Electrophysiological investigations of recognition memory: The role of pre-existing representations in recollection

Graham MacKenzie

University of Stirling

Submitted as a requirement for the degree of PhD

October 2007

Declaration

This thesis is submitted in fulfilment of the requirements for the degree of Doctor of Philosophy at the University of Stirling, United Kingdom. I declare that this thesis is based on my original work except quotations and citations which have been duly acknowledged. I also declare that this thesis has not been previously or concurrently submitted, either in whole or in part, for any other qualification at the University of Stirling or other institutions.

Publications

The following journal articles have been adapted from experimental work detailed in this thesis:

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

MacKenzie, G. & Donaldson, D.I. (submitted). Is recollection material specific? Faces and names elicit topographically dissociable ERP old/new effects.

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

MacKenzie, G. & Donaldson, D.I. (2006). Electrophysiological evidence that a centro-parietal old/new effect is elicited when a face looks familiar but you cannot remember its name. *Poster presented at the Cognitive Neuroscience Society Meeting, San Francisco, USA*.

MacKenzie, G. & Donaldson, D.I. (2007). Electrophysiological evidence that the neural correlates of recollection elicited by face and name retrieval cues are qualitatively distinct. *Poster presented at the Cognitive Neuroscience Society Meeting, New York City, USA.*

MacKenzie, G. & Donaldson, D.I. (2007). Do different retrieval processes support recognition of average and distinctive faces? Evidence from the Remember/Know procedure and Event-Related brain Potentials. *Poster presented at the joint Experimental Psychology Society/Psychonomic Society meeting, Edinburgh, UK.*

Acknowledgements

This thesis is dedicated to Nina MacKenzie for her support and inspiration.

I am indebted to past and present members of the Psychological Imaging Laboratory, University of Stirling. In particular, I would like to thank Professor David Donaldson for setting the cog-wheels of my mind in motion.

Thanks are due to Dr Ian Penton-Voak, Josephine Ross and Alana Davis for helping me to create stimuli. Thanks also to Stephen Stewart, Shona MacLean, Catriona Bruce, Bob Lavery and Bruce Sutherland for technical support.

Finally, I would like to take this opportunity to thank all the participants who volunteered to take part in experiments. I am indebted to them for their time and effort; this research project would not have been possible without them. "If any one faculty of our nature may be called more wonderful than the rest, I do think it is memory. There seems something more speakingly incomprehensible in the powers, the failures, the inequalities of memory, than in any other of our intelligences. The memory is sometimes so retentive, so serviceable, so obedient; at others, so bewildered and so weak; and at others again, so tyrannic, so beyond control! We are, to be sure, a miracle every way; but our powers of recollecting and of forgetting do seem peculiarly past finding out."

Jane Austen, Mansfield Park.

Abstract

Dual-process models of recognition memory propose that recognition memory can be supported by either a general sense of *familiarity* or the *recollection* of the encoding context. One source of evidence supporting dual-process models comes from event-related potential (ERP) studies of recognition memory, which have identified distinct patterns of neural activity associated with familiarity and recollection (the mid frontal and left parietal old/new effects, respectively). In this thesis, dual-process accounts of recognition memory were investigated in a series of ERP studies using three categories of stimulus: previously unknown faces, famous faces, and names.

For previously unknown faces, familiarity was associated with activity over posterior scalp electrodes while recollection was associated with topographically dissociable activity over anterior electrodes. These dissociable patterns of activity support dual-process models. However, the typical pattern of old/new effects was only observed for stimuli associated with pre-existing representations (i.e., names and famous faces), suggesting that the presence/absence of pre-existing representations may determine the particular retrieval processes that support recognition memory. Furthermore, recollection was associated with two different patterns of activity (anterior and left parietal effects), suggesting that recollection is not a homogenous process.

Dual-process theories may represent an important starting point for investigating recognition memory, but neither familiarity nor recollection appear to be functionally homogenous processes when theorizing is constrained by the analysis of scalp recorded electrophysiological activity.

V

Table of Contents

Declaration	i
Publications	ii
Acknowledgements	iii
Abstract	v
Table of Contents	vi
List of Figures	viii
Chapter 1 – Recognition Memory	1
Studying memory	2
Fractionating memory	
Episodic retrieval	9
Dual-process models	
Face recognition	
Process purity	
Conclusion	
Chanter 2 Event Related Potentials	28
Electrogenesis	
Volume conduction	
Recording the signal	
Extracting the signal from the noise	
Drawing inferences from ERPs	
Chapter 3 – ERPs and Recognition Memory	
The ERP old/new effect	
The neural correlate of recollection	
The neural correlate of familiarity	
Chapter 4 – General Methods	67
Experimental procedures	67
ERP data acquisition	72
Data analysis	
	0.0
Chapter 5 – EKP 1: Name/Other Specifics/No Specifics	
Introduction	
Method	
Behavioural Kesults	
EKP Kesults	
Discussion	

Chapter 6 – ERP 2: Manipulating Face Familiarity	106
Introduction	106
Pilot Experiment	108
Method	112
Behavioural Results	113
ERP Results	
Discussion	
Chapter 7 – ERP 3: Face versus Name Recognition	
Introduction	
Method	
Behavioural Results	
ERP Results	
Discussion	156
Chapter 8 – ERP 4: Famous Face Recognition	
Introduction	
Method	
Behavioural Results	
ERP Results	
Discussion	
Chapter 9 – ERP 5: Studied versus Famous Face Recognition	
Introduction	
Method	
Behavioural Results	
ERP Results	
Discussion	
Chapter 10 – General Discussion	
Summary of results	
Theoretical implications	
References	
Appendix I	252
Appendix II	254
11	-

List of Figures

Recognition Memory	
Figure 1: Signal detection model	11
Figure 2: Discriminability	12
Figure 3: Response bias.	13
ERPs and Recognition Memory	
Figure 4: The ERP old/new effect.	47
Figure 5: Example mid frontal and left parietal old/new effects	53
Figure 6: Yovel and Paller (2004) familiarity and recollection distributions	61
General Methods	
Figure 7: Morphing procedure for stimuli.	69
Figure 8: Example of famous face stimuli	70
Figure 9: Schematic illustration showing electrodes used for analysis.	77
Experiment 1	
Figure 10: Performance	86
Figure 11: Response time	87
Figure 12: Old/new effects.	88
Figure 13: Topography.	91
Figure 14: Dissociation between early and late frontal old/new effects	95
Experiment 2	
Figure 15: Familiarity rating.	110
Figure 16: Pilot performance	111
Figure 17: Performance	113
Figure 18: Sensitivity	114
Figure 19: Response time	115
Figure 20: Estimates of recollection and familiarity.	117
Figure 21: Remember and familiar response time	118
Figure 22: Familiar old/new effects	119
Figure 23: Remember old/new effects	122
Figure 24: Correct rejection waveforms.	124
Figure 25: Correct rejection contrast topography	126
Figure 26: Magnitude of familiar old/new effects, 300 – 500ms	127
Figure 27: Magnitude of remember old/new effects, 300 – 500ms	128
Figure 28: Familiar topography	129
Figure 29: Remember topography	130

Experiment 3

Figure 30: Performance	
Figure 31: Sensitivity.	145
Figure 32: Response bias.	146
Figure 33: Response time	147
Figure 34: Remember and familiar responses	149
Figure 35: Remember old/new effects for face and name cues.	151
Figure 36: Topography of face and name remember old/new effects	153

Experiment 4

Figure 37: Performance	173
Figure 38: Response time	173
Figure 39: Selected waveforms for can identify and familiar responses	175
Figure 40: Topography of can identify and familiar effects.	176

Experiment 5

Figure 41: Performance	
Figure 42: Remember and familiar responses.	
Figure 43: Response time	
Figure 44: Correct rejection and miss waveforms	
Figure 45: Famous face remember old/new effects	190
Figure 46: Studied face remember old/new effects	
Figure 47: Magnitude of anterior old/new effects, 500 - 700ms	195
Figure 48: Magnitude of parietal old/new effects, 500 - 700ms	196
Figure 49: Recollection topography.	197
Figure 50: Studied familiar old/new effects	
Figure 51: Magnitude of studied remember and familiar effects	
Figure 52: Studied remember and familiar topography	
Figure 53: Neural correlate of familiarity.	

General Discussion

Figure 5	54: Retrieval	of context	ual/associated	l information	
----------	---------------	------------	----------------	---------------	--

Chapter 1 – Recognition Memory

Memory refers to the way an organism's present state is influenced by previously learned information. It is important to note that memory is not a unitary phenomenon: human memory can be fractionated into several discrete sub-systems, each of which has distinct characteristics, and influences behaviour in its own particular fashion. One broad divide concerns whether the influence of the past is available to conscious awareness or not. Memory that we are conscious of is termed declarative memory, whereas memory that we are not conscious of (e.g., skills, habits, classical conditioning) is termed procedural memory. Declarative memory is considered to be comprised of two systems called semantic memory and episodic memory (Tulving, 1983); this thesis is concerned with understanding how information is retrieved from declarative memory. Episodic memory provides a record of personally experienced events, whereas semantic memory forms the basis of our facts and knowledge about the world. The research described in this thesis contributes to the on-going investigation of how information is retrieved from storage in the episodic memory system, and additionally assesses the question of whether there are common retrieval processes that can access both episodic and semantic memories.

This chapter will describe the organization of memory, with the aim of placing the retrieval of information from declarative memory in the context of memory as a whole. Next, current theories detailing how information is retrieved from episodic memory will be considered, along with some theoretical issues concerning the particular case of face recognition. First of all, the chapter will present a brief overview of how memory is studied in the laboratory.

Studying memory

Memory involves three discrete stages: encoding, storage and retrieval. Encoding refers to memory formation; storage involves the consolidation of memory as patterns of neural activity, or representations, in the brain; and finally, retrieval refers to the reactivation of previously learned information, where the past comes to bear upon the present. In order to remember some information, the encoding and storage stages must have been completed successfully; a failure to retrieve information may result from a disruption to any one of these three stages.

The focus of the research described in this thesis is on memory retrieval. While the successful encoding of information is an important determinant of whether information will later be retrieved, theoretical accounts of encoding are not directly tested in the studies presented in this thesis, and therefore attempts have been made to hold variables influencing encoding constant. For example, the amount of attention paid to information at encoding can determine the likelihood of subsequent retrieval (Naveh-Benjamin et al., 2007). To circumvent this issue, it is common to present participants with an encoding task to perform for each item of information to be committed to memory; the use of an encoding task is designed to ensure that the same strategies are used by participants when memorizing information, and also to foster comparable levels of attention for each item, thereby minimizing variability of a factor that is known to influence the likelihood of retrieval. Other factors are additionally capable of determining the probability of successful encoding, including the length of time that a stimulus is presented for (von Hippel & Hawkins, 1994), and the number of items that are required to be memorized (or list-length; Strong, 1912; Cary & Reder, 2003). Based on these

considerations, encoding conditions should be held constant when investigating memory retrieval to ensure that differential retrieval performance across experimental conditions is unlikely to result from variation in encoding.

Fractionating memory

Memory research in recent years has been concerned with 'fractionating' memory into constituent systems and the processes that support those systems. Much of this work has involved the neuropsychological assessment of memory function in brain damaged patients with memory deficits, referred to as amnesia. There are two main forms of amnesia: anterograde amnesia refers to the inability to form new memories and remember events that happened after brain damage, whereas retrograde amnesia refers to the inability to remember events that occurred prior to acquiring brain damage. It is difficult to generalize findings from brain damaged patients to the population as a whole because of a phenomenon called neural plasticity, which means that damaged brains may develop along idiosyncratic lines. However, neuropsychological evidence has been supplemented with convergent results from experimental psychology and neuroimaging using healthy participants. Based on evidence from a range of domains, the unitary phenomenon of memory has been steadily fractionated; the first important distinction is between the long-term memory system and the working memory system.

Long-term memory

While memory is often thought of as being concerned with events that occurred in the remote past, even everyday tasks like making a phone call require the use of memory because a multi-digit number must be kept in mind while

Recognition Memory

dialing. The distinction between memory for remote versus current information is formalized in the distinction between long-term and working memory. Neuropsychological evidence strongly suggests that long-term memory and working memory are separate systems. Patient H.M. had portions of his medial temporal lobes removed to treat epilepsy, and as a result he suffered from amnesia, which is a long-term memory deficit (Scoville & Milner, 1957). H.M.'s amnesia took both anterograde and retrograde forms: he was unable to form new memories or to remember what had happened immediately prior to undergoing surgery. In stark contrast to this long-term memory deficit, H.M. retained the ability to learn motor skills and to perform a digit span task, which require the maintenance of information in mind, and are considered to be supported by working memory. H.M. therefore provides an example of a single dissociation between long-term and working memory, with damage to his long-term memory and spared functioning of his working memory. The study of patient H.M. marked the beginning of memory research in the modern era, which has been largely concerned with fractionating memory into its constituent systems and processes.

