generic 'old-new' contrast illustrated in figure 10.1, raising the possibility that some prefrontal regions exhibit context-specificity during episodic retrieval.

Another region implicated in episodic memory and identified in the present study was the hippocampus. For reasons that remain unclear, hippocampal activation in episodic retrieval tasks is something of rarity in functional neuroimaging studies (for review see Rugg and Henson, in press), and this is one of the first event-related studies to report such activation. There are two possible kinds of interpretation for this finding. It may reflect a role for the hippocampus in the recollection of contextually- or information-rich memories. This interpretation is consistent both with the finding that items from negative vs. neutral contexts elicit greater 'recollection-related' effects (Ochsner, 2000; Maratos and Rugg, in press), and with the results of previous PET studies (Schacter et al., 1996a; Rugg et al., 1997a). Alternatively, the greater hippocampal activity for items from negative contexts may reflect processing 'downstream' from contextual retrieval. For example the activity might form part of a re-instatement of the initial encoding episode, or reflect 're-encoding' operations set in train by retrieval of emotionally arousing or salient information.

In summary, evidence is provided that neural activity mediating episodic retrieval and subsequent processing of information is modulated in at least two ways by emotion. First, there is enhancement of activity in networks supporting episodic retrieval of neutral information. Second, regions known to be activated when emotional information is encountered in the environment are also active when emotional information is retrieved from memory.

Discussion

The following discussion illustrates how the experimental findings in this thesis connect to the study of emotional memory. Summaries of the experiments begin the chapter to inform the reader of the main findings. Following this implications pertinent to research into emotional memory are discussed; first for the findings of the experiments investigating memory for emotional items (experiments 1 and 2) and secondly for the findings of the experiments investigating memory for emotional context (experiments 3 to 5). Specific issues relating to the behavioural and neuroimaging data for each experiment were dealt with in depth in the discussion sections for each chapter. Such issues will be revisited in the following discussions only where necessary. Finally, some directions for further research are proposed.

Experiment Summaries

Experiment 1: Electrophysiological correlates of Recognition Memory for Emotionally Negative and Neutral Words

Scalp recorded ERPs were used to investigate the neural activity elicited by emotionally negative and emotionally neutral words during performance in a recognition memory task. Behaviourally, the principal difference between the two word classes was that the false alarm rate for negative items was approximately double that for the neutral words. Correct recognition of neutral words was associated with three topographically distinct ERP memory 'old/new' effects: an early, bilateral, frontal effect which is hypothesised to reflect familiarity-driven recognition memory; a subsequent left parietally distributed effect thought to reflect recollection of the prior study episode; and a late onsetting, right-frontally distributed effect held to be a reflection of post-retrieval monitoring. The old/new effects elicited by negative words were qualitatively indistinguishable from those elicited by neutral items and, in the case of the early frontal effect, of equivalent magnitude also. However, the left parietal effect for negative words was smaller in magnitude and shorter in duration than that elicited by neutral words, whereas the right frontal effect was not evident in the ERPs to negative items. These differences between neutral and negative words in the magnitude of the left parietal and right frontal effects were largely attributable to the increased positivity of the ERPs elicited by new negative items relative to the new neutral items. Together, the behavioural and ERP findings add weight to the view that emotionally valenced words influence recognition memory primarily by virtue of their high levels of 'semantic cohesion', which leads to a tendency for 'false recollection' of unstudied items.

Experiment 2: Recognition Memory for Emotionally Negative and Neutral Words: The Effect of

Blocking Items at Test

Scalp recorded ERPs were used to investigate the neural activity elicited by emotionally negative and emotionally neutral words during the performance of a recognition memory task, however, in contrast to experiment 1, items were blocked at test according to class (negative, neutral). Consistent with the findings from experiment 1 the principal difference behaviourally between the two word classes was that the false alarm rate for negative items was approximately double that for the neutral words. Similarly, the amplitude of the N400 component was attenuated for negative relative to neutral items and, the parietally-based 'recollection-related' old/new effect was smaller in magnitude for such items. These findings provide further support for the proposal that emotionally valenced words influence recognition memory in a manner similar to lures in the Deese paradigm. In light of the results from the previous experiment, the ERP data also provide evidence that the arrangement of items at test (blocked versus mixed) affects the type of processing participants engage in when distinguishing between old and new emotional items. In contrast to the findings from the first experiment, the early frontal effect associated with familiarity-driven recollection was no longer evident in the ERPs to the negative items. Second, old/new differences for negative items were more apparent later in the recording epoch at right frontal sites. These findings suggest that when negative words are blocked at test, participants are less able to make recognition judgements on the basis of familiarity and compensate with post-retrieval processing tailored to distinguish features that differ between the old and new words. The experiment highlights methodological issues relating to the use of emotionally and neutrally valenced stimuli to allow cross-condition comparisons in investigations of emotional episodic memory. In effect, non-emotional factors such as semantic cohesiveness may interact with aspects of the experiment, such as arrangement of test items, thus influencing memory.

Experiment 3: Electrophysiological correlates of the incidental retrieval of emotional and non-emotional context

Scalp recorded ERPs were used to investigate the neural activity elicited by the incidental retrieval of emotional and non-emotional contextual information. In contrast to the previous experiments, the paradigm employed did not confound the emotional valence of the retrieval cues with the valence of the 'to-be-retrieved' information. Participants studied neutral words presented in negatively or neutrally toned sentences. At test, participants made old/new recognition judgements to these words. Left parietal old/new ERP effects were larger and more sustained when elicited by words that had been studied in negative sentences, and a right frontal old/new effect was elicited by these words exclusively. The findings indicate that incidental retrieval of emotional context gives rise to greater activation in neural systems supporting conscious recollection than does retrieval of non-emotional context.

Experiment 4: Electrophysiological correlates of the intentional retrieval of emotional and non-emotional context

This experiment addressed the effects of emotional vs. non-emotional study contexts on ERP old/new effects in a task where there was, in contrast to experiment 3, an explicit requirement for contextual retrieval. Participants studied words presented in negatively or neutrally toned sentences. At test, participants made old/new recognition judgements to these words. For words judged old they indicated whether the words had been studied in a neutral or a negative context. The left parietal and right frontal effects elicited by old words correctly assigned to their study context were equivalent in size regardless of the nature of the context. A third ERP old/new effect, maximal over posterior scalp regions, was elicited exclusively by words from negative contexts. These findings indicate that when contextual retrieval is intentional recollection of emotional and non-emotional information are associated with equivalent engagement of neural systems supporting conscious recollection. The findings are consistent with the existence of additional neural circuitry that is activated selectively by emotionally toned episodic information.

Experiment 5: Haemodynamic correlates of neural activity associated with episodic memory for emotional context

To address the question of which brain regions subserve retrieval of emotionally-valenced memories, efMRI was used to index neural activity during the incidental retrieval of emotional and non-emotional contextual information. At study, emotionally neutral words were presented in the context of sentences that were either negatively, neutrally or positively valenced. At test, fMRI data were obtained while participants discriminated between studied and unstudied words. Recognition of words presented in emotionally negative relative to emotionally neutral contexts was associated with enhanced activity in right dorsolateral prefrontal cortex, left amygdala and hippocampus, right lingual gyrus and posterior cingulate cortex. Recognition of words from positive relative to neutral contexts was associated with increased activity in bilateral prefrontal and orbitofrontal cortices, and left anterior temporal lobe. These findings suggest that neural activity mediating episodic retrieval of contextual information and its subsequent processing is modulated by emotion in at least three ways. First, there is enhancement of activity in networks supporting episodic retrieval of neutral information. Second, regions known to be activated when emotional information is encountered in the environment are also active when emotional information is retrieved from memory. Third, regions activated during retrieval of emotional episodic information differ according to the valence (positive, negative) of the information retrieved.

Implications

Memory for Emotional Items

The experiments investigating memory for emotional items provide evidence that neural activity differs during recognition of emotional words relative to neutral words. These differences involve the modulation of a common set of retrieval processes previously documented as subserving retrieval for neutral episodic information. The findings provide evidence that neutral and emotional stimuli differ on dimensions other than 'emotionality'. Specifically it appears that effects of emotion upon memory may, under some circumstances, be driven by emotionally-valenced words sharing higher levels of inter-item associations relative to neutral words in addition to (or instead of) 'specialised' emotional neural circuitry (see also LaBar and Phelps, 1998; Phelps et al., 1998)[1].

The most obvious implication of the findings concerns studies which employ contrasts between neutral and emotional retrieval cues in order to reveal the neural circuitry underlying emotional memory. Where such emotional and neutral retrieval cues are unmatched in terms of semantic-cohesiveness, behavioural and neuroimaging effects cannot confidently be attributed to the consequences of retrieving emotional vs. non-emotional memories.

In addition, the proposal that emotionality effects may be driven by mechanisms of semantic-cohesion has implications for researchers investigating the neural mechanisms underlying emotion enhancement of memory through pharmacological manipulations. Findings that the administration of pharmacological agents which block β-adrenergic receptors selectively reduce enhanced memory for emotional events are taken as support for the hypothesis that the enhanced memory associated with emotional systems is subserved by physiological arousal (e.g. Cahill et al., 1994; van Stegeren A.H., Everaerd W., Cahill, McGaugh and Gooren, 1998). Yet, although it is thought that arousal enhances memory by triggering physiological responses that

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[1] Differences in emotional and neutral words are also likely with respect to imagability and concreteness (Campos et al., 1999). Although this issue has not been discussed in this thesis, such variables may also interact with memory.

elaborate memory networks resulting in the strengthening of memory associations (see Bradley, 1994), little is known about the effects of pharmacological agents upon differential memory effects elicited by semantically-cohesive relative to non-related items. A recent study addressing this issue demonstrated that pharmacological agents (alcohol) may influence the level of remember (R) responses [relative to know (K) responses] for falsely recognised lure items in the Deese paradigm (Milani and Curran, 2000). Thus, to the extent that emotionally valenced items influence memory by virtue of high levels of semantic cohesion (in a manner similar to associative lures in the Deese paradigm), findings from experiments assessing effects of pharmacological agents upon differential memory retrieval for emotional versus neutral events (e.g. β-adrenergic antagonists block enhancement effects of emotional content) will be difficult to interpret unless either: a) it is demonstrated that the pharmacological agent does not also influence memory effects driven by semantic-cohesiveness; or b) neutrally-valenced items employed match the emotionally-valenced items in terms of associative relatedness.

Not only does the finding that emotional memory may be mediated through mechanisms of semantic cohesion have implications for investigations into the neural basis of emotional memory, the finding also has implications for studies of emotional memory in affective disorders [e.g. depression or generalised anxiety disorder (GAD)]. Many of these studies note enhanced recall of and more liberal response biases for negative information in depressed/anxious patients relative to controls (see McNally, 1997 for review). For example, Zuroff, Colussy and Wielgus, (1983) (cited in Baddeley, 1997) demonstrated that depressed participants retrieved more emotionally negative items in a test of free recall relative to non-depressed participants and in a test of recognition memory the patients also falsely recognised more negative items. The differences between high and low depressed groups were attributable to differences in bias (β) as opposed to sensitivity (d′).

The bias differences were interpreted to reflect mood-congruity effects in the clinical groups, (i.e. predisposition toward attending to, recalling and recognising negative information congruent with current depressed mood). However, since depressed patients often have generalised impairments in cognitive processing (including memory), the negative bias could instead reflect a greater susceptibility in the depressed/anxious groups to the lure properties of emotional words. Consistent with the findings of Zuroff et al. (1983), in a task of recognition such a susceptibility would lead to an increase in hits and false alarms and thus be evident in bias (β) measures. Furthermore, this 'cognitive processing' explanation of negative bias in depressed patients is better able than 'mood-congruency' theories to account for observations that, similar to controls, depressed patients may recall more positive than neutral information (e.g. Danion et al., 1995; Calev, 1996).

A further methodological limitation with employing emotional and non-emotional stimuli in recall or recognition tasks is that the emotional attributes of the retrieval cues are confounded with the emotional attributes of the information to be retrieved. This is problematic for neuroimaging experiments since it may be difficult or impossible to distinguish between neural activity associated with accessing emotional vs. non-emotional memories, and activity associated with the representation and further processing of these memories [Taylor et al. 1998; Dolan et al., 2000 for a specific example of this confound; see also Rugg and Wilding (2000) for a general discussion of these and related issues]. For example, the PET study by Taylor et al. (1998) revealed enhanced activity in the lingual gyrus during recognition of emotional relative to neutral slides. However, the finding is difficult to interpret since enhanced activity in visual cortex is also observed during visualising and perceiving emotional images (Paradiso, Robinson et al., 1997; Kosslyn, Shin et al., 1996). Although, the recent experiment investigating emotional episodic retrieval by Dolan et al. 2000 attempted to control for effects elicited by the perception of emotional stimuli (e.g. target effects) by subtracting from the effects a perceptual comparison condition, in practice it could not be demonstrated that interactions between the accessing and further processing of episodic memory were not occurring.

A final issue demonstrated through comparison of the results of the first two experiments is that when emotional and neutral items are employed as retrieval cues, the arrangement of item presentation at test (e.g. blocked versus mixed) might influence cognitive processing and memory-related neuroimaging effects. Specifically, it was demonstrated that the arrangement of the emotional items at test influenced the type of retrieval processing employed to distinguish between old and new emotional items. The effect of test format on emotional memory has been considered previously, predominantly with regard to habituation. By contrast, here the effect of test format was interpreted in light of the emotional items acting as associative lures and were thus proposed to result from modulation of generalised cognitive processing subserving memory retrieval rather than specialised emotion sensitive neural circuitry .

In summary, as participants perform memory tasks they need to retrieve information from memory and process information (e.g. represent and evaluate information) in a form specific to the task and the behavioural goals evoked by the task. Thus, cognitive processes employed are determined by the behavioural context such as the design and structure of the memory task (recognition, recall, blocked/mixed etc, intentional versus incidental retrieval task). Expanding upon this, it is easy to envisage other examples of how the arrangement of item presentation in memory tasks might influence various aspects of cognitive processing differentially when emotional and neutral items are employed as stimuli without necessarily affecting emotion-specific processing (such as amygdala habituation to repeated emotional stimuli). For example, another form of emotional influence upon cognitive processing could occur if emotional items are blocked at study. With such a design of memory task, the repeated presentation of negative items might induce a negative mood state which reduces effort at encoding for such items (see Johnson and Magaro, 1987). Thus at retrieval, memory performance for such items would be impaired relative to when such items were mixed, but again such effects would not necessarily be item-specific.

A further issue to be discussed regards the finding that recognition memory was impaired for stimuli with emotional (relative to neutral) content. This finding appears inconsistent with the widely held generalisation that emotional experiences are well remembered relative to non-emotional experiences (see McGaugh, Roozendaal and Cahill, 2000; see also Christianson, 1992). As discussed above, the contradiction is accounted for by the proposal that the semantic-cohesiveness of emotional items impairs recognition by increasing false alarm rates for such items, a proposal supported by the findings of the final three experiments which demonstrated that once effects of semantic-cohesiveness are removed, emotion has an enhancing effect on neural activity subserving recognition memory.

Although differences between effects of emotion and effects of semantic cohesion have been emphasised in this thesis (and previously by Phelps and colleagues), problematically, this distinction is not consistently noted in the emotional memory literature. This neglect has resulted in interactions between emotion and memory being over-generalised to include many kinds of emotional stimuli and many types of retrieval tasks. However, it is possible that many studies employing recall of emotional and neutral words unwittingly and erroneously report enhancement effects of emotion (upon memory) by neglecting to compensate for intrusion errors (spurious recall).[2] To my knowledge, it has never been reported that the elevated recall rate for emotional words is unaccompanied by an elevated rate of intrusion errors for emotional relative to neutral words, as would be expected if emotion rather than mechanisms of semantic-cohesion were mediating the enhancement effects. Notably, data from a study conducted with regard to this issue (Maratos and Rugg, unpublished observations) indicated higher levels of spurious recall for emotional relative to neutral words. The results proved indeterminate as to whether the finding of enhanced recall rate for negative relative to neutral words was offset by the enhanced rate of intrusion errors for such items.

In part, this bias towards reporting enhancement effects for emotion may stem from the fact that it is generally accepted that the main mechanism mediating the effects of emotion upon memory is arousal. Thus, enhancing effects of emotion upon memory are compatible with established findings that arousal enhances memory (e.g. Soetens, D'Hooge and Hueting, 1993) and as such may receive less scrutiny. It is of interest to note that in the 1960/70's when psychoanalytical theories of repression were more popular in the emotional memory literature, experiments were more frequently reported where emotionality manipulations impaired memory performance. For example, Levinger and Clark, (1961) found that associative recall was poorer for emotionally toned-words relative to neutrally toned words. The findings were interpreted as demonstrating Freudian repression, that is emotional words (anxiety-laden 'complexes') promote repression relative to neutral words.[3]

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[2] Although discrimination indices sensitive to differential false alarms rates are systematically employed in tasks of recognition memory, the vast majority of studies reporting enhancing effects of emotion upon memory have done so through reports of enhanced recall for emotional relative to neutral stimuli wherein intrusion errors are generally ignored.

[3] It was subsequently suggested that the emotionality effects found by Levinger and Clark do reflect arousal mechanisms (rather than repression) following the findings that the effects are reversed when a longer delay is employed between study and recall (see Baddeley, 1997, pp 275 - 277 for discussion).

Memory for Emotional Context

Whereas experiments 1 and 2 addressed mechanisms underlying retrieval of emotional items, the final three experiments employed a design suitable for assessing differences in the neural activity elicited by retrieval cues according to their affective encoding context. It was demonstrated again that retrieval of emotional contextual information engages much of the same neural circuitry that supports the retrieval of non-emotional information. However, in addition the findings also support the proposal that retrieval of emotional memories is subserved by activity in neural circuitry additional to that engaged during retrieval of emotionally neutral information (LeDoux, 2000). A final conclusion (arising from a comparison of the findings from the final two ERP studies), is that emotional information does not necessarily lead to enhanced activity in this retrieval network; rather, when greater retrieval effects are observed for emotional information, this may be because such information is more likely to be retrieved, and, once retrieved, more likely than non-emotional information to receive post-retrieval processing (see discussion of experiment 4).