The single dissociation between performance on tasks thought to require long-term and working memory provided by consideration of patient H.M. does not in itself imply that the two forms of memory depend on different parts of the brain, and therefore engage different cognitive operations; it may simply be the case that long-term memory tasks are more difficult than working memory tasks, with both tasks relying on the same cognitive operations. The demonstration of a double dissociation of function (see below) between performance on tasks assumed to be supported by long-term memory and working memory would provide stronger evidence that the two memory systems are distinct. Shallice and Warrington (1970)

described patient K.F. who had damage to brain regions involved in speech perception; K.F. performed poorly on working memory tasks but performed longterm memory tasks without impediment. Thus, the differing patterns of performance on tasks assessing long-term memory and working memory represent a double dissociation.

A double dissociation refers to a case where one factor affects performance on task A but not task B, while a second factor affects performance on task B but not task A. If it is assumed that each task is process pure (i.e., is supported by a single cognitive process) and that particular mental functions are supported by discrete brain regions, then a double dissociation provides evidence that the processes supporting tasks A and B are separate. Dunn and Kirsner (2003) criticized double dissociations on a variety grounds, including the requirement that only pure neuropsychological cases can be used (i.e., where only a single process is damaged). It is important to note that the requirement to use pure neuropsychological cases is particularly difficult to ensure (Coltheart & Davies, 2003). However, double dissociations remain a useful means of constraining theorizing (Baddeley, 2003). Based on these considerations, the double dissociation of function between patients H.M. and K.F. provides strong evidence that long-term memory and working memory are functionally distinct systems.

Declarative memory

Long-term memory is itself comprised of several component systems. One important distinction is between the declarative and procedural memory systems: declarative memory refers to the system that allows previously experienced information to influence the present via consciousness, whereas procedural memory

refers to the system that allows past experience to influence the present without conscious awareness. It should be noted, however, that the products of retrieval from procedural memory may sometimes be available to consciousness, although this is not a defining feature of procedural memory.

Declarative and procedural memory are assessed by explicit and implicit memory tasks, respectively. Explicit memory tasks require a participant to remember a previously encountered item, such as a word studied in a list. An example of an explicit memory task is recognition memory, where a list of items is studied and later a test list comprising studied and unstudied items is presented to participants; the task is to indicate whether each item on the test list is 'old' or 'new' (i.e., whether the item was present in the study list or presented for the first time in the test list). In contrast, implicit memory tasks do not require participants to probe their memory for previously encountered information. In implicit memory tasks, participants typically make non-mnemonic responses to a series of items (e.g., by assessing perceptual information) and the influence of a form of procedural memory called priming is gauged by facilitated processing (i.e., enhanced performance or speeded response time) of repeated items compared to items presented for the first time. An example of an implicit memory task is gender identification for a series of faces, including some faces that are repeated; evidence for priming would be provided where gender decisions were faster for repeated faces compared to faces presented for the first time.

Many patients with damage to their temporal lobes suffer from amnesia, and such amnesic patients can perform implicit memory tasks but are unable to perform explicit memory tasks as well as non-amnesic controls. For example, patient H.M.

was able to learn a motor skill while being impaired on explicit memory tests (Corkin, 1968). Dissociations between performance on explicit and implicit memory tasks have also been observed with healthy participants; one example comes from a levels of processing manipulation, where the idea of 'depth of processing' refers to the amount of semantically meaningful processing given to an item during encoding; a deep encoding condition requires an item to be processed at the level of its semantic meaning, whereas a shallow encoding condition requires an item to be processed at the level of its perceptual features. Jacoby and Dallas (1981) found that recognition memory was superior after deep encoding than after shallow encoding, whereas performance on a perceptual identification task was not affected by the levels of processing manipulation. However, as described above, it should be noted that such single dissociations do not necessarily imply that declarative memory and procedural memory rely upon discrete cortical regions.

Episodic and semantic memory

A further fractionation of memory occurs within declarative memory itself, which is considered to be comprised of two distinct systems: semantic memory and episodic memory. In both cases, the products of retrieval are available to consciousness, but the difference between the two forms of memory concerns whether the information being retrieved is specific to a particular event or not. A typical example used to distinguish between semantic and episodic memory is provided by considering the question 'What is the capital of France?' If the correct answer 'Paris' comes into mind as a fact that is simply known, it would be argued that information from semantic memory has been retrieved. In contrast, if a particular episode involving the fact that Paris is the capital of France comes into

mind, it would be argued that information from episodic memory has been retrieved. On a broader scale, semantic memory forms the basis of facts and knowledge about the world, whereas episodic memory provides a record of personally experienced events that can be reinstated in consciousness. The semantic and episodic memory systems interact with one another under normal circumstances (Greve et al., 2007), although attempts are made to isolate the two systems in the laboratory. One problem concerns ensuring that retrieved information is purely episodic or purely semantic, given that the difference between the two forms of memory is simply couched in terms of whether information is associated with the encoding context or not.

Some neuropsychological evidence supports the distinction between semantic and episodic memory. A double dissociation of function is provided by considering patients L.P. (De Renzi et al., 1987) and K.C. (Tulving et al., 1991). L.P. was unable to name objects and identify famous people while having normal recognition memory, whereas K.C. was able to learn new facts while suffering from a recognition memory deficit. This pattern of spared functioning and impairment demonstrates that L.P had impaired semantic memory and spared episodic memory, whereas in contrast, K.C. had spared semantic memory and impaired episodic memory; this double dissociation provides evidence that the semantic and episodic memory systems are separate. Furthermore, patients who suffered damaged to the hippocampus early in life (at birth, for one patient) were able to learn language and factual knowledge while suffering from severe anterograde amnesia (Vargha-Khadem et al., 1997); this report provides evidence of a further dissociation between semantic and episodic memory. However, some theorists maintain that damage to medial temporal lobe structures affects semantic and episodic memory to

the same degree, and that damage to the frontal lobes is required before dissociations between semantic and episodic memory can be observed (Squire & Zola, 1998). Whatever the neuro-anatomical substrates of semantic and episodic memory are, there is compelling neuropsychological evidence that fosters the conclusion that the two forms of declarative memory are dissociable.

This thesis is primarily concerned with how information is retrieved from episodic memory. However, the close relationship between semantic and episodic memory is important to note, particularly because retrieval from the two systems is directly compared in one of the experiments presented here. The following section describes several theoretical accounts of episodic retrieval.

Episodic retrieval

Episodic memory is typically studied using a recognition memory task called the study-test paradigm. In the study-test paradigm, a list of items is studied and after some delay a mixture of studied and unstudied items is presented on a test list; the participant's task is to make old/new discriminations between studied (old) and unstudied (new) items. Two competing theoretical accounts attempt to explain patterns of performance on recognition memory tasks: single-process and dualprocess models. Single-process models assert than one single retrieval process supports recognition memory (Gillund & Shiffrin, 1984; Hintzman, 1988; Murdock, 1997), whereas dual-process models maintain that two dissociable processes called familiarity and recollection combine under normal circumstances to support recognition memory (Atkinson & Juola, 1974; Jacoby & Dallas, 1981; Mandler, 1980; Tulving, 1985; Yonelinas, 1994). Although a wide range of evidence refutes the single-process view of recognition memory (see Yonelinas, 2002), it is

important for the purposes of this thesis to consider how single-process models account for recognition performance.

Several single-process models of episodic retrieval attempt to explain performance on recognition memory tasks by proposing that a strength-based retrieval process supports recognition. Examples of single-process models include MINERVA 2 (Hintzman, 1988), TODAM (Murdock, 1997), and SAM (Gillund & Shiffrin, 1984). Most single-process models are based on signal detection theory. Signal detection theory (Green & Swets, 1966; Macmillan & Creelman, 1991; Snodgrass & Corwin, 1988) has been adapted to interpret a variety of psychological phenomena, including recognition memory. A basic signal detection model is outlined below in Figure 1; studied and unstudied items are grouped as two normally distributed frequency functions, with the distribution of studied items lying further along a memory strength continuum than the distribution for unstudied items, due to the previous presentation of the studied items.

During performance on a recognition memory task, participants assess memory strength for each item and set a decision criterion; if an item's memory strength is above the decision criterion then an 'old' response is made, whereas if memory strength is below the criterion then a 'new' response is made. In the scenario depicted in Figure 1, the studied and unstudied distributions overlap such that some unstudied items are associated with greater memory strength than some studied items, and conversely some studied items are associated with less memory strength than some unstudied items.



Figure 1: Signal detection model.

Frequency distributions for unstudied (red) and studied (green) test list items are plotted separately. The x-axis represents a continuous memory strength variable and the y-axis represents the frequency of the test items. Participants place a decision criterion based on some value of perceived memory strength; items associated with memory strength above the criterion are given 'old' responses and items associated with memory strength below the criterion are given 'new' responses. The area under the curve to the left hand side contains correct rejections ('new' response to unstudied item) and the area under the curve to the right hand side contains hits ('old' responses to studied items). In this example, the area of overlap between the two distributions contains items that are given incorrect responses: the area under the studied distribution to the left of the criterion contains misses ('new' response to studied item), while the area under the unstudied distribution to the right of the criterion contains false alarms ('old' response to unstudied item).

Studied items associated with memory strength falling below the decision criterion and unstudied items associated with memory strength falling above the criterion receive incorrect responses. Old and new responses to studied and unstudied items therefore form a matrix of four response conditions: hit, miss, correct rejection and false alarm. Hits and correct rejections reflect correct responses to studied and unstudied items, respectively, whereas misses and false alarms reflect incorrect responses to studied and unstudied items, respectively.

Signal detection models of recognition memory incorporate two important measures of memory performance: discriminability and response bias. Discriminability refers to how well studied items can be distinguished from unstudied items, and is modeled as the distance between the unstudied and studied distributions (see Figure 2); it is easier to discriminate studied items from unstudied items with increasing discriminability.



Figure 2: Discriminability.

Two signal detection models provide examples of low discriminability (left) and high discriminability (right). In both cases, frequency distributions for unstudied (red) and studied (green) test list items are plotted separately; the x-axis represents a continuous memory strength variable. Discriminability is a measure of how well studied items can be distinguished from unstudied items, and is modeled by the distance between the mean memory strengths of the unstudied (red) and studied (green) distributions.

Response bias refers to how liberal or conservative participants are in making an 'old' response in cases of uncertainty; response bias is reflected in decision criterion placement (see Figure 3). When a decision criterion is placed relatively high on the memory strength continuum, a conservative response bias operates (i.e., test items are only given 'old' responses if they are associated with high levels of memory strength), whereas when a decision criterion is placed relatively low on the memory strength continuum, a liberal response bias operates (i.e., items are given 'old' responses even if they are associated with low levels of memory strength).



Figure 3: Response bias.

The two signal detection models provide examples of decision criterion placement associated with conservative (left) and liberal (right) response biases. Frequency distributions for unstudied (red) and studied (green) test list items are plotted separately; the x-axis represents a continuous memory strength variable. If the decision criterion is relatively high on the memory strength continuum, only items associated with high levels of memory strength are given 'old' responses and a conservative response bias operates, whereas if the decision criterion is relatively low on the memory strength continuum, items associated with a wider range of memory strengths are given 'old' responses and a liberal response bias operates.

Single-process models of recognition memory are attractive because they are relatively simple and can account for the decision processes used by participants performing a recognition memory test (Macmillan & Creelman, 1991); however, such single-process models fail to account for all of the observed data. One example is that single-process models fail to provide a satisfactory explanation of the mirror effect, which refers to the common observation that distinctive stimuli lead to an increased hit rate and a concomitant decrease in the false alarm rate (Glanzer & Adams, 1985). In addition, single-process models do not account for the relationship between decision confidence and the pattern of hits and false alarms observed when Receiver Operating Characteristics (ROC; see below) are studied (Yonelinas, 1994). In consequence, a number of dual-process models of recognition memory have come to prominence in an attempt to explain a wider range of memory phenomena.