The first point to note concerning these studies is that the paradigm employed to investigate emotional memory (i.e. retrieval of emotional context through presentation of neutral retrieval cues) appears to offer some advantages over methods employed in other neuroimaging studies (experiment 1 and 2 included) which employ emotional items as retrieval cues. Crucially, by employing a single type of test item (emotionally neutral words), it was possible unequivocally to attribute differences in the neural activity elicited by the items to their encoding context; specifically, in the present case, to whether the context had a negative, neutral or positive affective valence. Furthermore, the experimental manipulation revealed memory effects (behavioural and neuroimaging) consistent with emotion having an enhancing effect upon memory.

The data from these three experiments has implications for the choice of experimental paradigms employed in studies of affective disorders whose symptoms include traumatic intrusive memories. These disorders include, but are not limited to depression, generalised anxiety disorders and prototypically, post-traumatic stress disorder (PTSD).

It has been proposed that are two distinct types of traumatic intrusive memory

(Brewin, Dalgleish and Joseph, 1996). The first type of intrusive memory consists of ordinary episodic memories, albeit that can also be retrieved, represented and edited 'at will'. The second type is characterised by automatic, involuntary retrieval elicited by internal or external cues. This second type of memory is proposed to underlie 'flashback' memories - intense 're-living' of the traumatic episode. More specifically, these 'type 2' memories have been likened to the acquisition of a CFR in that internal and external cues present at the time of the original traumatic event (conditioned stimulus) may later give rise to the CER (Pitman, Shalev and Orr, 2000).

Occurrences of second type of memory have been proposed as distinguishing PTSD from other affective disorders such as depression (Brewin, Hunter, Carroll and Tata, 1996). However, recently Reynolds and Brewin (1999) reported that there appears to be considerable overlap in the types of traumatic intrusive memories reported by patients with depression and patients with PTSD (although the study could not rule out the possibility of differences in the intensity/quality of the emotion reported in the two conditions). For example, some patients with PTSD report vivid and detailed recollections of the traumatic experience ('type 1' memories). Furthermore, intrusive 'type 2' memories are reported by trauma survivors who are not diagnosed with PTSD (Foa, Riggs and Gershuny, 1995), persist after PTSD diagnoses are removed (McFarlane and Yehuda, 1996 cited in vanOyen Witvliet, 1997) and are also reported by patients suffering from major depression (Reynolds and Brewin, 1999). Finally, these two types of emotional memory do not appear to be mutually exclusive and some reports of traumatic intrusive memories appear to include components of both types memory (Pitman et al., 2000).

The above synopsis highlights the importance of studying traumatic intrusive memories as an emotional memory phenomena in their own right rather than specific to a particular disorder such as PTSD (see vanOyen Witvliet, 1997 for a similar proposal). To date, research into traumatic intrusive memories has primarily taken one of three forms. One line of research has addressed the nature of flashbulb memories of culturally significant events [e.g. the assassination of JFK, (Brown and Kulik, 1977); the Challenger disaster, (Bohannon, 1988)]. The second line of research has addressed memory for personal autobiographical episodes, for example incidents of childhood physical or sexual abuse (Kuyken and Brewin, 1994; Shin, McNally et al., 1999), rape (Tromp, Koss, Figueredo and Tharan, 1995; Dancu, Riggs, Hearst-Ikeda, Shoyer and Foa, 1996) or combat (Pitman, Orr et al., 1996). Finally, the third line of research has addressed episodic memory for emotional stimuli, for example, neutral versus emotional slides (Christianson, Loftus, Hoffman and Loftus, 1991) or films (Horowitz and Wilner, 1976).

All three kinds of research have contributed to our understanding of the properties of emotional memories and the relationship between emotional memories and intrusive memories. However, as discussed above these approaches are not without confounds, for example between the emotionality of the encoding episode and the distinctiveness of the autobiographical event (approaches 1 and 2) or between the nature of the retrieval cue and the nature of the information to be retrieved (approach 3). Indeed, in a review of the relevant literature, vanOyen Witvliet (1997) similarly remarks on the absence of suitably controlled studies and identifies the need for studies with 'standardised instruments ......to assess rigorously the specific features of intrusions' (pp 528). In addition, the review notes the importance of examining non-clinical populations to establish normative data on traumatic memories.

On the basis of the experiments from this thesis, it is suggested that the paradigm employed in experiments 3 and 5 (incidental retrieval of emotional contextual information) offers an alternative 'suitably controlled' method for investigating the properties of traumatic intrusive memories both in normal subjects and also with inter-group comparisons (e.g. clinical versus normal, PTSD versus depression). Crucially, the experimental paradigm has been demonstrated to elicit enhanced emotional (negative) memory superfluous to behavioural requirements thus emulating the 'intrusive' characteristics of such memories. Furthermore, the design of the experiment is 'standardisable' such that it is easy to replicate experiments both within and across groups (normals, PTSD, depression) and across methodologies (electrophysiological, haemodynamic, pharmacological).

Further Research

There are a number of aspects of the mechanisms underlying emotional memory that remain poorly understood. It is proposed that experimental manipulations can be applied to the 'retrieval of emotional context' paradigm in order to elucidate further neural mechanisms underlying emotional memories (and also dysfunction thereof in disorders such as PTSD).[4] As described above, reasons for employing this paradigm 'as standard' arise predominantly from concerns about interpreting contrasts between different types of retrieval cue (emotional, non-emotional). However, it is not the case that comparisons involving emotional and neutral words should be universally avoided. Indeed, it could be argued that the use of emotional stimuli in memory tasks under some circumstances corresponds well to re-encountering emotional episodes in real life and thus experiments which attempt to control for factors such as semantic-cohesiveness are counter-intuitive as they exclude characteristics of 'real-life' emotion.

In answer to this issue it is proposed that the best way to understand a phenomenon as complex as emotional memory is to reduce the number of components in the emotional memory which may interact with the experimental variables. Well-defined manipulations can then be applied to the design, which selectively alter variables of interest, and concomitant changes in neural activity can be monitored. The following discussion outlines the form that such manipulations might take in future studies of emotional context retrieval. Once emotional memory is understood in its 'purest' form, researchers can turn their attention to naturalistic environments. [It is noted that a similar approach has been promoted before with the suggestion that emotions are best investigated by reducing them to 'sub-components' of avoidance and approach rather than as phenomena in their own right (e.g. sadness, happiness, anger) (see Ortony and Turner, 1990; Turner and Ortony, 1992 *vs* Ekman, 1992; Izard, 1992; Panksepp, 1992 for debate with regard to this issue)].

There are a number of variables which interact with cognitive processing underlying emotional memory. This thesis has addressed; a) type of emotional memory (i.e. whether emotional memory is operationalised as memory for items or memory for context); b) behavioural context in which the emotional memories are retrieved (for example, the arrangement (blocked/mixed) of the information at encoding or retrieval, or whether retrieval is incidental or intentional) and c) valence (whether the emotional

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[4] It is suggested that in the studies proposed below emotional context retrieval should be incidental to the task requirements (as in experiments 3 and 5) rather than an explicit requirement (as in experiment 4) since it was demonstrated that only the incidental retrieval of emotional context gives rise to greater activation in neural systems supporting conscious recollection (experiment 3 and 5). By contrast, when contextual retrieval is intentional retrieval of emotional and non-emotional information are associated with equivalent engagement of neural systems supporting conscious recollection.

memory was positive or negative). There follows a summary of issues raised by the experiments in this thesis that could be addressed in future studies.

It was noted in the discussion of the fMRI study that there was no attempt to determine the extent to which valence effects found in that study might have reflected differences between in the capacities of the contexts to evoke emotional 'arousal' (negative contexts were more emotionally arousing than positive contexts). Thus one direction for further research is the delineation of the relative contributions of valence and arousal to emotional memory (and their respective underlying neural mechanisms). It is proposed that the effects of valence and arousal upon emotional memory could be determined by modifying the experimental paradigm (and analyses thereof) such that the study sentences are systematically varied across the two dimensions; arousal and valence. On the basis of the findings from experiment 5 it is predicted that the level of amygdala activation should be correlated with 'arousal' rather than valence, whereas medial orbitofrontal activation should be valence specific (to retrieval of positive memories).

Secondly, it has been noted previously that delay between encoding and retrieval may play an important role in the interaction between the emotional type and amount of material retrieved (Kleinsmith and Kaplan, 1963; Phelps et al., 1998). More specifically it appears that this pattern reflects the robustness of emotional memories (relative to neutral memories) to forgetting, rather than any increment in the strength of emotional memories (Phelps et al., 1998). Thus, a second variable that could incorporated into future studies of the neural circuitry underlying retrieval of emotional context is time between encoding and retrieval. It will be of interest to determine whether differences in the neural activity mediating memory for neutral and memory for emotional information are most apparent immediate to encoding or whether differences increase with time (from immediate recall to delayed recall).

A third variable of interest, whose influence upon emotional memory has yet to be comprehensively addressed, is the environment of the stimuli at encoding. As discussed previously, this environment can relate to the arrangement of the items to be encoded (blocked, intermixed). However, behavioural studies of emotional memory have shown that arousal in the environment that is not related to a particular stimulus may still lead to enhanced recollection of that stimulus. For example, studies have shown that arousal due to white noise (Berlyne, Borsa, Craw, Gelman and Mandell, 1965) or physical exercise (Baron and Moore, 1987) will lead to enhanced recall for neutral words. Thus, a future experiment might assess whether non-specific emotional arousal in the environment also leads to enhanced activity in the neural systems supporting conscious recollection similar to when the emotionality manipulation was integral to the study task.

The final proposal for future research more specifically addresses the employment of the retrieval of emotional context paradigm in studies of intrusive emotional memories. Reynolds and Brewin (1999) suggested that traumatic emotional memories are based at least partly on perceptual representations of information (see also Kosslyn et al., 1996; Taylor et al., 1998). In support of this, the fMRI study in this thesis revealed that during retrieval or emotional information a similar pattern of enhanced activity to that normally observed during perception/encoding of emotional information is observed, even to the extent of heightened activity in sensory systems. It does appear therefore that emotional memories are best characterised in terms of the active generation of representations of the past (cf. correspondence views of memories versus storehouse views, Koriat and Goldsmith, 1996b). A critical question therefore that the paradigm can be used to address is whether patterns of neural activity during intrusive traumatic memories (operationalised as incidental retrieval of emotional contexts) also differ a) between clinical populations and normal populations and b) between different subgroups of clinical populations (e.g. PTSD versus depression). The need to resolve this issue with respect to PTSD and depression has been noted previously (see Reynolds and Brewin, 1999). If activity during intrusive emotional memories is greater in PTSD/depressed patients relative to controls this would be consistent with theories of a sensitivity to emotional information in such patients (Holmes, Chronopoulos et al., 1993; Hovdestad and Kristiansen, 1996; Grillon, Southwick and Charney, 1996, for reviews see Pitman et al., 2000; Buckley, Blanchard and Neill, 2000).

Conclusion

The research outlined in this thesis has provided a framework within which emotional episodic memory can be viewed and further investigated. The finding that the ERP correlates of retrieval of emotional words are sensitive to the arrangement of emotional and neutral items at test indicates that researchers should be cautious when interpreting neuroimaging data as indices of emotional memory. A more significant finding is that emotional episodic memory may be mediated by at least two mechanisms. One of these mechanisms – semantic cohesion – is dependent upon the same neural circuitry which mediates episodic retrieval for neutral information. By contrast, mechanisms underlying the retrieval of emotional contextual information are dependent both upon neural circuitry known to mediate episodic retrieval for neutral information and in addition dissociable neural structures. It was further determined that, where retrieval of emotional memory is incidental, activity in networks supporting episodic retrieval of neutral information is enhanced. Finally, the findings suggested that dissociable brain regions are sensitive to the affective nature (positive or negative) of the emotional memory, specifically it appears that regions which are known to be activated when emotional information is encountered in the environment, are also active when emotional information is retrieved from memory. This last conclusion corresponds well to subjective experience of emotional memory in that we often 'feel' emotions while 'remembering' them. Thus returning to the lines of Nekrassov with which the thesis began, 'Revolted, Maddened, horror-stricken, At memories of foul disgrace.', it does indeed appear that that emotions are relived in their memory.

Abbreviations

ANOVA = analysis of variance

BA = Brodmann area

Br = Bias index

BOLD = blood oxygenation level-dependent

CER = conditioned Emotional Response

CFR = conditioned fear response

CS = conditioned stimulus

EEG = electroencephalography

EOG = electro-oculogram

ERP = event-related potential

EPI = echoplanar imaging

GLM = general linear model

hEOG = horizontal electro-oculogram

HRF = haemodynamic response function

IAPS = international affective picture system

K = know

l = left

LTP = long-term potentiation

NMRI = nuclear magnetic resonance imaging

fMRI = functional magnetic resonance imaging

efMRI = event-related functional magnetic resonance imaging

FHWM = full width half magnitude

HRF = haemodynamic response function

MIP = maximum intensity projections

MNI = Montreal Neurological Institute

PET =positron emission tomography

Pr = discrimination index

PTSD = post-traumatic stress disorder

r = right

R = remember

RT = reaction time

SCR = skin conductance response

SD = standard deviation

SMF = source monitoring framework

SPM = statistical parametric mapping

SOA = stimulus onset asynchrony

ST = Site

SPM = statistical parametric mapping

TE = echo time

TR = repetition time

US = unconditioned stimuli

UR = unconditioned response

vEOG = vertical electro-oculogram

Appendices

Critical words from experiments 1 and 2

Neutral:	Negative:
absorb	abandoned
academy	abuse
account	accident
acquaint	accuse
agency	ache
aluminium	afraid
average	alienate
banana	anxiety
barbecue	ashamed
bathe	avoided
brandy	awful
bread	bad
buck	bankrupt
bus	blame
butter	bomb
butterfly	bored
chicken	burden
civilian	conflict
concert	confused
conclude	corpse
context	cramp
cousin	crime
cup	crisis
customers	cry
deduct	curse
degrees	damage
diplomats	danger
document	demands
dune	depressed
dutch	despair
earring	desperate
ebony	died
eel	dire
factory	dismay
fan	disturb
fathom	doom
flame	doubts
fluid	dud
followed	failure
fragment	fearful
gateway	feeble
gear	forgotten
gene	fright
glanced	funeral

grass
green
grouped
handle
hat
heel
herd
inch
incline
indirect
installed
iron
jacket
juice
kitty
ladder
lawn
lens
library
liquid
lock
lunch
maple
margin
measure
mention
moth
normal
nearby
neutral
novel
onion
orange
oyster
package
palm
parking
pave
pen
pianist
placed
porch
pottery
quarter
quote
recruit
refund
replace
resident
restore

gloom
grave
grief
guilty
gun
harm
helpless
hopeless
horror
hurt
ill
inhibit
injury
intense
isolated
killed
lonely
loss
misery
murder
nervous
ominous
pain
panic
pathetic
penalty
petrified
poverty
punish
regret
rejected
restless
risk
sad
scared
shame
shock
shy
sick
solemn
sorry
strain
stress
stupid
suffering
suffocate
suicide
tears
tension
terrible

retained
salad
sandwich
scan
signal
slope
solar
somehow
sooner
starling
steel
submarine
swimming
taste
theory
throw
total
transfer
terror
threat
torture
tragedy
trap
troubled
ugly
uneasy
unhappy
upset
urgent
victim
violence
warning
waste
weakness
widowed
worried

Critical Words and Sentences from Experiments 3 and 4

	Neutral	Negative
academy	The boys went to the academy to learn sketching and fine art.	The soldiers from the academy were gunned down.
address	She wrote down her address for the receptionist.	The murderer found her address and hid there.
agency	She went to the agency to enquire about changing profession.	The agency sacked all its employees.
aircraft	The engineers gave the aircraft a final check over before takeoff.	The aircraft exploded and everyone on board was burned to death.
aluminium	The set of pans were made of aluminium with plastic lids.	Senile dementia is caused by aluminium.
animal	The children drew an animal during their art class at school.	They poured acid over the caged animal.
apartment	The apartment was in the town centre.	They apartment had been the scene of a brutal murder.
arm	He stretched out his arm and yawned.	She screamed as he hammered the nail through her arm.
artist	It took five days for the artist to complete his work.	The artist mutilated his face with a knife.
author	The payments were issued to the author on receipt of his work.	The author was accused of pornography.
bag	She rummaged through her bag and pulled out her purse.	The mugger snatched her bag and stabbed her to death.
baker	The baker woke at 6am everyday.	The baker was found frozen in the deep freezer.
glider	On Saturday evening they went to see the glider.	The glider had a heart attack and crashed.
banana	He put the banana on the table.	The banana had worms burying into it.
bank	He went to the bank every Tuesday to check his balance.	The robbers held up the bank and threatened to kill every one.
bar	Charlie went to the back to the bar to buy some peanuts.	The drunk fell onto the bar and smashed his head open.
barbecue	They bought the barbecue at the supermarket.	The visitors vomited over the barbecue.
beach	They went for a walk along the beach in the afternoon.	The beach was covered with raw sewage.
bear	The bear lived in the forests.	The bear sunk his teeth into the man.
beef	The mother bought 1lb beef from the supermarket.	Eating beef will give you mad cow disease.
bench	They all sat on the bench and listened to the headmaster.	The bench snapped under their weight crushing them on the floor.
bird	The bird flew low looking for insects on the ground.	They fed the live bird to the snake.
block	The toddler fitted the block into the puzzle.	The disturbed toddler poked the block into his eye.
boat	The boat was painted a blue and red colour.	They clung to the boat as it sank into the ocean.
bone	They gave a bone to the cat to eat.	He howled as they sawed through the gangrenous bone.
bottle	She washed up the bottle and put it into the cupboard.	He smashed the bottle against her face.
box	She loaded the box up with books.	They kept the boy trapped in a box.
brain	They learned about the brain in their biology lesson.	He screamed in agony as they drilled through his brain.