Dual-process models

A number of dual-process models have been proposed to account for recognition memory performance. According to these models, recognition memory is supported by a memory strength-based process called familiarity and a second process called recollection that retrieves the context within which an item was previously encountered. While models of familiarity resemble the strength-based retrieval processes as described by single-process models, recollection retrieves qualitative information about previous events.

Mandler (1980) characterized familiarity in the classic 'butcher-in-the-bus' phenomenon; he described a scenario where encountering someone in an unusual context is sufficient to generate a feeling of familiarity but does not lead to the retrieval of contextual information such as where or when the person was encountered previously. What Mandler wanted to illustrate is that there are two retrieval processes that support recognition memory: familiarity and recollection. Familiarity is recognition of an item without retrieval of any contextual information, whereas recollection is the retrieval of both an item and contextual information, such as where the item was encoded or other associated details.

It should be noted that all dual-process models are similar in positing familiarity and recollection as dissociable retrieval processes; however, each model makes different predictions about how each of these processes operate, and about the relationship between familiarity and recollection. Three possible relationships between familiarity and recollection have been proposed: independence, exclusivity, and redundancy (Joordens & Merikle, 1993; Knowlton, 1998). An independent relationship between familiarity and recollection assumes that each retrieval process

provides an independent source of information about previous occurrence; an exclusive relationship, in contrast, assumes that either process alone can provide a source of mnemonic information, and that the two processes do not co-occur; finally, a redundant relationship assumes that information provided by familiarity is redundant when recollection operates. The following sections describe the various dual-process models as they were originally formulated, including the proposed relationships between familiarity and recollection.

The conditional search model

Atkinson and Juola (1974) proposed that two processes support recognition memory in their conditional search model. According to this model, familiarity and recollection deal with perceptual and semantic information, respectively. Furthermore, familiarity is a relatively fast-acting process that assesses memory activation levels to look for a match between a current stimulus and stored representations. If an item has been encountered previously, then its memory representation will be more active than representations for new items. In contrast to the relatively automatic nature of familiarity, the recollection process is slower and requires some effort, assessing semantic information rather than perceptual information. In the Atkinson and Juola model, recollection only comes into operation if familiarity fails to support recognition: recollection is therefore conditional¹ upon the failure of familiarity. This model assumes that familiarity is the default process, and that recollection only operates in cases of uncertainty.

¹ The relationship between familiarity and recollection outlined by Atkinson and Juola is neither independent, exclusive nor redundant. Rather, the relationship is best conceived of as being one of contingency, with recollection being contingent upon the failure of familiarity.

The intra-item/inter-item model

Mandler (1980) proposed that familiarity and recollection provide independent sources of mnemonic information. According to this model, familiarity reflects intra-item perceptual integration whereas recollection is the search process whereby inter-item information is retrieved. Rather than proposing a conditional search model along the lines of Atkinson and Juola, the Mandler model states that both familiarity and recollection operate in parallel, although the computation of familiarity is faster than that of recollection. In short, the conditional search and intra-item/inter-item models essentially differ on the question of whether the two processes onset in parallel or serially, and also on the relationship between familiarity and recollection.

The perceptual fluency heuristic

In a seminal model, Jacoby and Dallas (1981) also proposed that familiarity and recollection are initiated in parallel, with familiarity representing the automatic assessment of perceptual fluency and recollection representing a controlled process that recovers the context within which an item was encoded. Where the conditional search and intra-item/inter-item models hold that familiarity relates to the assessment of previously stored representations, the perceptual fluency hypothesis states that familiarity can also reflect a quality of the stimulus itself: some stimuli are more familiar than others because of the ease with which they are processed. Item recognition can be supported by the automatic assessment of perceptual fluency because prior exposure facilitates subsequent recognition, or because the stimulus has certain perceptual characteristics that facilitate processing.

States of awareness: knowing and remembering

Tulving (1985) argued that familiarity and recollection provide two different phenomenological experiences: knowing and remembering, which map onto familiarity and recollection, respectively. Familiarity and recollection were originally proposed to derive from two functionally distinct memory systems: the semantic and episodic memory systems, respectively. The semantic memory system controls the conscious experience of knowing that a retrieval cue has been encountered previously (i.e., familiarity) and the episodic memory system controls the conscious experience of remembering specific episodic information (i.e., recollection). The two systems are proposed to operate independently and in parallel at the time of retrieval. The relationship between familiarity and recollection is complex, and differs at phenomenological and process levels of analysis. At a phenomenological level, familiarity and recollection are considered to provide exclusive sources of mnemonic information: an item is recognized because it is either remembered or known. However, at the process level, a trade-off relationship between independent sources of mnemonic information is proposed; for example, where semantic cue information is impoverished it can be compensated by the retrieval of episodic context information, and as a corollary, where episodic context information is difficult to retrieve then semantic cue information can compensate to support recognition memory.

The signal detection/threshold process model

Finally, Yonelinas (1994) argued that familiarity and recollection differ in the types of information they provide at retrieval time. Familiarity yields quantitative information concerning the previous occurrence of a stimulus and

recollection provides qualitative information about the context of an encoding episode. Familiarity is modeled as a signal detection process while recollection is modeled as a threshold process where information is retrieved on an all-or-none basis. This dual-process model is primarily based on the analysis of ROC curve data (described below), and is attractive in its simplicity. The relationship between familiarity and recollection is one of independence, with both processes initiating in parallel, and with quantitative familiarity information becoming available more quickly than qualitative recollection information.

Each of these models represents the weighing of different sorts of empirical evidence (discussed below). There have been many different experimental paradigms that have attempted to gauge whether familiarity and recollection are indeed separate processes, and how they relate to one another. In essence, these different models have attempted to define familiarity and recollection, as there is a wide consensus that the two processes exist and are dissociable (see Yonelinas, 2002, for a review).

Measuring Familiarity and Recollection

Recognition memory is investigated by requiring participants to discriminate between studied and unstudied items. A straightforward item recognition experiment should in theory be sufficient to provide a glimpse of the contribution of familiarity to recognition performance. One view stresses that while the correct identification of old items (hits) should be supported by a combination of familiarity and recollection, the incorrect endorsement of new items as old (false alarms) is likely to be made on the basis of familiarity alone (Dobbins et al., 2000). Any conclusions drawn from such experiments are assumption-laden because false

alarms may also result from recollection (Gallo et al., 2004). Limitations such as this have led to the creation of a number of experimental procedures designed to estimate the relative contributions of familiarity and recollection to recognition, the most prevalent of which are the process dissociation procedure (Jacoby, 1991; Jacoby & Kelley, 1991) and the remember/know paradigm (Tulving, 1985).

The process dissociation procedure requires participants to perform two similar recognition experiments under differing instructions (inclusion and exclusion tasks). Items are presented in one of two conditions, for example, in a male or female voice. In the inclusion task, participants are required to give 'old' responses to all recognised items, regardless of how they were encountered in the study phase. In contrast, the exclusion task requires participants to give 'old' responses only to those previously presented items that were encountered in one of the two conditions. The exclusion task requires participants to remember both the item and the context in which it was encountered, and is thus designed to elicit recollection because dual-process theories state that contextual retrieval can only be supported by recollection. The inclusion task is designed to employ both familiarity and recollection. The results of both tasks are entered into two equations to yield estimates of the relative contributions of familiarity and recollection (for details of these equations, see Jacoby, 1991). It is noteworthy, however, that this paradigm relies upon the premise that familiarity and recollection are independent processes, and only supports dual-process theories because of this assumption. Any conclusions drawn from the process dissociation procedure alone are therefore open to the criticism of circularity.

Tulving (1985) designed the remember/know procedure to assess the relative contributions of familiarity and recollection to recognition performance. Rather than simply endorsing recognised items as old, participants make remember/know discriminations. "Remembering" is defined as the retrieval of both item and context information, while "knowing" is the generation of a strong feeling that an item has been encountered previously, without the concomitant retrieval of context. Know responses are held to index familiarity while remember responses result from recollection (or a combination of recollection and familiarity). This paradigm does not require that familiarity and recollection are independent, as the process dissociation procedure does, although participants are required to internalize the distinction between the two classes of response and introspect during the experiment. One potential problem with the remember/know procedure concerns whether participants erroneously use the response options on the basis of their confidence that an item was studied, rather than on the basis of their phenomenological experience of mnemonic states (Gardner et al., 2002). However, the results of the remember/know paradigm tend to be in broad alignment with other process estimation procedures (Yonelinas, 2002).

A further process estimation method used to isolate familiarity- and recollection-based recognition comes from the analysis of Receiver Operating Characteristics (ROC; Yonelinas, 1994). ROC studies involve plotting the probability of hits and false alarms at a range of different confidence values after participants rate on a scale how confident they are that a test item is old or new. ROC curves for familiarity are relatively more symmetrical, whereas recollection curves are relatively more asymmetric, primarily due to recollection responses being made with high confidence.

In addition to experimental methods where behavioural outputs represent the primary dependent variables that constrain theorizing, brain imaging techniques complement behavioural measures with more direct measures of neural activity. For example, functional magnetic resonance imaging (fMRI) studies have demonstrated activity in different brain regions for conditions thought to selectively engage familiarity and recollection (Rugg & Yonelinas, 2003). Furthermore, the analysis of event-related potentials (ERPs; see Chapters 2 & 3) has demonstrated differential patterns of activity that are considered to reflect the operation of familiarity and recollection. Indeed, Donaldson and Curran (2007) argue that ERPs have provided the strongest source of evidence in support of dual-process models.

Evidence for dual-process models

A wide range of evidence supports dual-process models of recognition memory. Evidence has been reviewed extensively elsewhere (Yonelinas, 2002) and so this section will present a brief outline of the empirical basis for the preference for dual-process models over single-process models. Sources of evidence include: behavioural experiments testing memory function in healthy adults; the patterns of spared and defective memory performance in neuropsychological patients; lesion studies involving rats and non-human primates; and brain imaging studies.

As described above, several behavioural methods have been used to separate memory performance supported by familiarity and recollection, but the rationale for the development of these methods comes in part from studies using the response deadline technique (Reed, 1973). In this procedure, old/new decisions are required at varying lengths of time after test stimulus onset, and the number of false alarms is higher after short delays following stimulus onset than after longer delays. If it is

assumed that false alarms result from the familiarity of unstudied items, and that with longer delays after stimulus onset a second process can be engaged that is capable of over-riding familiarity assessment, then data from the response deadline technique suggest that more than one process supports recognition performance. In addition, these studies suggest that familiarity is a faster process than recollection (Hintzman & Curran, 1994; Rotello & Heit, 2000). Furthermore, studies have found that item recognition is preserved at short delays, while context recognition requires longer processing time (Hintzman et al., 1998).

The study of amnesic patients provides another strand of evidence supporting dual-process theory. Although amnesic patients' memory performance may be explained by the operation of a single memory strength process, healthy controls appear to make use of an additional retrieval process (Huppert & Piercy, 1978). Furthermore, item recognition appears to be relatively spared in amnesic patients but memory for contextual information is impaired (Mayes, 1992).

Animal studies have provided evidence that the processes supporting discrimination between old and new items relies upon different brain regions to memory for associations (Eichenbaum et al., 1994; Fortin et al., 2004). These studies suggest that regions of the medial temporal lobes are differentially involved in familiarity and recollection; parahippocampal structures support familiarity while the hippocampus itself supports recollection. Further neuro-anatomical dissociations include the view that familiarity is supported by the perirhinal cortex and dorsal medial nucleus of the thalamus, whereas recollection depends upon the integrity of the hippocampus, fornix, mamilliary bodies and the anterior nucleus of the thalamus (Aggleton & Brown, 1999).

Finally, evidence from fMRI investigations of memory performance in healthy adults suggests that familiarity and recollection rely upon distinct regions of prefrontal, lateral parietal and medial parietal cortices (Yonelinas et al., 2005). This brief review of the literature clearly demonstrates that dual-process models of recognition memory receive support from a range of diverse methods. However, as noted above, arguably the strongest source of evidence in support of dual-process theory comes from the study of ERPs (see Chapters 2 & 3).

The remainder of this chapter will describe some issues of general importance for understanding the research described in this thesis. Two issues in particular, face recognition and process purity, will be considered briefly.