branch	The children swung from the branch.	They gauged her eye out with a branch.
brandy	The children learned how to make brandy snaps at school.	The mother bought brandy instead of food for her children.
bread	The loaves of bread are on the third aisle in the supermarket.	He laughed as the starving child begged for the bread.
breakfast	The hotel served breakfast from eight until ten in the morning.	He vomited his breakfast over the table.
bride	The hire car pulled up and the bride got in.	The bride was left screaming at the altar.
bridge	They think the bridge was built before the war.	They clung to the bridge as it collapsed into the canyon.
brother	She went to ask her brother to come for his tea.	The brother beat his younger sister.
brush	He went to fetch a brush from the house.	He used the brush to batter his wife.
buck	The buck roamed around the forest during the summer.	The hunters enjoyed shooting at the buck.
bus	The bus went from Salford to Manchester.	The bus crashed into the wall killing the children.
butter	The supermarket sells butter and other groceries.	Cockroaches crawled over the uncovered butter.
butterfly	The cabbage white is the most common butterfly in England.	He set fire to the trapped butterfly and watched it melt.
camera	They took their camera away on holiday with them.	He photographed the torture with his camera.
camp	They went off to a camp during the summer.	The concentration camp stunk of burning bodies.
captain	They went to ask the captain about the length of the journey.	The captain laughed as they threw the stowaway overboard.
ceiling	The ceiling was painted a sky blue colour within a week.	The ceiling was mouldy and water leaked through it.
chain	She oiled the chain on her bike and set off for the next town.	She whipped his back with the chain until it was raw.
chair	He pulled his chair up closer to the radio.	He tied her to a chair and threw knives at her.
chapter	He finished the chapter and then rolled over and went to sleep.	The chapter was banned as it depicted paedophilic activities.
chest	The tailor measured his chest.	She split his chest in two with the axe.
chicken	They fed the chicken by scattering bran and barley on the ground.	The battery chicken pulled out its feathers and pecked itself.
china	They were bought the china as a wedding present.	She slashed his face with the broken china.
clay	They sold clay bowls in the supermarket.	They forced clay into his cat.
coal	She put some more coal onto the hearth.	He screamed as they placed the burning coal on his body.
coffee	She went for a break and made a coffee.	Coffee manufacturers starve third world workers.
column	The building had one main supporting column.	The column fell onto the tourists crushing them to death.
communist	He believed in most communist principles.	The communist screamed as they tortured him with a red-hot poker.
concert	At the concert the choir sang music from the classical era.	Ten thousand people died when the concert was bombed.
concrete	The pavement was made quickly out of concrete.	He screamed as they buried him alive in the concrete.
cook	The restaurant hired an extra cook for the Friday nights.	The cook went to the toilet and did not wash his hands.
corn	The farmer went out to harvest his corn that morning.	They farmer was shredded when he fell into the corn grinder.
cotton	The shirt was made from cotton and had short sleeves.	The operation revealed a ball of cotton in his intestines.
cousins	The cousins lived nearby to one another.	The cousins were tied to the railings and shot.

credit	Her account statement showed that she was in credit.	She exceeded her credit limit and went bankrupt.
crew	The crew of the yacht were sent on a training course.	The crew of the yacht drowned when it capsized.
crowd	She mingled in with the crowd as they watched the fireworks.	The angry crowd tore the paedophiles limbs off.
cup	The man bought a cup from the supermarket.	The cup contained a mixture of bile, pus and sick.
customer	The customer picked up a basket from by the door.	The customer strangled the checkout assistant.
dancer	The dancer warmed up before stating her routine.	The dancer was raped as she returned home from a show.
desk	She sat at the desk in the middle of the class.	The headmaster pinned the child to the desk and caned her.
detective	The inquiry was handed over to the local detective.	The prisoner beat up the detective.
dinner	They normally sat down to eat dinner in the early evening.	His dinner was full of blood and excreta.
diplomat	The speech was given by a diplomat in Greece.	They poured petrol over the diplomat and burnt him alive.
doctor	Their father worked as a doctor in the local hospital.	The doctor molested the patient.
document	The document contained information about the town's history	He put the gun in the policeman's mouth and demanded the document.
dog	The dog slept every night in front of the fire.	They trained the dog to assault the women.
drawing	The hung the drawing in the living room.	They stuffed the drawing into his mouth.
dress	She bought the dress mainly for work.	He ripped off her dress and tied her down with it.
drink	He got up to get a drink of water.	His drink had been laced with poison.
driver	The driver of the taxi was middle aged.	The driver of the taxi was a serial killer.
dune	The sand dunes mark out the landscape of the coast.	The sand dunes collapsed burying the toddler.
dust	He made sure the house was dust free.	Household dust is formed of dead mites and lice.
earring	She wore the earring she had bought the previous day.	During the fight the earring ripped through her ear.
eel	The eel swam at the bottom of the tank.	He ate the live eel for a bet.
election	There is a general election every 5 years.	The Nazis cancelled the next election.
engine	He warmed up the engine slowly as it was freezing.	The boy was mangled when he fell into the engine.
factory	The jumpers are being ordered from the factory for the catalogue.	The slaves worked in the factory until they died from exhaustion
fan	The head office contained a fan that was often on.	They forced her head into the fan and blood splattered everywhere.
fashion	The book was aimed at people who were interested in fashion.	He clubbed the seal's head open for the sake of fashion.
fiction	The fiction section is on the second floor.	The fiction had been based upon a true serial killing.
fig	The girl ate a fig whilst reading her book.	The girl spat out the fig as it tasted rotten.
film	They showed a film every evening.	The film showed the hostages being stripped naked and beaten.
finger	She pointed at the view with her finger and they stared for a while.	They chopped off his finger and blood splurted from the stump.
fish	They had a fish for tea as it was traditional for a Friday.	They slit open the fish and pulled out its gut.
flame	The candle flame flickered in the breeze.	They held the flame against his eye.
flesh	The chef carefully prepared the flesh for stewing.	The crematorium smelt of burning flesh.

lung	They looked at the x-ray of the lung.	They siphoned the fluid out of his pneumonic lung.
foam	Before shaving he lathered the foam onto his face.	The foam gathered around his rabid mouth.
foot	She hopped on one foot around the playground.	Her foot was blown off by the land mine.
fort	They visited the fort on a school outing and spent a day there.	The fort had been built by slaves most of whom died in the process.
fragment	They fitted the last fragment into the puzzle.	She carried around a fragment of his skull.
frame	She hung the frame on the wall and made sure it was straight.	The frame fell of the wall and knocked him unconscious.
fruit	They ate a piece of fruit everyday in the morning.	Razor blades had been hidden inside the fruit.
gallery	The gallery hosted a series of collections over the summer.	They firebombed the gallery in protest of the displayed prints of castrated men.
gas	She put a pan on the stove and turned on the gas.	She put her head in the oven and turned on the gas.
gateway	The park gateway opens at 10am every morning.	They tied the beaten woman and her baby to the park gateway.
gear	When changing gear it is necessary to use the clutch	He yelled at her to change up a gear but she ignored him.
gene	In biology the children learned that a gene may determine eye colour.	The politicians funded research into gene selection techniques.
glass	The glass was bought for her as a leaving present when she changed jobs.	The glass from windows lacerated their faces when the bomb exploded.
gold	The security men put the gold into the safe.	They stripped any gold off the murdered Jews.
golf	The highlights of the golf tournament were being reported on the radio.	The golf ball hit him in the face and smashed his teeth in.
grass	Every Sunday it was Charlie's job to cut the grass before washing the windows.	The bully stuffed grass into his mouth until he choked.
guest	The put the guest in the spare room at the end of their hall.	The guest was unaware that they planned to torture him.
handle	She turned the handle and entered the room.	She screamed as they turned the handle on the stretching rack.
hat	He put his hat and coat in the cloakroom.	They filled his hat with excrement.
heel	The Dalmatian walked at the heel of his master.	She screamed as they sliced off her heel.
herd	The whole of the herd were rounded up into the barn.	The pack of wolves ravaged the farmer's herd.
hill	They walked up the hill at a gentle pace most days.	He died of a heart attack half way up the hill.
horn	She sounded her horn to indicate she was ready.	The crash trapped her head against the car horn.
iron	She got up early to iron her clothes for the meeting.	He pressed the hot steam iron onto her face.
jacket	He went to the cloakroom to get his jacket from where he had hung it.	He wrapped the jacket around her head and suffocated her.
joint	He rolled a joint of tobacco as he spoke.	He rolled a joint of heroin in the school toilets.
juice	During the interval they were served juice.	Her teeth were rotten from too much juice.
jury	The jury reached a decision quickly.	The jury were blackmailed by the gangster's friends.
key	He put the key inside for safekeeping.	He forced her to swallow the key.
kid	The kid delivered the papers every morning in the local neighbourhood.	The kid terrorised the elderly people on the estate.
kitchen	He went into the kitchen to start preparing the evening meal.	The kitchen was crawling with rats and mice.

kitty	They kept a kitty to buy tea and biscuits with.	They accused the grandma of stealing from the kitty.
knee	He tied a pad to his knee before the cricket game started.	The gunman shot at his knee which exploded.
ladder	He climbed up the ladder to fix the drainpipe.	The father fell off the ladder and was permanently paralysed.
lady	The tomboy figured that she'd act like a lady when she grew up.	The burglars hung the lady of the manor from the banister.
lawn	They went to play bowls on the lawn as it was a nice day.	They went to play bowls but the lawn had been dug up by vandals.
lawyer	He was training to be a lawyer at one of the oldest firms in the city.	They stabbed the lawyer's eyes with needles.
league	She turned on the radio to check the league results.	His favourite team was relegated from the premier.
leg	He stood on one leg and counted to five.	They tied him down and amputated his leg.
lens	She put in her contact lens before going out.	She lost her contact lens behind her eye.
library	They went to the library after school to do their homework.	He stood in the middle of the library screaming and shouting.
fragment	She poured the liquid into the container.	They poured scalding liquid into his ears.
literary	She got medium marks for literary at school.	She always found literary really boring at school.
loan	She started paying off her loan when she got a job.	The student was forced to get a loan from the government.
lock	She fixed the lock on the shed that weekend.	He put a lock on her door so that she could not escape.
lunch	They went out for lunch every fortnight.	The boss kept them behind and they missed lunch.
magazine	She went to her bedroom to read a magazine.	The magazine contained a lot of pornography.
maid	The maid came on a Wednesday to help clean the house.	The husband frequently raped the maid.
manager	She went to ask the manager about her training schedule.	They tied up the manager and threw him down the lift shaft.
maple	The maple tree grew in the middle of the orchard.	They nailed the mother and child to a maple tree.
margin	The boy drew in a margin before he began writing.	The headmaster caned the boy for ruling a slanted margin.
marriage	Everyone said that the marriage had gone smoothly.	The marriage was a sham and they both had affairs.
match	He lit the stove carefully with the match.	He liked to burn himself slowly with a match.
mayor	The mayor helped with the town planning and budgeting.	The mayor swindled money from the council.
meat	He got the meat out of the freezer to defrost it.	Maggots and flies crawled over the uncovered meat.
message	She left a message for her friend at the reception.	The message said that she would be raped.
milk	They went out to get some milk first thing.	The milk poured out in lumps and smelt rancid.
minister	They said hello to the minister on the way home.	The minister was sleeping with most of the congregation.
model	The model had a lot of work that season.	The model was anorexic and hardly ate.
moth	The moth flew out of the window into the garden.	The moth burnt its wings as it flew around the light.
mountain	They often visited the mountain at the weekend.	They were found dead from hypothermia on the mountain.
mud	The frogs climbed onto the mud to catch flies.	He screamed as the mud enveloped his head.
muscle	He flexed his muscle before lifting the weight.	They injected the steroid into his muscle.
museum	The local museum had a fossil collection.	The museum was crammed with decaying war victims.

furnace	They put the paper into the furnace.	They put the child in the furnace.
neck	She put a scarf around her neck.	He wrung her neck slowly until he heard it snap.
newspaper	He sat down on the tube and read his newspaper.	They found out that their father was a transsexual from the newspaper.
nose	He blew his nose with his new handkerchief.	The punch plastered his nose over his face.
object	They examined the object and put it aside to think about.	He said he treated her like an object because she was stupid.
onion	He chopped the onion finely and added it to the pan.	They placed pieces of onion under his eyelids.
opera	The tickets for the opera cost ten pounds.	He took his mistress to the opera on his wife's birthday.
orange	At half time they had an orange and some water.	The orange fell on the ground and the ants crawled over it.
orchestra	The orchestra practised the overture most out of the piece.	The orchestra were line up and shot.
oxygen	Water is formed form hydrogen and oxygen.	The astronaut ran out of oxygen and asphyxiated.
oyster	She chose oyster for her starter and lasagne for her main course.	Those who had eaten oyster got chronic diarrhoea.
package	He asked for the package to be sent to his home.	The package exploded and blowing off his hands.
page	He read to the end of the page and then turned off the light.	Written on the page were names of aids victims.
painting	They hung the painting above the fireplace.	The painting was of a starving child.
palace	They went to see the palace while they were in London.	The palace was burned to the ground during the revolution.
palm	She placed the leaf on her palm and it blew away.	She slashed at her palm with the knife and watched it bleed.
parking	She didn't mind parking a little out of town.	She ran over the toddler while parking.
passage	The passage led from the master bedroom to the study.	The passage was full of muggers and drug dealers.
path	She took the same path to school everyday.	The girl was dragged off the path on her way to school.
pen	She picked up her pen and started writing the letter.	She stabbed the pen into her girlfriend's eye.
belt	He put the belt around his waist.	The inmate hung himself with his belt.
pianist	The pianist liked to play when he got home from work.	No one suspected that the pianist was a rapist.
pilot	The pilot was thinking about retiring.	The hijackers butchered the pilot and took over the plane.
platform	He climbed to the highest platform and dived.	He committed suicide by jumping off the highest platform.
player	They needed one more player to make the sides even.	They lost the tournament when after a player was sent off.
pocket	He put his money inside his pocket.	He lost the money through a hole in his pocket.
poet	He was a poet in his spare time.	The poet was dying of aids.
pope	They went to Italy to see the pope.	The pope was assassinated by the Mafia.
porch	They stood in the porch and chatted before going out.	He dragged her onto the porch and strangled her.
pottery	Every Tuesday night they went to pottery lessons.	The vandals smashed the priceless pottery.
prince	The prince travelled the world to find a suitable wife.	The prince was castrated by his enemies.
rain	The forecaster predicted no rain for a while.	They were forced to stand naked in the rain for hours.
relative	The elderly relative was still the loudest member of the house.	When her last relative died she went to a home for orphans.

resident	The resident of the house walked down the hallway.	They found the resident of the house handcuffed in a corner.
rice	She put the rice on to boil and set the time for 20 minutes.	They scrambled in the dirt for grains of rice.
ring	She put the ring on her dressing table.	She ripped the ring off his nipple.
rock	She sat on the rock and tied her shoelace.	He smashed open the cat's head with a rock.
salad	She decided to have a salad for a snack.	There was a huge slug wriggling in her salad.
salt	She added some salt to her soup for flavour.	He screamed as they ground salt into his wounds.
sandwich	She toasted the sandwich until it was light brown.	The sandwich had gone mouldy in the fridge.
scan	They took the scan into the laboratory.	They looked at the scan showing the tumour.
seed	They planted the seed in the garden and left it to grow.	The Nazi scientists planted a seed in her womb.
shadow	She looked at the sundial and read the time by its shadow.	She froze when she saw the maniac's shadow in her garden.
sheet	She hung the sheet out on the line to dry.	She tied the sheet around his head and suffocated him.
drum	He put his drum on the rack.	The noise of the drum deafened him.
shop	They went to work in the local shop.	They masked gunmen ransacked the shop.
shore	They walked along the shore up to the cliffs.	They were made to dig their own graves on the shore.
shoulder	He rotated his shoulder before throwing the discus.	The stretching rack ripped his shoulder out of its socket.
signal	The car moved off when the signal turned green.	The car ignored the signal and smashed into a pram.
site	They went to the site where they had the best view.	They went to the site where the stabbing had happened.
skin	She put the moisturising lotion on her skin.	Her skin was covered in sores and oozing scabs.
slope	They left the building and walked along the downward slope.	He dragged her by her hair up the slope.
smoke	The smoke rose from the buildings into the night.	The clouds of black suffocating smoke choked them.
snow	They went out for a walk in the snow.	They buried him alive in the snow.
soil	She turned the soil over with the garden fork.	They made him eat soil.
speaker	They were stood quite near to the speaker so could hear the speech.	They forced his head next to the speaker and his eardrum exploded.
stairs	He carried the child down the stairs and into the nursery.	He threw the woman down the stairs and watched her hit every step.
starling	The starling hopped along the ground looking for small insects.	The starling became tangled up in the netting and starved to death.
steel	The knives and forks were made of steel and were quite hardwearing.	He poured the molten steel slowly over the screaming prisoner.
stick	He used the stick to lean as he chatted to the farmer.	He used the stick to beat the cat with until its back bled.
stomach	He patted his stomach and remarked that he was now full.	They sliced open his distended stomach and sucked out the pus.
stone	The stone skimmed across the water before sinking.	The stone hit him between the eyes splitting open his skull.
store	They kept most of the grain in a store after Autumn.	The store was infested with rats and cockroaches.
stream	They walked along by the stream for about half a mile.	He pushed her head into the stream and held it as she struggled.
studio	He went to the studio to do some work for the day.	He filled his studio with emaciated and diseased bodies.
submarine	They designed the submarine to be watertight.	The submarine was hit by a torpedo and exploded.