Face recognition

The majority of recognition memory research to date has used word lists as stimuli. One problem with this approach was highlighted by Yovel and Paller (2004), who argued that words are associated with pre-existing levels of familiarity due to exposure outside the laboratory. Such pre-existing familiarity may confound the results of recognition memory testing. While researchers typically control word frequency as a means of limiting variability in recognition performance, another approach is to use stimuli that are not associated with pre-existing levels of familiarity. In theory, faces of unknown individuals should not be associated with familiarity due to previous experience, and as such represent an excellent means of investigating recognition memory.

This thesis is primarily concerned with investigating patterns of electrophysiological activity generated by the brain in response to recognizing items

on the basis of familiarity and recollection. Crucially, faces have been chosen as stimuli for recognition memory testing as a result of Yovel and Paller's proposal that previously unknown faces should be devoid of pre-existing conceptual representations. The particular case of face recognition is therefore incidental to this thesis; given the focus of this research on memory retrieval, faces are simply used as a particular type of stimulus and are not of particular theoretical interest. However, some consideration of alternative accounts of face recognition is important for placing Experiments 4 and 5 in context.

Face recognition is accounted for in a seminal model of the organization of semantic memory (Bruce & Young, 1986). This model states that a variety of aspects of face recognition are coded separately in a distributed fashion within the brain (e.g., gender, emotion, identity). It is important to note, however, that this model is not concerned with how information is retrieved from semantic memory; rather, it proposes a model of how information about known faces is stored in the brain. Furthermore, the term "face recognition" in this context refers to identification rather than to recognizing an item from a previous encoding context. The focus of the present research is on the retrieval of information from declarative memory rather than on the organization of memory storage. Therefore, although a semantic memory face recognition literature exists, it will not be considered in further detail here.

Of greater importance is the concept of process purity, which has already been alluded to in consideration of the influence of procedural memory on explicit memory tasks. The following section describes process purity in more detail.

Process purity

If there are multiple memory systems and supporting processes then designing a task that isolates one single process represents a fundamental challenge to the experimentalist. Tight experimental design should in theory lead to 'pure insertion', or process purity, which means that the contrast between two experimental conditions will reveal the operation of a single process of interest. Given that both procedural and declarative memory systems operate in concert during everyday functioning, then it is unlikely that any one memory task will be supported by a single memory process (Jacoby & Kelley, 1991; Richardson-Klavehn & Bjork, 1988). For example, when asked to name a picture of a famous face, which should in theory require semantic retrieval, the possibility that episodic memory supports naming cannot be ruled out.

In terms of recognition memory, which is a task designed to isolate episodic retrieval, it remains possible that both explicit and implicit memory processes can contribute to performance on a study-test task. For example, the influence of semantic memory may be observed where unstudied words that are semantically related to genuinely studied words give rise to false alarms (Roediger & McDermott, 1995). In a similar vein, implicit memory processes may be engaged during a recognition memory test; an example comes from the phenomenon of priming, where studied words may be processed faster than unstudied words. It has been argued that priming may influence performance on recognition memory tasks (e.g., Yovel & Paller, 2004); however, priming effects may differ depending upon the degree of match between tasks performed on initial and subsequent processing of an item (Gabrieli et al., 1999). In recognition memory tasks using an encoding

manipulation that differs from the recognition task, the influence of priming may be minimized. In addition, it has been demonstrated that brain regions involved in a conceptual priming task differ from those involved in recognition memory (Donaldson et al., 2001); however, task differences across conditions mean that the role of conceptual priming in recognition performance cannot conclusively be ruled out. In fact, several of the predictions made by dual-process models suggest that non-episodic processes do influence recognition performance: Tulving (1985) originally viewed familiarity as reflecting output from the semantic memory system, and Jacoby and Dallas (1981) argue that familiarity results from perceptual priming.

The studies described in this thesis use variants of the remember/know procedure (Tulving, 1985), which require participants to introspect upon the quality of their memory experience and endorse recognized items as having been supported by familiarity or recollection. As discussed above, the remember/know procedure is problematic because of the nature of the response options. Any given item can either be given an exclusive *remember* or a *know* response, despite many dualprocess models proposing that familiarity and recollection have an independent relationship. It is likely that *remember* responses are supported by both familiarity and recollection, and therefore the analysis of electrophysiological activity related to *remember* responses will reveal the operation of more than one retrieval process. Thus, process purity is inherently difficult to ensure when using the remember/know procedure. However, the procedure is straightforward, and suffers no more from process purity concerns than other methods.
Conclusion

This chapter has described a range of evidence suggesting that memory is not a unitary phenomenon. Findings from experimental psychology have demonstrated that: working memory and long-term memory are separate systems; long-term memory can be divided into declarative memory and procedural memory systems; declarative memory is itself comprised of episodic and semantic systems; and finally, the retrieval of information form episodic memory may be supported by two independent processes called familiarity and recollection.

The aim of the research described in this thesis is to test the validity of dualprocess accounts of recognition memory. Specifically, the proposal that familiarity and recollection represent dissociable retrieval processes will be tested experimentally in a series of event-related potential (ERP) studies of recognition memory which primarily use faces as stimuli. Before describing the specific experimental work, the ERP method (Chapter 2) and studies using ERPs to investigate recognition memory (Chapter 3) will be reviewed.

Chapter 2 – Event-Related Potentials

This chapter will describe important methodological issues concerning the recording and processing of event-related potentials (ERPs), and will then turn to address the types of inference that can be drawn from ERPs. First of all, however, this chapter will describe what ERPs are.

Brain activity generates electrical fields that can be detected at the scalp. The activity of the brain can be observed by recording the difference in electrical potential (i.e., voltage) between two electrodes placed on the scalp. Electrodes conduct fluctuations in voltage, which are amplified and then plotted against time as an electroencephalogram (EEG). The EEG amplitude ranges from -100 to 100 microvolts (µV), and EEG frequency ranges from DC to over 40 Hertz (Hz; Coles & Rugg, 1995). The EEG contains the sum of all scalp-detectable electrical activity occurring at any point in time; however, amplitude changes associated with individual cognitive operations are relatively small (in the order of $5 - 10\mu$ V; Kutas & Dale, 1997). The EEG must therefore be processed in order to extract the record of neural activity related to any one specific event of interest (the "signal") from background brain activity ("the noise"). The process of extracting the signal from the noise involves two stages: first, the EEG is segmented into epochs, which are periods of EEG that are time-locked to the presentation of an event of interest (e.g., the presentation of a stimulus); and second, epochs are averaged together to form an event-related potential (ERP). Assuming that background EEG activity occurs randomly, the averaging process is assumed to attenuate noise and enhance the signal elicited by the event of interest. Thus, ERPs provide a non-invasive measure of the brain's response to an event.

ERPs provide an invaluable source of information in the study of cognition because they allow the time-course of brain activity to be traced with near millisecond precision. As such, ERPs have an advantage over haemodynamic techniques (fMRI, PET, etc.) which have relatively poor temporal resolution. Electrical transmission in the brain is several orders of magnitude faster than the blood flow measures used by haemodynamic techniques, and therefore the exploitation of electrical transmission by the ERP technique is one of its major benefits. The major drawback of the ERP technique, however, is its poor spatial resolution. At best, ERPs provide ambiguous information about the intra-cerebral sources of scalp-recorded electrical activity through the use of source localization procedures, which attempt to identify ERP sources through mathematical solutions informed by biological constraints. Only the synchronous firing of neurons organised into open fields can be detected by scalp electrodes, and because bone is a poor conductive material, the electrical activity smears as it travels through the skull. As a result, the scalp recorded EEG is at best a partial and distorted record of underlying brain activity that is difficult to model precisely.

Attempts to model the source of scalp-recorded neural activity have so far failed to surmount this problem. It should be noted that poor spatial resolution is only a problem when research is primarily neuroscientific rather than cognitive in orientation. If research aims to address cognitive questions then ERP sources are arguably only of interest because they might provide a dependent variable capable of producing dissociations between two or more experimental conditions that are being compared. ERPs not only provide amplitude and temporal variables, but in addition, where simultaneous recordings are made from several electrodes at the same time, the topographic distribution of ERPs provides a third variable that is

crucial in providing dissociations that can distinguish between experimental conditions. Thus, one key assumption that guides ERP research is that qualitatively distinct distributions are the result of activity from at least partially non-overlapping neural populations, and that non-overlapping neural populations imply the engagement of dissociable cognitive processes (Coles & Rugg, 1995). Whereas amplitude and temporal differences with respect to a common baseline provide evidence that a common cognitive operation is differentially engaged across conditions, topographic differences provide evidence that different cognitive operations are engaged across conditions.

Before detailed consideration is given to the type of inference that can be made on the basis of ERP data, it is important that the relationship between the brain and scalp-recorded electrical activity is considered. The next section will describe the neuronal electrogenesis of ERPs.

Electrogenesis

Neuronal electrogenesis is the production of electrical fields from the activity of neurons, or populations of neurons, in the brain. This section will describe the relationship between scalp-recorded EEG and electrical activity generated in the brain. First of all, the way in which individual neurons generate electrical fields will be discussed, before consideration is given to the activity of large populations of neurons. The exact relationship between brain activity and scalp-detectable electrical fields is not yet fully understood, but some discussion of neuronal electrogenesis is important in providing constraints on the inferences that can be drawn from the analysis of ERP data.

Individual neurons

The voltages measured by scalp electrodes result from chemical changes within neurons in the brain. When a neuron fires, it produces an action potential and ions flow across the cell membrane, generating internal and external electromagnetic fields. Scalp electrodes are thought to measure extracellular electrical fields, which primarily consist of post-synaptic potentials; however, action potentials can also be detected when they occur in cortical structures close to the scalp (Allison et al., 1986; Wood, 1987; Wood & Allison, 1981).

The presence of extracellular potentials at the scalp depends upon several important factors. First, net inward current flow at active regions of the neuron produces a negative potential in adjacent extracellular space. Net inward current flow is balanced by net outward current flow producing positive extracellular potentials in passive regions. Second, the propagation of the extracellular potentials is relatively instantaneous, but the specific potential recorded at any given scalp electrode depends on that electrode's location with regard to both the generator of the potential and the reference electrode (Kutas & Dale, 1997). Accordingly, the observed polarity at any given moment in time is a function of the spatial relationship between the recording electrode and neural generator, and therefore does not convey any meaningful information about underlying cognitive processes (Allison et al., 1986; Wood & Allison, 1981). Third, although the amplitude of extracellular potentials decreases with distance from their origin, Helmholtz's principle of superposition (Allison et al., 1986; Wood, 1987) dictates that when a number of neurons fire synchronously, the resultant potentials will summate and may be large enough to be detected at a considerable distance from their origin. The

period over which transmembrane current flow occurs also influences whether potentials are recordable at the scalp; the shorter the period of current flow, the greater the degree of synchronization required (Wood & Allison, 1981).

Populations of neurons

There are many factors that determine whether neural activity can be detected at the scalp, including synchronous firing as described above. Neurons are frequently complex, with dendrites and axons of irregular size, shape, number and orientation from the cell body. All of these variables influence the distribution of the electrical field potential (Wood, 1987), but the physical organization of neurons is the most important factor that determines whether an electrical field potential will be detected at the scalp.

Populations of neurons can be organized into open or closed fields. Electrical activity from open field configurations can be detected outside the population of neurons. One example of an open field configuration is where neurons are aligned in parallel; if the neurons in an open field fire synchronously then the electrical fields from each individual neuron sum together to form a dipole that can be detected at some distance from the neural source (Lorente de Nó, 1947). The majority of the pyramidal neurons in the cortex are organized into open field configurations, and these populations of neurons are considered to be the primary source of electrical activity detected at the scalp (Kutas & Dale, 1997).

In addition to open field configurations, populations of neurons are often not aligned in parallel, and do not produce dipoles capable of projecting electrical fields. For example, a closed field configuration is found in structures where the cell

bodies are assembled at the centre and the dendrites extend radially away from the cell bodies. Even if the neurons in a closed field fire synchronously, the individual dipoles cancel each other out, and therefore the activity of closed fields cannot be detected at the scalp.

Based on the preceding considerations of the electrogenesis of field potentials it follows that the failure to detect a difference in ERPs between two conditions does not necessarily imply that the brain does not differentiate the two conditions. Rather, it may simply be the case that the neural population that differentiates the two conditions is organized into a closed field. Null results may arise for a number of further reasons, however; a null result may imply that the brain does not differentiate between two conditions. A further possibility may be that the magnitude of effect is small and may require increased power to be detected. Thus, null results in ERP analysis should be interpreted with caution (Rugg & Coles, 1995; Kutas & Dale, 1997; Otten & Rugg, 2005).

Volume conduction

ERPs recorded at the scalp reflect the summed activity of populations of neurons somewhere in the brain where the requirements of synchronicity and cell alignment are met. The electrical activity of dipole sources is propagated to the scalp because the brain and its coverings (the meninges, skull and scalp) are volume conductors. The brain, meninges and scalp are all efficient conductors; however, the skull is less conductive than brain tissue and causes smearing (attenuation and spreading) of the electrical field potential over the scalp (Koles, 1998).

It is difficult to identify the neural source of ERPs detected at the scalp for two principal reasons. First, the brain, meninges, skull and scalp vary in their conductivity; and second, the size and shape of individual heads vary. Given that ERP research in the field of cognitive neuroscience typically involves collecting data from multiple participants and averaging individual ERPs to produce grandaverage ERPs, then variance in individual skull size and shape is problematic. Thus, ERPs are a poor tool for investigating the neuro-anatomical sources of scalp detected electrical activity.

Recording the signal

Active electrodes

An ERP waveform is a measurement of the difference in electrical potential between an active and a reference electrode that is plotted as a function of time. ERPs recorded at two different active electrodes positioned at different scalp locations may vary in their morphology (amplitude, latency and polarity) and therefore simultaneous recording from a montage of electrodes covering multiple scalp locations allows the distribution of ERPs to be characterized. A montage of electrodes also permits ERPs to be differentiated on the basis of their distribution, and eye movement artefacts are more readily observed (Picton et al., 2000).

Electrode placement is typically based on the International 10-20 system (Jasper, 1958). The 10-20 system exploits features of the skull (e.g., the nasion, inion, etc.) to position electrodes on the scalp and assumes that the skull is symmetrical. The 10-20 system accommodates up to 75 electrodes, one of which normally serves as a ground. The system covers around two-thirds of the cortex.

Some authors argue that a minimum of 128 electrodes is necessary to accurately depict scalp topography (Srinivasan et al., 1998), and recently dense arrays of 128 or 256 electrodes have been developed to improve spatial resolution (e.g., Tucker, 1993).

Reference electrodes

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

Previous recognition memory studies have typically used the mastoid processes behind each ear to site reference electrodes, and have used the average of the two mastoid electrodes as a virtual reference electrode. This linked mastoid reference provides a virtual reference at the midline and therefore the recording is not biased to either one of the hemispheres (Miller et al., 1991). In practice, the EEG is often recorded using a left mastoid reference and algebraically reconstructed

off-line to re-create a linked mastoid reference. Algebraically re-referencing in this way circumvents two potential problems associated with recording using a linked reference. First, the low-resistance current path between the linked electrodes may distort the scalp potential (Katznelson, 1981). Second, if the two reference electrodes had different impedance values (electrical resistance), then the linked mastoid reference would not be symmetric, and would move towards the electrode with the lowest impedance (Miller et al., 1991).

It is important to recognize that the position of the reference electrode influences the pattern of electrical activity observed at each active electrode. In particular, amplitudes at active electrodes proximal to the reference electrode are attenuated more than amplitudes at more distal active electrodes. The research reported in this thesis uses the linked mastoid reference to facilitate comparison with previous recognition memory research.

Analogue-digital (A/D) conversion

Modern ERP research involves the collection of vast quantities of data and therefore the analogue signal is digitized so that it can be processed by computer. Digitization proceeds by sampling the analogue signal at a particular frequency (e.g., 250Hz, or every 4 milliseconds) and assigning a numerical value representing the amplitude to each sample. The signal is amplified (either before or after digitization) because only extremely small voltages are detected at the scalp, and then the signal is passed through two filters: a high-pass filter attenuates low frequencies (which might block A/D converters) and a low-pass filter attenuates high frequencies, which might result in aliasing. One problem with digitization is aliasing, which may occur if the analogue signal contains high frequencies and the

sampling rate is too low, resulting in the production of spurious low frequencies (which alias as veridical data) after digitization (Picton et al., 1994). Because this problem arises when a signal is under-sampled the Nyquist Theorem states that aliasing is eliminated when the sampling rate is at least twice the highest frequency present in the analogue signal (Luck, 2005).

Extracting the signal from the noise

The EEG contains activity from concurrent brain activity and artefacts (e.g., muscle activity and eye blinks) in addition to the ERP. The ERP is likely to be so obscured by electrical fields that are not of interest that the ERP signal must be extracted from the background noise. The following section describes the methods used to extract the ERP signal from the background noise across the experiments described in this thesis, and discusses alternative methods where appropriate.

Ocular artefact reduction

Ocular artefacts are the major source of electrical contamination in the EEG. Ocular artefacts stem from eye movement and blinking, and are measured with the electro-oculogram or EOG. The EOG records differences in electric potential (in the order of millivolts, rather than the microvolts generated by brain activity) between electrodes placed above and below one of the eyes (vertical EOG, or VEOG) and also between electrodes positioned on the outer canthi to the left of the left eye and to the right of the right eye (horizontal EOG, or HEOG). Eye movement and blinking produce artefacts that contaminate the EEG, and are most pronounced at frontal and inferior electrodes.

It is extremely important to minimize the influence of EOG artefact on the ERP. One approach is to ask participants not to blink during critical periods during the recording, and to minimize eye movements by fixating on a central location. Trials containing EOG artefact can then excluded from the averaging process that produces ERPs. This method is not preferred because a substantial amount of data may be lost and the remaining artefact-free trials may not be representative of the complete data set (Gratton, 1998). Furthermore, residual EOG activity may contaminate the accepted trials, and instructing participants to refrain from blinking may create muscle tension and interfere with brain activity by creating a secondary task for the participant (Verleger, 1991).

The foregoing considerations have led to the development of several EOG correction procedures. The majority of these procedures assume a linear relationship between EOG and EEG; they use regression techniques to compare EEG with EOG and to compute regression coefficients for each active electrode. These regression coefficients can then be used to remove a proportion of EOG from each active electrode channel. The major benefit of this approach is that it allows for the retention of much more data than asking participants to refrain from blinking; however, if ERP effects are observed at fronto-polar electrodes close to the eyes, then this method may contaminate veridical data with artificial data.

Averaging

In addition to the signal of interest, the EEG that has been corrected for ocular artefacts still contains background electrical noise from concurrent mental processes, muscle activity, etc. The ERP signal is relatively small, and therefore it cannot readily be distinguished in the EEG. The most commonly technique for

enhancing for extracting the signal from the noise is averaging, which summates the electrical activity occurring over a specific epoch following the onset of multiple events of interest. Four assumptions underlie averaging (Glaser & Ruchkin, 1976; Spencer, 2005): first, the signal and noise sum linearly to produce the recorded waveform; second, the signal is the same for each event of interest; third, the noise is sufficiently irregular from event to event to be considered as statistically independent samples of a random process; fourth, the noise is stationary (i.e., the means and variance of each sample are similar). If these assumptions are met, then the square root rule of averaging will apply, which states that reduction of noise is directly proportional to the root mean square of the noise and inversely proportional to the square root of the number of samples (Perry, 1966).

In practice, noise tends not to be stationary. An example is provided by consideration of muscle activity, which is unlikely to occur systematically throughout the recording. Although muscular artefacts can be minimized by rejecting epochs prior to averaging, some residual artefact is likely to remain. Another breach of the rationale behind signal averaging is that the signal is unlikely to be constant; periods of fatigue, boredom and attention lapses will introduce variance as the recording session progresses (Ruchkin, 1988), and the signal may even be absent from some trials (e.g., as a result of guessing in a memory experiment).

Another important consideration is that inter-trial variations in the onset of a signal (or jitter) can distort the averaged waveform. Latency jitter reduces the amplitude of an averaged signal and causes it to spread out in time. In practice, jitter decreases as the number of trials contributing to the average signal increases. To

enhance the signal-to-noise ratio, and to minimize the effect of latency jitter, participants can be excluded from contributing data to grand-average ERPs if they fail to contribute a sufficient number of trials to individual participant ERPs. Thus, across the studies described in this thesis, a criterion of 16 artefact-free trials per condition was set before an individual's data were included in grand-average ERPs.

Component selection

This section describes how waveforms can be measured after forming grandaverage ERPs from a sample of participants. Previously, positive and negative peaks in the waveform were assumed to be the neural correlates of cognitive functions, but this approach is no longer favoured because a peak contains contributions from all the parallel cognitive operations occurring during a particular task. One solution to this issue is to define the component of interest as the difference in activity between two separate experimental conditions. Definition of a component according to this functional approach is based solely on its relationship with experimental variables. Subtraction of the ERPs elicited by two conditions isolates the component that reflects the cognitive process underlying the experimental manipulation.

The subtraction method is predicated on two assumptions: first, the latency of the equivalent component in separate conditions is identical; a difference in latency in the same component would produce separate peaks in the subtraction waveforms, spuriously suggesting that the underlying functions differed qualitatively (Coles & Rugg, 1995). Second, the experimental conditions under comparison must vary with respect to one cognitive process alone. This second assumption is known as the pure insertion principle (Donders, 1868). Pure insertion presupposes that cognitive functions are additive and act independently of each

other (Sternberg, 1969; 2001). However, one problem with this assumption is that cognitive functions are often not additive (Friston et al., 1996; Price & Friston, 1997). By definition, the two conditions being subtracted will have several overlapping components, but the manifestation of these shared components will be affected when additional non-overlapping components are present. The difference between two conditions will therefore comprise the interaction between the overlapping and non-overlapping components, in addition to the overlapping components themselves. Although the principle of pure insertion may not be strictly adhered to in electrophysiology, this problem is not unique to ERP data. For instance, comparisons of behavioural measures between two conditions also depend on this principle.

The research described in this thesis uses the subtraction method to extract ERP components of interest, with experimental conditions being carefully designed so that the contrast between conditions reveals a specific cognitive operation of interest. Each component is quantified by averaging the amplitude of the difference between two waveforms over a particular latency period. This area measure is less sensitive to noise than simply assessing the maximum deflection of a component (Handy, 2005).

Drawing inferences from ERPs

Cognitive neuroscience research is based on the assumption that there is a direct mapping between neural activity and cognitive operations. This assumption implies that differences in ERPs reflect differences in underlying cognitive operations. It is further inferred that a one-to-one relationship exists between

cognitive function and brain structure (Rugg & Coles, 1995). This section describes how the cognitive neuroscientist draws inferences from differences between ERPs.

Making inferences from quantitative differences

Where ERP waveforms associated with two experimental conditions differ in magnitude then it can be inferred that the cognitive operation underlying the ERP is differentially engaged across conditions. In practice, the first point in time at which the waveforms diverge only provides an upper-bound estimate of the time it takes the brain to differentiate between the two conditions: earlier differences may have been present in brain regions but the signal may not have propagated to the scalp (Rugg & Coles, 1995; Otten & Rugg, 2005). Amplitude differences can be used to infer that a cognitive operation is more active in one condition than in another. Inferential statistics are used to assess the reliability of amplitude differences. However, where amplitude differences are identified it is important to assess whether the distributions of the ERPs are equivalent, because qualitative differences in the distribution of ERPs are assumed to reflect the operation of different cognitive operations across conditions.

Making inferences from qualitative differences

Qualitative (or topographic) differences between ERPs refer to changes in the scalp distribution of components across conditions. The inverse problem refers to the difficulty in determining neuro-electric sources on the basis of the pattern of scalp recorded electrical activity. Although the inverse problem implies that firm conclusions cannot be drawn about neural generators, a qualitative difference between two conditions generally indicates at least partially non-overlapping neural

populations are engaged. Assuming a one-to-one mapping between brain activity and cognitive operations leads to the conclusion that qualitatively different ERPs reflect the activity of discrete cognitive operations.

As with quantitative differences, inferential statistics are used to assess the reliability of apparent topographic differences. However, the ANOVA model typically used to assess differences between conditions is inherently incompatible with ERP data. The ANOVA model is additive whereas ERP data are multiplicative (McCarthy & Wood, 1985). If ERP data were additive, an increase in the activity of a neural generator would add a constant voltage to each electrode. In fact, an increase in the activity of a neural generator has a greater impact at electrodes where the dipole projects to than at electrodes further away from the dipole projection; the ANOVA model interprets such a pattern of difference. In this manner, spurious interactions are likely to result from the analysis of raw ERP data. To circumvent this issue, ERP data are normalized, which eliminates amplitude differences between conditions but preserves the relative pattern of differences across electrodes differences between conditions but preserves the relative pattern of differences across electrodes are between conditions but preserves the relative pattern of differences across electrodes differences between conditions but preserves the relative pattern of differences across electrodes across electrodes. Normalizing ERP data in this manner prior to assessing qualitative differences reduces the likelihood of Type 1 error.