sugar	She put a spoon of sugar into her tea and stirred.	They injected sugar into his veins.
suit	He put his best suit on for the night out	He found that his favourite suit had been cut to shreds.
swimming	They decide to go swimming for some exercise.	She got severe cramp whilst swimming and drowned.
symphony	He was commissioned to write the symphony by the king.	The king hated the symphony and cut off the composer's ears.
tape	The played the tape they had just bought in the car.	The tape contained a recording of the screams of the dead children.
teacher	The teacher told the children to get their books out.	The teacher repeatedly molested the young boys.
telephone	He went to the telephone to call his mother.	She had been receiving threatening dirty calls on her telephone.
television	He sat down in front of the television to eat his tea.	He electrocuted her by throwing a television into her bath.
temple	They went to the temple to admire the architecture.	The congregation was killed when the temple collapsed..
theatre	They went to the theatre for a birthday treat.	The woman was taken to a disused theatre and gang raped.
throat	She cleared her throat before starting the speech	He held the knife to her throat and slowly sliced it open.
thyroid	The young medics learned how the thyroid gland worked.	The thyroid disorder made his eyes bulge.
tissue	She pulled out a tissue and wiped her brow.	The tissue was covered in blood and pus.
tongue	She rested the boiled sweet on her tongue.	They chopped off his tongue and posted it to his wife.
tool	He looked for the right tool to fix the sink with.	He used the tool to puncture the skull with.
traffic	The child waited for the traffic before crossing.	The child ran out into the oncoming traffic.
train	The train travelled at one hundred miles per hour.	The train arrived full of rotting corpses covered in excreta.
tray	She carried the tray of plates into the dining room.	He hammered the tray against her head.
trip	They went on the trip as a break from work.	They went on a trip away and were kidnapped.
truck	The truck was bound for Lyon in France.	They dragged the girl into the truck and drove away.
uncle	She used to visit her uncle on a Thursday night.	They lived with their uncle who beat them frequently.
uniform	They wore a uniform most days to school.	The bullies urinated over his uniform.
valley	They walked along the valley to the next town.	They were found dead from hypothermia in the valley.
village	The used to go to the village at weekends.	The village was hit by the black death and its inhabitants died.
vitamin	She used to take a vitamin in the morning with some water.	She took her daily vitamin and choked to death on it.
wagon	They hired a wagon to take their belongings to the new farm.	The wagon drove over the tramp and broke his back.
wash	She had a wash and changed into her outfit for the evening.	She never had a wash and smelt disgusting.
watch	She took her watch off before she washed the pots.	He tore the watch off her and smashed it on the floor.
wave	The painter used blue and wait to paint the wave.	The wave hit the surfer full on and broke his back.
weather	The weather that day was the same as usual.	The weather was so cold that he froze to death.
wheel	They rolled the wheel along the pavement.	The wheel rolled over his hand crushing it.
willow	The willow was planted at the end of the garden.	They hung the girl bleeding from a willow tree.
wind	The wind blew their hair out of place.	The wind blew the shelter down killing the family.

winter	The winter was fairly short that year.	The winter killed off most of the elderly.
wire	He tied the wire to the post and went for some tea	He pulled the wire around her head and her face went blue.
wood	He used the wood to make a shelf.	He used the wood to smash her face in.

Critical Words and Sentences from fMRI Experiment

	Negative	Neutral	Positive
animal	They poured acid over the caged animal.	The children learned to spell animal during their English lesson.	The animal rolled happily in the hay.
arm	She screamed as he hammered the nail through her arm.	He stretched out his arm and yawned.	He seductively kissed her arm.
artist	The artist mutilated his face with a knife.	It took five days for the artist to complete his work.	The artist celebrated after he sold his first painting
baker	The baker was found frozen in the deep freezer.	The baker woke at 6am everyday.	The baker was overjoyed at winning the lottery.
banana	The banana had worms burying into it.	He put the banana on the table.	The banana split looked and tasted fantastic
bear	The bear sunk his teeth into the man.	The bear lived in the forests.	The magnificent bear played tenderly with her cubs.
block	The disturbed toddler poked the block into his eye.	The toddler fitted the block into the puzzle.	The toddler gurgled happily as he played with the block.
boat	They clung to the boat as it sank into the ocean.	The boat was painted a blue and red colour.	They spent a blissful day aboard the boat.
bone	He howled as they sawed through the gangrenous bone.	The medics looked at the x-ray of the bone.	The cat purred excitedly when its owner gave it a bone.
bottle	He smashed the bottle against her face.	She washed up the bottle and put it into the cupboard.	They celebrated with a bottle of champagne.
box	They kept the boy trapped in a box.	She loaded the box up with books.	They laughed as the kitten jumped into the box.
brain	He screamed in agony as they drilled through his brain.	They learned about the brain in their biology lesson.	He had a brilliant brain.
branch	They gauged her eye out with a branch.	The children swung from the branch.	The children playfully swung from the branch.
bread	He laughed as the starving child begged for the bread.	The loaves of bread are on the third aisle in the supermarket.	The baking bread smelled delicious.
breakfast	He vomited his breakfast over the table.	The hotel served breakfast from eight until ten in the morning.	The breakfast tasted delicious.
bride	The bride was left screaming at the altar.	The bride stepped over the curb.	The bride was deeply in love with her fiancée.
bridge	They clung to the bridge as it collapsed into the canyon.	They think the bridge was built before the war.	The architecture of the bridge was spectacular.
bus	The bus crashed into the wall killing the children.	The bus went from Salford to Manchester.	The friends chatted and laughed on the bus.
butter	Cockroaches crawled over the uncovered butter.	The supermarket sells butter and other groceries.	The grocer sang joyfully as he stacked the butter.
butterfly	He set fire to the trapped butterfly and watched it melt.	The cabbagewhite is the most common butterfly in England.	A beautiful butterfly settled onto the flowers.
camp	The concentration camp stunk of burning bodies.	On their way through the forest they passed a scout camp.	The scouts were thrilled about going off to camp.
chair	He tied her to a chair and threw knives at her.	He pulled his chair up closer to the radio.	The grandmother rocked peacefully in her chair.
chest	She split his chest in two with the axe.	The tailor measured his chest.	She lovingly caressed her sweetheart's chest.
clay	They forced the clay into his cat.	They sold clay bowls in the supermarket.	She blissfully moulded the clay into a beautiful pot.
coffee	Coffee manufacturers starve third world workers.	She went to the kitchen to make a coffee.	They laughed at the hilarious jokes as they drank their coffee.
column	The column fell onto the tourists crushing them to death.	The building had one main supporting column.	The little girl giggled as she hid behind the column.
concert	Ten thousand people died when the concert was bombed.	They rehearsed the concert on a Tuesday evening.	They eagerly cheered the brilliant concert.

concrete	He screamed as they buried him alive in the concrete.	The pavement was made quickly out of concrete.	He laughed at his cat's paw marks in the drying concrete.
corn	They farmer was shredded when he fell into the corn grinder.	The farm labourers began harvesting the corn.	The farmer was overjoyed with his bountiful crop of corn.
cousin	The cousins were blindfolded and shot.	The cousins lived in different cities.	The cousins loved playing out together.
crowd	The angry crowd tore the paedophiles limbs off.	She made her way through the crowd.	The crowd ecstatically cheered their hero.
cup	The cup contained a mixture of bile, pus and sick.	The man bought a cup from the supermarket.	The winners proudly raised the cup above their heads.
customer	The customer strangled the checkout assistant.	The customer picked up a basket from by the door.	He was thrilled at winning the millionth customer prize.
dancer	The dancer was raped as she returned home from a show.	The dancer warmed up before stating her routine.	The remarkable dancer received a standing ovation.
dinner	His dinner was full of blood and excreta.	They normally sat down to eat dinner in the early evening.	The dinner was the most delicious he had ever tasted.
diplomat	They poured petrol over the diplomat and burnt him alive.	A diplomat in Greece gave the speech.	The diplomat negotiated everyone's release.
doctor	The doctor molested the patient.	Their father worked as a doctor in the local hospital.	The doctor miraculously saved the life of the child.
dune	The sand dune collapsed burying the toddler.	The sand dune marked out the landscape of the coast.	The lovers rolled passionately in the sand dune.
earring	During the fight the earring ripped through her ear.	She wore the earring she had bought the previous day.	The devoted lover bought her some beautiful earrings.
engine	The boy was mangled when he fell into the engine.	He warmed up the engine slowly as it was freezing.	The mechanic cheerfully fixed the engine.
fan	They forced her head into the fan and blood splattered everywhere.	The head office contained a fan that was often on.	Standing next to the fan felt refreshing on the hot day.
fashion	He clubbed the seal's head open for the sake of fashion.	The book was aimed at people who were interested in fashion.	The girl looked stunning dressed in the latest fashion.
film	The film showed the hostages being stripped naked and beaten.	They showed a film in the evening.	The film made them laugh uncontrollably.
flame	They held the flame against his eye.	The candle flame flickered in the breeze.	The flame of the candle danced prettily in the lantern.
flesh	The crematorium smelt of burning flesh.	The chef carefully prepared the flesh for stewing.	The cool peach flesh was sweet and succulent.
fruit	Razor blades had been hidden inside the fruit.	They ate a piece of fruit everyday in the morning.	They quenched their thirst with the cool succulent fruit.
gas	She put her head in the oven and turned on the gas.	She put a pan on the stove and turned on the gas.	The old man sat blissfully in front of the gas fire.
gateway	They tied the beaten woman and her baby to the park gateway.	The park gateway opens at 10am every morning.	The gateway of their house was covered with pretty roses.
glass	The glass from windows lacerated their faces when the bomb exploded.	The glass was bought for her as a leaving present.	She was delighted with the crystal glass.
gold	They stripped any gold off the murdered Jews.	The security men put the gold into the safe.	The miners cheered and hugged when they struck the gold.
guest	The guest was unaware that they planned to torture him.	The put the guest in the spare room at the end of their hall.	The guest felt extremely welcome at the party.
handle	She screamed as they turned the handle on the stretching rack.	She turned the handle and entered the room.	She grabbed the suitcase handle and set off on her dream holiday.
heel	She screamed as they sliced off her heel.	The Dalmatian walked at the heel of his master.	His lover massaged his heel tenderly.
hill	He died of a heart attack half way up the hill.	They walked over the hill and round a corner.	The children rolled playfully down the hill.
horn	The crash trapped her head against the car horn.	She sounded her horn to indicate she was ready.	The children laughed uncontrollably as the clown beeped a horn.
juice	Her teeth were rotten from too much juice.	They poured out the juice in time for the interval.	They sipped the ice-cold juice in the hot sunshine.
jury	The jury were blackmailed by the gangster's friends.	The jury reached a decision quickly.	Justice was done when the jury acquitted the innocent man.
kid	The kid terrorised the elderly people on the estate.	The kid delivered the papers every morning in the local neighbourhood.	The kid loved to help his grandmother with the cooking.
ladder	The father fell off the ladder and was permanently paralysed.	He climbed up the ladder to fix the drainpipe.	Climbing to the top of ladder made her feel brave and daring.
lady	The burglars hung the lady of the manor from the banister.	The tomboy figured that she'd act like a lady when she grew up.	The lady kissed him passionately.