The issue of data normalization is contentious, with some authors (e.g., Haig et al., 1997; Urbach & Kutas, 2002) arguing that the procedure fails to consider differences in variance between conditions, and that normalization can therefore obscure genuine differences (maximum/minimum method), or produce spurious differences (vector method). Other authors (Ruchkin et al., 1999; Wilding, 2006), however, advocate that normalization should be performed prior to topographic

analyses, but that significant results should only be interpreted as confirming the presence of distributional differences between conditions. The nature of these differences should then be inferred from the pattern observed in the quantitative analysis of raw ERP data. Although normalization may produce conservative results, the topographic analyses reported in this thesis employ the maximum/minimum method (McCarthy & Wood, 1985).

Conclusion

The precise nature of the relationship between cognitive operations and ERP components remains unclear. However, the assumption of one-to-one mapping between brain structure and cognitive function allows meaningful inferences about cognitive operations to be drawn. Having described how ERPs are used to study cognitive operations generally, the following chapter will describe evidence from ERP studies of recognition memory.

Chapter 3 – ERPs and Recognition Memory

This chapter presents a selective review of research in which event-related potentials (ERPs) have been used to investigate recognition memory. The majority of the research described in this chapter has been concerned with establishing neural correlates of episodic retrieval processes (i.e., recollection and familiarity), and more recently these candidate neural correlates have begun to be used as biomarkers to investigate psychological questions (e.g., Azimian-Faridani & Wilding, 2004). While a neural correlate of recollection has been established for some time, the neural correlate of familiarity remains a matter of debate (Paller et al., 2007; Rugg & Curran, 2007). It is therefore important that a consensus is achieved in validating neural correlates of both recollection and familiarity before they can be accepted as valid biomarkers to investigate psychological questions.

The experiments described in this thesis were designed to test some of the implications of the research described in this chapter, and therefore consideration of previous recognition memory research using ERPs is essential for placing this thesis in its proper context. This chapter will first describe the basic ERP phenomenon observed in studies of recognition memory, and will then present evidence that has been used to establish a neural correlate of recollection before the somewhat more controversial area of establishing a neural correlate of familiarity will be considered. Finally, two issues will be discussed: the conceptual priming hypothesis of the mid frontal old/new effect, and the material specificity of the ERP old/new effect.

The ERP old/new effect

The ERP old/new effect is typically observed in study-test paradigms, in which participants memorize a list of items and after some delay a number of previously studied ('old') items are intermixed with unstudied ('new') items and presented in a test list. Participants are required to make old/new discriminations to each item on the test list, responding 'old' if they recognize the item and 'new' if they do not. When ERPs are compared for correctly recognized old items and correctly rejected new items, there is typically a more positive-going amplitude associated with the old waveforms, especially during an early latency period (300 – 800ms post-stimulus). The reliable difference² between the amplitudes for old and new items, termed the 'ERP old/new effect' (see Figure 4), can be observed during different latency periods after stimulus onset, and at different scalp locations.

The ERP old/new effect is typically observed during tests of explicit memory (where retrieved information is consciously experienced) although some components may reflect implicit memory processes (where prior experience affects behaviour without any awareness of the past). ERPs have been used in a number of different explicit and implicit memory paradigms (for a review, see Rugg, 1995); this chapter will focus on explicit tests of recognition memory involving the studytest paradigm.

² While the ERP old/new effect is typically considered to be the difference between old and new waveforms, some authors argue that mid frontal potentials directly reflect familiarity (Windmann et al., 2002; Azimian-Faridani & Wilding, 2004; and see also Woodruff et al., 2006). However, this approach is inconsistent with the traditional method of interpreting the ERP old/new effect, and more importantly this approach has not been demonstrated to be valid: it has simply been assumed on the basis of a signal detection model of familiarity (Yonelinas, 1994). The data presented in this thesis are interpreted with the difference between old and new waveforms representing indices of recollection and familiarity, for reasons outlined in Chapter 2.



Figure 4: The ERP old/new effect.

Grand-average waveforms for correctly recognized studied items (old) and correctly identified unstudied items (new) are plotted as a function of time (taken from MacKenzie & Donaldson, unpublished data). Changes in voltage (in microvolts) are plotted on the y-axis and time (in milliseconds) is plotted on the xaxis. The 0 ms point marks the onset of stimuli. From approximately 300 – 700ms, the old waveform is more positive-going than the new waveform. The ERP old/new effect refers to the reliable difference between the waveforms.

Until the mid 1990s the ERP old/new effect was considered to reflect a single cognitive process, but subsequent research has attempted to examine the old/new effect where recognition supported by either recollection or familiarity is isolated (Rugg & Curran, 2007). Today it appears that the typical positive-going deflection from approximately 300 - 800ms might reflect two independent components of the ERP old/new effect: an early component maximal over mid frontal electrodes from 300 - 500ms ('the mid frontal old/new effect') has been proposed as an index of familiarity, while a later component maximal over left parietal electrodes from 500 - 800ms ('the left parietal old/new effect') is widely considered to provide an index of recollection. While other components have been identified (e.g., the late posterior negativity and the late right frontal effect) the cognitive operations that support these effects are peripheral to this thesis; accordingly, the evidence that has identified these effects will not be reported here.

The neural correlate of recollection

The left parietal old/new effect is a positive-going deflection of the old waveform relative to the new waveform that onsets approximately 400ms poststimulus and is maximal at recording sites over temporo-parietal cortex on the left hemisphere. The left parietal effect is widely considered to provide an index of processing associated with, or contingent upon, recollection. The left parietal effect is only found for old items that are recognized ('hits'), and therefore does not simply reflect the repetition of stimuli; the effect is not always associated with unstudied items incorrectly endorsed as 'old' ('false alarms'), and so the effect is not solely related to processes linked with making an 'old' response. Across a number of studies, it has been argued that the left parietal effect varies in a manner consistent with recollection (Allan, Wilding & Rugg, 1998).

One source of evidence in support of a recollection interpretation of the left parietal effect comes from studies using the remember/know procedure (Tulving, 1985). In the remember/know procedure, items that are recognized can be given either one of two exclusive responses: items are given a remember response if specific details of the study episode are retrieved and a know response is made when an item is recognised in the absence of the retrieval of contextual information about the study episode. As such, know responses are assumed to be supported by familiarity alone, while remember responses are likely to be supported by recollection (or a combination of recollection and familiarity, if independence is assumed – see Jacoby et al., 1997). ERP studies using the remember/know

know responses³ (Smith, 1993; Düzel et al., 1997; Mark & Rugg, 1998). Duarte et al. (2004) operationalised the neural correlate of recollection as the difference between remember and know waveforms, and observed a left parietal effect in the critical contrast. In a paradigm adapted from the remember/know procedure, the left parietal effect was larger for items that were fully recollected compared to partially recollected (Vilberg et al., 2006).

Source memory paradigms provide another strand of evidence that the left parietal effect reflects recollection. In a typical source memory paradigm, items are studied in either one of two contexts (e.g., in either red or green font) and are presented again at test without the study context (e.g., all items in white font). In the test phase, not only must a studied item be recognized, but the context in which the item was studied must be retrieved. The left parietal effect has been shown to be larger for correct source judgments compared to incorrect source judgments (Wilding et al., 1995; Mark & Rugg, 1998; Senkfor & Van Petten, 1998). In an exclusion task (i.e., a type of source memory task where items from only one source are designated as targets) a reliable left parietal effect was observed for the target items but not for non-target studied items (Dzulkifli & Wilding, 2005). Fraser et al. (2007) also found that targets alone elicited a left parietal effect, but only when there was a high probability of correctly identifying targets; when identifying targets was more difficult, left parietal effects were observed for both targets and nontargets. This interesting finding suggests that the processes sub-serving the left parietal effect can be engaged flexibly in response to task demands.

³ Although these studies support the view that the left parietal effect reflects recollection, findings that the neural correlates of recollection and familiarity only differ quantitatively are problematic for dual-process theories, which propose that recollection and familiarity are qualitatively distinct. As such, qualitative differences between ERPs might be expected for the two putative retrieval processes, rather than simply quantitative differences.

Theoretically, associative recognition should be supported by recollection, although it has been argued recently that familiarity may support associative recognition in circumstances where the individual memory traces are represented in adjacent cortical areas (Mayes et al., 2007). In associative recognition, pairs of items are studied, and at test participants must discriminate between intact and rearranged pairs; while familiarity may be sufficient to correctly identify an intact pair, recollection is required to identify a rearranged word pair. Left parietal effects have been observed in several associative recognition paradigms (e.g., Donaldson & Rugg, 1998, 1999; Opitz & Cornell, 2006; Rhodes & Donaldson, 2007), suggesting once again that the left parietal effect reflects processes contingent upon recollection.

A range of behavioural manipulations have been employed to investigate the functional significance of the left parietal effect. For example, the left parietal effect has been observed for items studied under deep encoding conditions but not under shallow encoding conditions (Rugg et al., 1998). Similarly, the effect was reduced in magnitude following divided attention at study (Curran, 2004). Based on observations across a wide range of studies, therefore, the left parietal effect appears to be modulated in a manner that would be expected of a neural correlate of recollection (Rugg & Curran, 2007).

The neural correlate of recollection and the brain

ERPs may have excellent temporal resolution, but they do not provide detailed information about the intra-cerebral sources that generate components. Source localization techniques have thus far failed to surmount this problem. One approach to identifying ERP sources comes from studies of neuropsychological

patients who have brain lesions. This approach is problematic, however. If an ERP component is observed then it can be concluded that the neural population where the lesion is located does not generate the component. However, the converse is not true: if an ERP component is attenuated or absent then it is not necessarily the case that the neural population where the lesion occurs is the source that generates the component. Rather, the lesion could be in a region that is downstream from the source, rather than the source of the component *per se*.

This point is illustrated with the following evidence, which suggests that the medial temporal lobe and hippocampus represent the loci of recollection processing. Patients with medial temporal lobe lesions show either attenuated or absent left parietal effects (Rugg et al., 1991; Mecklinger et al., 1998). Furthermore, a patient with hippocampal damage did not display the left parietal effect (Düzel et al., 2001). Convergent evidence from fMRI studies is perhaps more compelling, however. It has been shown that activity in the left inferior parietal lobe correlates with recollection (Wagner et al., 2005). As discussed in Chapter 2, scalp detectable neural activity is thought to originate in areas of cortex close to the skull. The medial temporal lobes and the hippocampus are sub-cortical structures whose activity is unlikely to project electrical field potentials to the scalp. Based on these considerations, it appears that medial temporal lobe structures may project activity to the cortex, and that the left parietal effect directly reflects the activity of the left inferior parietal lobe.

The neural correlate of familiarity

A large body of evidence suggests that the mid frontal ERP old/new effect provides an index of familiarity (Rugg & Curran, 2007). The mid frontal effect is

manifest as a positive-going deflection for correctly recognized old items compared to a correct rejection baseline, maximal from 300 – 500ms post-stimulus onset at bilateral frontal electrodes surrounding the midline. One problem with accepting the mid frontal effect as a neural correlate of familiarity concerns the lack of specificity given to characterisations of familiarity in dual-process models. Familiarity has been cast variously as an assessment of the strength of node activation (Mandler, 1980), an implicit memory process reflecting assessments of perceptual fluency (Jacoby & Dallas, 1981), output from the semantic memory system (Tulving, 1985) and the retrieval of quantitative information about a test stimulus (Yonelinas, 1994). Until the cognitive operations supporting familiarity can be delineated more precisely, an uncontested neural correlate of familiarity is unlikely to be identified.

A series of studies by Curran (1999; 2000; Curran & Cleary, 2003) provide arguably the strongest evidence in favour of a familiarity interpretation of the mid frontal effect. The association between the mid frontal old/new effect and familiarity was formalized by Rugg et al. (1998) who designed a levels of processing (Craik & Tulving, 1975) study based on the view that memory after both shallow and deep encoding is supported by familiarity but only deep encoding enables the use of recollection.

Figure 5 shows mid frontal old/new effects (300 - 500ms) for both shallow and deep hits, while there is a significant left parietal effect (500 - 800ms) for deep hits only. This dissociation between the mid frontal and left parietal effects suggests that the mid frontal effect is an index of a process common to recognition memory after both shallow and deep encoding. Rugg et al. linked the early frontal effect found in the shallow and deep hit conditions with the early frontal effect described



by Wilding and Rugg (1997), and surmised that the effect may be related to familiarity.

Figure 5: Example mid frontal and left parietal old/new effects. Grand-average ERP waveforms for correctly recognized items that were studied under deep (deep hit) and shallow (shallow hit) encoding conditions are plotted along with correctly identified unstudied items (new) at representative frontal (RF) and left parietal (LP) electrodes. The components observed at these two electrodes are modulated differently: at the frontal electrode, the waveforms for deep and shallow hit conditions are equivalent from 300 - 500ms, whereas at the left parietal electrode, the waveform for the deep hit condition is more positive-going than the waveform for the shallow hit condition. This dissociation between the mid frontal and left parietal effects has provided strong evidence for the view that the effects reflect familiarity and recollection, respectively. Figure adapted from Rugg et al. (1998).

As mentioned above, arguably the strongest evidence in support of a familiarity interpretation of the mid frontal effect comes from work conducted by Curran. Curran (1999) designed a study to see whether the left parietal old/new effect was sensitive to task demands; participants were required to make a lexical decision to words or to perform a recognition memory task. While equivalent left parietal effects were observed for both tasks, an unpredicted frontal effect was also identified (300 - 500ms). Curran's experiment had included both words and pseudowords so that the lexical decision task could be performed. The left parietal effect was only found for words while a mid frontal effect was found for both word classes. Curran argued that words are more likely than pseudowords to be

recollected while pseudowords are as likely as words to be recognized on the basis of familiarity, supporting the claim that the mid frontal effect reflects familiarity.

Curran (2000) designed a second experiment to explicitly test the hypothesis that the mid frontal old/new effect reflects familiarity. The experiment used plurality-reversed lures; for example, the word "cookie" occurred as a study item and then the unstudied word "cookies" was presented as a lure in the test phase. Curran reasoned that recollection is required to recall the specific plurality of words, while plurality-reversed lure words could be recognized on the basis of familiarity. The magnitudes of the mid frontal effects for same and plurality-reversed words were equivalent. By contrast, the left parietal effect was only reliable for words that retained their plurality from the study phase. This result was interpreted as reflecting similar levels of familiarity for words from these two conditions, with recollection only being present when participants correctly remembered the exact plurality of the words. Supporting evidence comes from studies employing an analogous design, which presented old words along with lure words that were semantically related to study items; mid frontal effects (300 – 500ms) were of equivalent magnitude for lures and true hits (Nessler, Mecklinger & Penney, 2001; Geng et al., 2007).

In another study, Curran and Cleary (2003) used pictures as stimuli. Between study and test, some of the pictures were mirror-reversed. This manipulation was intended to be analogous to switching word plurality, and was designed to elicit recognition supported by familiarity for mirror-reversed lures. Again, the magnitudes of the mid frontal effects for same and mirror-reversed pictures were equivalent, while only same pictures were associated with a reliable left parietal effect. This finding is important not simply for supporting a familiarity

account of the mid frontal effect, but also because it demonstrates that the mid frontal effect is not material specific: it is elicited by both words and line drawings of objects.

Taken together, these studies which have specifically manipulated the similarity of lures to studied items suggest that the mid frontal effect indexes a process sensitive to conceptual variables rather than to perceptual variables. If perceptual fluency (which is one candidate underlying computation of familiarity) underpinned the effect, then mirror-reversed pictures would have elicited a smaller mid frontal effect than studied pictures. By contrast, if the conceptual (e.g., semantic) representation associated with study items generates the effect, then equivalent old/new effects should be expected. The mid frontal effect has been elicited in tests using words and line drawings of pictures as stimuli, and it is clear that both these categories may have pre-existing semantic representations attached to them. However, the mid frontal effect was also observed for pseudowords (Curran, 1999) and therefore an account in terms of semantic representations is not straightforward, and critically depends on the assumption that pseudowords activate pre-existing semantic representations due to shared features with known words.

One caveat to be placed upon the familiarity interpretation of the mid frontal effect is that the effect has also been interpreted as being sensitive to novelty rather than familiarity (Tsivilis et al., 2001). According to the novelty hypothesis, the mid frontal effect represents an attenuation of a negative-going deflection by previously encountered stimuli. In most recognition paradigms, the modulation of the mid frontal effect varies in a manner consistent with familiarity because the tasks are relatively simple: in discriminating old items from new, the waveforms for old

items are more positive than waveforms for new items. In more complex tasks, the effect fails to vary in a manner consistent with familiarity, and so requires to be interpreted within a new framework. The framework proposed by Tsivilis et al. is that the mid frontal effect indexes a process downstream from familiarity: a process sensitive to the conjunction of components of the prior episode (for further discussion of the novelty hypothesis, see Schloerscheidt and Rugg, 2004). If this is the case, then it would appear that the neural correlate of familiarity itself has yet to be identified.

Another view of the mid frontal effect is that it reflects the summed activity of a fronto-polar priming mechanism and a more posterior implicit memory correlate (Curran & Dien, 2003). This argument is based on a Principal Components Analysis of the ERP old/new effect, but has not been replicated and therefore remains highly speculative. What this argument does highlight, however, is that there may be more than one cognitive operation responsible for the mid frontal effect, and possibly also more than one route to familiarity.

On the whole, these findings converge on the view that the mid frontal old/new effect reflects the activity of a cognitive process that distinguishes old items from new items while failing to distinguish items that seem to be old on the basis of their similarity to genuinely studied items (Curran, 2000; Curran & Cleary, 2003; Nessler et al., 2001; Geng et al., 2007). Studies that have specifically set out to manipulate the familiarity of stimuli and elicited reliable mid frontal effects provide the most convincing evidence in support of a familiarity interpretation. Familiarity is characterized as a process that crudely assesses the relationship between incoming information and prior experience, but is insensitive to the retrieval of specific details

of the study episode. The relationship between incoming information and prior experience is not sensitive to perceptual variables, but rather seems to gauge whether the concept coded by the stimulus has been encountered before. The idea that conceptual fluency is indexed by the mid frontal old/new effect is consistent with the view that familiarity reflects retrieval from semantic memory, as proposed by Tulving (1985), and more recently expounded by Mecklinger (2000). However, there is currently great debate concerning whether the mid frontal effect reflects familiarity or conceptual priming (Yovel & Paller, 2004; Voss & Paller, 2006; Woodruff et al., 2006). This issue will be addressed more fully after the neural substrate of the mid frontal effect is considered.

The neural correlate of familiarity and the brain

A further strand of evidence that lends weight to a familiarity interpretation of the mid frontal old/new effect comes from electrophysiological investigations into spared memory functioning in amnesic patients. Behavioural data from amnesic patients provide evidence for a dissociation between familiarity and recollection; both forms of retrieval are affected by amnesia, but recollection seems to be more adversely affected (Yonelinas et al., 1998). Düzel et al. (2001) compared ERPs for an amnesic patient who had suffered a focal injury to the hippocampus with control subjects. The patient and controls displayed mid frontal effects but only the controls showed a left parietal effect.

Not all amnesic patients display mid frontal old/new effects, however. Mecklinger et al., (1998) investigated memory function in a group of amnesic patients who had suffered hypoxia as a result of myocardial infarction. The study used an object versus spatial memory task and contrasted ERPs for a group of

amnesic patients with age-matched controls. Behaviourally, all but one of the patients performed the recognition tasks at above chance level, yet this group failed to display any old/new effects. An oddball task, which involves processing stimuli of one category and then introducing occasional stimuli that differ from the category, was performed to see if the patient group suffered from a general inability to produce ERP effects, but a P300 correlate of oddball detection was obtained. The authors argued that recognition performance for the amnesic patients was supported by implicit memory in the form of skill learning, and cited increasing accuracy across experimental blocks as supporting evidence.

However, Düzel et al. (2001) reported that familiarity was spared in an amnesic patient, based on the observation of a mid frontal old/new effect for that patient. The patient had suffered from localized damage to the hippocampus in early life, while the patients in the Mecklinger et al. study suffered from global ischemia as a result of cardiac arrest. Such global ischemia tends to damage medial temporal lobe structures, but it is conceivable that both hippocampal and para-hippocampal structures were damaged in these patients. Neuropsychological data are often equivocal because patients suffer from heterogeneous deficits. Amnesic patients are not the only group who suffer from memory problems: Alzheimer's disease offers a sample of patients whose mnemonic decline follows a more homogenous course.

Tendolkar et al. (1999) compared ten patients with mild Alzheimer's disease with control subjects on a source memory test. The Alzheimer's disease patients had reduced hippocampal volumes compared to the controls. Overall recognition rates were above chance for both groups but only the control subjects made correct source judgments. The ERP old/new contrasts differed between the two groups:

only the control group displayed the left parietal old/new effect. The control group and the Alzheimer's disease patient group displayed mid frontal effects.

Together, these findings from neurological patients are most consistent with the view that recognition performance relies upon processes in addition to recollection. The absence of left parietal effects, coupled with above-chance recognition performance, indicates that some other process must operate to support recognition. Dual-process theory suggests that familiarity should support recognition memory in patients with hippocampal damage, and the observation of mid frontal effects for these patients is consistent with this view.

The conceptual priming hypothesis

The studies reviewed so far converge on the view that the mid frontal old/new effect is the neural correlate of familiarity. Recently, however, this view has been challenged by the claim that the mid frontal effect reflects conceptual priming rather than familiarity (Yovel & Paller, 2004). By this argument, the repetition of a test item that was studied earlier in a study phase leads to a facilitation of processing of that item during its second presentation in the test phase. The observation of mid frontal effects for semantically related lures can be explained by this facilitation of processing generalising to unstudied items that share conceptual features with genuinely studied items. The phenomenon of priming is normally restricted to the facilitation of performance in the absence of awareness, which reflects implicit memory. The conceptual priming hypothesis has met with resistance primarily because the mid frontal effect is exclusively observed in explicit memory tests. Recently, the hypothesis has been reformulated, and now its principal advocate interprets the mid frontal effect in terms of conceptual implicit memory, rather than as a priming phenomenon (Voss & Paller, 2006).

The conceptual priming hypothesis stems from a study conducted by Yovel and Paller (2004), who designed a recognition memory test using faces as stimuli. Yovel and Paller argued that words should not be used as stimuli to investigate familiarity because they are already familiar due to pre-experimental exposure. The authors argued that the use of faces that have never been encountered before should in theory eliminate the confounding factor of pre-experimental stimulus familiarity. Participants viewed faces, each of which was paired with a unique occupation that was presented auditorily at stimulus onset. In the test phase, old and new faces were presented alone, and participants made an old/new discrimination. If participants decided a face was old, they were given a further three-way response choice: no specifics, other specifics, or occupation. Participants made a 'no specifics' response if they recognized that the face was old but were unable to recall any information from the study event: this response was assumed to be supported by familiarity. An 'other specifics' response was made if the participant recalled some aspect of the study event but was unable to retrieve the occupation that was paired with the face. An 'occupation' response was made only when the participant actually recalled the occupation: after selecting this response option the participant was asked to say aloud the recalled occupation. Recollection was inferred from trials where either an other specifics or an occupation response was made.



Figure 6: Yovel and Paller (2004) familiarity and recollection distributions. Topographic maps show the distribution of the old/new difference for familiarity (left) and recollection (right). Each cartoon shows activity averaged across a 200ms latency period; dots represent recording electrodes and the data are interpolated between electrodes to illustrate the distribution of the effects. The scale bar indicates the range of activity. No reliable differences in distribution were observed, consistent with a single-process model of recognition memory. Figure adapted from Yovel and Paller (2004).

Yovel and Paller found that the ERPs associated with familiarity and recollection differed only quantitatively: both effects had parietal maxima (see Figure 6). The only differences between the effects were that familiarity was associated with a lower amplitude and a shorter duration. There was no evidence of a mid frontal effect. The authors concluded that they had induced pure familiarity, which was uncontaminated by pre-experimental exposure, and that familiarity is supported by a subset of the neural generators that support recollection. Further, the functional significance of the mid frontal effect was proposed to be related to conceptual priming rather than to familiarity: it was argued that facial test stimuli removed the influence of conceptual representations contaminating the old/new effect, and therefore no mid frontal effect was observed.