lawyer	They stabbed the lawyer's eyes with needles.	He was training to be a lawyer at one of the oldest firms in the city.	The kind lawyer gave them legal aid for free.
leg	They tied him down and amputated his leg.	He stood on one leg and counted to five.	He stroked her leg seductively.
liquid	They poured scalding liquid into her ears.	She poured the liquid into the container.	He loves the taste of the liquid nectar
manager	They tied up the manager and threw him down the lift shaft.	She went to ask the manager about her training schedule.	He was overjoyed when he received the manager of the year award.
maple	They nailed the mother and child to a maple tree.	The maple tree grew in the orchard.	The leaves of the maple trees look magnificent in Autumn.
message	The message said that she would be raped.	She left a message for her friend at the reception.	The message bought her extremely good news.
mud	He screamed as the mud enveloped his head.	The frogs climbed onto the mud to catch flies.	The children happily splashed in the puddles washing mud off their boots.
neck	He wrung her neck slowly until he heard it snap.	She put a scarf around her neck.	He gently brushed his lips on the nape of her neck
orchestra	The orchestra were line up and shot.	The orchestra practised the overture most out of the piece.	The orchestra enthralled the audience with their astounding talent.
oxygen	The astronaut ran out of oxygen and asphyxiated.	Water is formed form hydrogen and oxygen.	The oxygen fuelled him and powered his ascent up the mountain.
package	The package exploded blowing off his hands.	He asked for the package to be sent to his home.	She opened the package in joyful anticipation.
parking	She ran over the toddler while parking.	She didn't mind parking a little out of town.	He was pleased to have found a free parking space so easily.
path	The girl was dragged off the path on her way to school.	She took the same path to school everyday.	Lucy skipped happily down the path.
pen	She stabbed the pen into her girlfriend's eye.	She picked up her pen and started writing the letter.	The pen was the nicest present the writer had ever had.
pencil	The inmate stabbed the guard through the hand with the pencil.	He sharpened the pencil before beginning to draw.	She could sketch magnificent portraits with the pencil.
pilot	The hijackers butchered the pilot and took over the plane.	The pilot was thinking about retiring.	The expert pilot flew the plane with immense skill
platform	He committed suicide by jumping off the highest platform.	They fitted the platform to the wall.	Amy eagerly waved at her mother from the diving platform.
porch	He dragged her onto the porch and strangled her.	She put her hat on in the porch.	The neighbours laughed cheerfully in the porch.
relative	When her last relative died she went to a home for orphans.	The elderly relative was the loudest member of the house.	He was excited about seeing his favourite relative.
rice	They scrambled in the dirt for grains of rice.	She put the rice on to boil and set the time for 20 minutes.	The bride smiled affectionately as they threw the rice and confetti over her.
ring	She ripped the ring off his nipple.	She put the ring on her dressing table.	On her birthday she received a beautiful diamond ring.
rock	He smashed open the cat's head with a rock.	She sat on the rock and tied her shoelace.	The boys enjoyed playing on the rock.
scan	They looked at the scan showing the tumour.	They took the scan into the laboratory.	They father smiled at the scan of his unborn baby.
seed	The Nazi scientists planted a seed in her womb.	The tiny seed was a brown colour.	The seed grew into a beautiful blossom tree.
shadow	She froze when she saw the maniac's shadow in her garden.	She looked at the sundial and read the time by its shadow.	The girl laughed at her long shadow in the midday sun.
sheet	She tied the sheet around his head and suffocated him.	She hung the sheet out on the line to dry.	The lovers wrapped themselves in the silk sheet.
ship	Everyone aboard the ship died of typhus.	The ship docked in the harbour.	The magnificent ship sailed away into the sunset.
shoulder	The stretching rack ripped his shoulder out of its socket.	He rotated his shoulder before throwing the discus.	He passionately kissed her bare shoulder.
signal	The car ignored the signal and smashed into a pram.	The car moved off when the signal turned green.	The signal told her that she had won the race.
speaker	They forced his head next to the speaker and his eardrum exploded.	They were stood quite near to the speaker so could hear the speech.	The guitarist was overjoyed with his new speaker.
stairs	He threw the woman down the stairs.	He carried the child down the stairs and into the nursery.	The kitten playfully chased the ball of wool down the stairs.
starling	The starling became tangled up in the netting and starved to death.	The starling looked for small insects.	The starling chirped happily in the garden.
steel	He poured the molten steel slowly over the screaming prisoner.	The knives and forks were made of steel and were quite hardwearing.	Their grandmother was immensely pleased with her steel cutlery.

stick	He used the stick to beat the cat with until its back bled.	He used the stick to lean as he chatted to the farmer.	The girl excitedly watched him twirling the candyfloss around the stick.
stomach	They sliced open his distended stomach and sucked out the pus.	He patted his stomach and remarked that he was now full.	He gently caressed his pregnant wife's stomach.
stone	The stone hit him between the eyes splitting open his skull.	The stone skimmed across the water before sinking.	She looked lovingly at the sparkling precious stone.
stream	He pushed her head into the stream and held it as she struggled.	The stream was diverted under the road.	The hikers paddled in the cool mountain stream.
studio	He filled his studio with emaciated and diseased bodies.	He went to the studio to do some work for the day.	The aspiring musician excitedly toured the studio.
sugar	They injected sugar into his veins.	She put a spoon of sugar into her tea and stirred.	The girl joyfully added the sugar to her birthday cake.
symphony	The king hated the symphony and cut off the composer's ears.	The symphony was written on manuscript.	They symphony was met with a standing ovation.
teacher	The teacher repeatedly molested the young boys.	The teacher told the children to get their books out.	The children sat enthralled as the teacher read a story.
temple	The congregation was killed when the temple collapsed..	The temple was in the old part of the town.	They admired the wondrous architecture in the temple.
theatre	The woman was taken to a disused theatre and gang raped.	They passed the theatre on their way home.	They went to the theatre for a birthday treat.
throat	He held the knife to her throat and slowly sliced it open.	She cleared her throat before starting the speech	The feathers round the birds throat were exquisite.
tissue	The tissue was covered in blood and pus.	She pulled out a tissue and wiped her brow.	He joyfully tore the tissue off the present.
tongue	They chopped off his tongue and posted it to his wife.	She rested the boiled sweet on her tongue.	She stuck out her tongue playfully
tool	He used the tool to puncture the skull with.	He looked for the right tool to fix the sink with.	The mechanic happily polished his tool.
traffic	The child ran out into the oncoming traffic.	The child waited until the traffic had cleared before crossing.	Happily there was no traffic on her peaceful route.
train	The train arrived full of rotting corpses covered in excreta.	The train travelled at one hundred miles per hour.	He ate a delicious meal in the first class buffet of the train
truck	They dragged the girl into the truck and drove away.	The truck was bound for Lyon on France.	The truck was crammed with gifts for the children
uncle	They lived with their uncle who beat them frequently.	She used to visit her uncle on a Thursday night.	His uncle won four million pounds and shared it amongst their family.
uniform	The bullies urinated over his uniform.	They wore a uniform most days to school.	The boy scout was very proud of his new uniform.
village	The village was hit by the black death and its inhabitants died.	The used to go to the village at weekends.	The village is a beautiful and relaxing place to spend the weekend
wagon	The wagon drove over the tramp and broke his back.	The wagon transported the goods into the city.	They sang cheerfully as the wagon took them home.
weather	The weather was so cold that he froze to death.	The weather that day was the same as usual.	The weather was beautifully warm and sunny
willow	They hung the girl bleeding from a willow tree.	The willow grew near the wall.	He slept contentedly under the willow tree
wind	The wind blew the shelter down killing the family.	The wind blew their hair out of place.	The kite danced merrily in the wind
winter	The winter killed off most of the elderly.	The winter was fairly short that year.	They loved skiing in the winter.
wire	He pulled the wire around her head and her face went blue.	He tied the wire to the post and went for some tea	The bird chirped merrily on the wire.
wood	He used the wood to smash her face in.	He used the wood to make a shelf.	He carved a beautiful ornament out of the wood.

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