The association between the mid frontal effect and conceptual priming receives further support through the demonstration that the repetition of famous faces leads to activity over mid frontal electrodes (Voss & Paller, 2006). Evidence against the conceptual priming hypothesis comes from a study employing a variant of the remember/know procedure, where separate waveforms were made for items that were not remembered and were endorsed with different levels of familiarity; it was shown that the mid frontal effect varies in a graded manner for different levels of familiarity (Woodruff et al., 2006). Purportedly meaningless stimuli have also been used in a recognition memory test: such stimuli were assumed to be bereft of pre-existing conceptual or semantic representations, yet frontal activity was observed and interpreted as an instance of the mid frontal effect (Groh-Bordin et al., 2006). However, these same stimuli were later rated on a scale to determine how much meaning could be extracted from them, and it was shown that mid frontal potentials vary with how much meaning is associated with stimuli (Voss & Paller, 2006).

The evidence in support of a conceptual priming interpretation of the mid frontal effect is therefore mixed. However, it does seem that the cognitive operations that lead to the mid frontal effect may depend in part upon the existence of semantic representations. It is assumed that there may be more than one way of generating a feeling of familiarity with a test item (Mayes et al., 2007; Rugg & Curran, 2007), therefore perhaps sensitivity to conceptual representations represents just one way in which familiarity can be computed. The relationship between semantic representations and the mid frontal effect clearly requires further investigation to assess the conceptual priming hypothesis.

Material specific retrieval processes

The ERP old/new effect is considered to reflect mnemonic processes that operate on all types of information, i.e., that the effect is material independent. This view has been derived from failed attempts to establish material specific old/new
effects (e.g., Schloerscheidt & Rugg, 2004). However, two strands of evidence suggest that the old/new effect may indeed differ across stimuli variables. In a study using words studied in two different contexts, it has been shown that recollection is associated with the left parietal effect and additional context-specific old/new effects (Johnson et al., in press). This finding has been interpreted as implying that the left parietal effect reflects a material independent correlate of recollection, while other effects may reflect material specific recollection processes. Further evidence that recollection can be associated with different old/new effects comes from a study using characters and symbols as stimuli (Cycowicz & Friedman, 2007). The stimuli were rated for meaning in a separate study; following incidental encoding instructions, recollection was only associated with a left parietal effect for meaningful stimuli; meaningless stimuli were associated with a more anterior distribution. This study suggests that the typical left parietal index of recollection may only be observed under circumstances where the information to be retrieved is associated with pre-existing semantic representations.

The pattern of old/new effects observed when faces are used as stimuli also suggests that the ERP old/new effect may be material specific. Posterior effects have been reported for familiarity for faces (Paller et al., 2001; Yovel & Paller, 2004, Voss & Paller, 2006) and additional anterior activity was observed for faces that were studied along with biographical information (Paller et al., 2000). These effects are difficult to interpret because a number of studies have reported the typical pattern of effects for faces (Münte et al., 1997; Johansson et al., 2004; Nessler et al., 2005). However, parietal effects in two of these studies were not lateralized to the left hemisphere, which necessarily implies that different neural populations are active relative to the generators of the left parietal effect. In addition, given reports of posterior familiarity effects for faces, it may be the case that the parietal effects interpreted as neural correlates of recollection actually reflect familiarity.

On the whole, the evidence concerning the material specificity of the old/new effect is inconclusive. Further experimentation to define the boundaries within which left parietal and mid frontal effects index recollection and familiarity is clearly required in order to adjudicate between the material specific and material independent viewpoints.

ERPs and semantic memory

Given that much of the preceding discussion concerns whether semantic representations and semantic processing influence the ERP old/new effect, some consideration of the neural correlates of semantic memory is warranted. However, there is little evidence concerning the neural correlates of semantic retrieval. Semantic memory research is typically interested in the organization of semantic memory rather than in semantic retrieval, and as such there is a paucity of relevant literature.

ERPs have been recording in tests of semantic integration, where words are presented that are either predictable from the preceding context or not. The contrast between ERPs associated with predictable and non-predictable words has revealed a neural correlate of semantic integration called the N400 (Kutas & Hillyard, 1980). The N400 is a negative-going deflection of the waveform which is distributed over centro-parietal electrodes and maximal 400ms post-stimulus onset. Importantly, the N400 effect is attenuated for words that are predicted by the preceding context, and

absent following disfluent speech (Corley et al., 2006) suggesting that the effect depends on the continuity between previous linguistic context and the word to be processed. The N400 has been observed during the study phase of a recognition memory test (Rhodes & Donaldson, in press) but has not been clearly observed during a test phase, possibly due to contamination with explicit memory processing.

A number of studies have attempted to identify neural correlates of the face processing modules described by the Bruce and Young (1986) model (e.g., Huddy et al., 2003). Almost exclusively, a priming procedure has been employed whereby a perceptual judgement has been made to faces presented for the first or second time and inferences about semantic access have been made on the basis of the ERP contrast between conditions. Explicit and implicit face recognition tasks have been compared (Trenner et al., 2004), but this study involved the short-term repetition of faces as the explicit memory task, and therefore is not comparable to the episodic retrieval literature reviewed in this chapter.

One recent study attempted to identify a neural correlate of conceptual priming (Voss & Paller, 2006). The neural correlate of conceptual priming bore close resemblance with the mid frontal old/new effect widely considered to be an index of familiarity, and on this basis the authors concluded that the mid frontal effect reflects conceptual priming rather than familiarity. However, task differences mean that a direct comparison between the effects is difficult. Nevertheless, this demonstration of the *prima fascia* involvement of semantic memory processing in a recognition memory task highlights the difficulty of ensuring process purity in explicit memory tasks.

On the whole, there is a gap in the literature concerning the retrieval of information from semantic memory. Two of the studies described in this thesis (ERP 4 & ERP 5) make a contribution towards identifying neural correlates of semantic retrieval.

Conclusion

The conclusions drawn from the studies reviewed here critically depend on the assumed relationship between the left parietal effect and recollection, and between the mid frontal effect and familiarity. The conceptual priming hypothesis has been criticized (e.g., Woodruff et al., 2006) and defended (Paller et al., 2007), with the debate being somewhat polarized. There appears to be little attempt to integrate these disparate hypotheses. Rugg and Curran (2007) consider the possibility that the phenomenological experience of familiarity may actually be supported by more than one cognitive process; for example, it remains theoretically possible that under certain circumstances perceptual priming supports familiarity, and that under other circumstances conceptual priming provides the computational mechanism underlying familiarity. These two possibilities are not exclusive. Some evidence suggests that the mid frontal effect supports familiarity, while other evidence points towards a posterior effect. As an alternative to the view that there are different ways in which familiarity can be computed is the view that the ERP old/new effect differs according to the type of information to be retrieved. These issues represent the background against which the experiments described in this thesis are presented.

Chapter 4 – General Methods

This chapter describes the core methods used in the experiments described in this thesis. Where individual experimental procedures deviate from these core methods, specific details are described in the relevant chapters. Here, details of the experimental procedures are provided, before the chapter moves on to consider how ERP data were acquired. Finally, the methods used to analyze both behavioural and ERP data are discussed.

Experimental procedures

Participants

The ethics committee at the University of Stirling approved all experiments prior to the recruitment of participants. Participants were either recruited from the student population at the University of Stirling (including undergraduate psychology students who took part for course credit, as well as non-psychology undergraduate students) or friends who were not enrolled at the university. All participants were right-handed, native English speakers who reported having normal or corrected-to-normal vision, and whose ages ranged from 17 to 35. Participants gave informed consent prior to taking part in an experiment, and were remunerated at a rate of £5 per hour (or given two credits for the first hour). All participants were fully debriefed at the end of the experimental session.

General Methods

Stimulus materials

Three sets of stimuli were used across the experiments described in this thesis: two sets of faces ('previously unknown' and 'famous') and one set of proper names. The pool of previously unknown faces was created from 330 colour photographs of young adults, of whom half were female. All faces were of Caucasian individuals who did not wear any jewelry, glasses or facial hair. Facial images were cropped to remove background, hair and ears, before being resized and positioned in the centre of the display. Facial stimuli were controlled in this way to ensure that the faces alone supported recognition, rather than extrinsic features such as background information, or intrinsic non-facial features such as jewelry. To eliminate gross differences in luminance between individual stimuli, faces were morphed 25% towards average colour using Psychomorph software (Tiddeman et al., 2001). Morphing technology computes an average face from templates marking the features of individual faces; individual faces can then be transformed relative to the average face. In addition to colour transformations, each face was morphed 50% towards average face shape to make an 'average' version of the face. From 330 source photographs, therefore, 660 facial stimuli were created, with one distinctive and one average version of each face (see Figure 7).



Figure 7: Morphing procedure for stimuli. The figure shows three images of the same face. Original photographs first had salient features delineated in Psychomorph before a 25% colour transformation was performed and a mask was applied, to yield a 'distinctive' face. Next, each face was transformed 50% towards average shape to produce an 'average' version.

The pool of famous face stimuli was created from 210 photographs of famous people taken from the internet. The famous people used included actors, musicians, politicians, etc.; these people were chosen in the hope that they would be identifiable by a cohort of student participants (see Appendix I for details of the people used). As with the images of previously unknown faces described above, the famous faces were cropped of hair, ears and background and placed in the centre of the display. Due to the fact that some photographs were grayscale while others were colour, all images were converted to grayscale. For both sets of stimuli, faces were presented against a black background, and from a viewing distance of approximately one meter they subtended a maximum horizontal visual angle of 2° and a maximum vertical visual angle of 5° . See Figure 8 for an example of the famous face stimuli.



Figure 8: Example of famous face stimuli. The figure shows two examples of famous face stimuli. Images were taken from the internet and cropped of hair, ears and background. Faces were resized, positioned in the centre of the display, and set against a black background.

The pool of proper names comprised 216 names taken from a website detailing the most common names of babies registered with US social security services in the 1970s (US Social Security Records, 2004). Names are listed in Appendix II: male names were spoken in a male voice and female names were spoken in a female voice. Auditory samples were edited to ensure that face and word onset coincided. In Experiment 3, these same names were presented in the visual domain in white letters (18 point bold Courier New font) set against a black background.

Experimental paradigm

Study and test items were presented together in small blocks. With the exception of Experiment 3, names were not presented again as retrieval cues. Each block contained an equal number of male and female faces. The test status of the faces was rotated across participants such that each face had an equal chance of

General Methods

being new at test. Within each block there was random selection of faces to counter against order of presentation effects.

Experiments 1 - 3 and 5 included a study phase in which previously unknown faces were paired with names and participants rated whether or not the face and name fit well together. On each trial, a grey fixation cross (+) was presented in the centre of the screen against a black background for 1000ms. The fixation cross was followed immediately by a face presentation which lasted for 2000ms. In experiments 1, 2 and 5, a name was presented auditorily at the same time as the face onset. In experiment 3, a name was presented visually directly below the face. After stimulus offset, participants made a binary judgment as to whether the face fit the name, having been told that stimulus assessment was more important than response speed. Participants responded with one of two buttons, and their response terminated the trial. Button presses were counterbalanced across participants. Participants were told that the judgment was arbitrary, and that the task was designed to help them remember face - name associations for the test phase.

In the test phase, each trial began with a grey fixation cross presented against a black background for 1500ms. The fixation cross was replaced by a face presentation that lasted for 500ms. After face offset, a black screen was displayed for 2000ms, while participants indicated whether they thought the face was 'old' or 'new' by pressing one of two buttons. Accuracy was emphasized over speed, but participants were asked to respond as soon as a recognition decision was made. The correspondence between button and response was fully counterbalanced across participants. If a 'new' response was made, the trial terminated. If an 'old' response was made, the black screen was followed by a prompt indicating further response

options designed to isolate recognition supported by recollection and familiarity. Specific details of response options will be given in each empirical chapter.

Experiment 4 differed from the other experiments in that it did not have a study phase. Experiment 4 can be considered to be a *test phase only* paradigm. All other aspects of the procedure are described in the relevant empirical chapters.

ERP data acquisition

Participants were fitted with an electrode cap prior to the experiment, before being seated in a sound attenuated room in front of a 17" LCD colour monitor. A button box was placed on the desk in front of the monitor, and participants were instructed to minimize muscle movements by keeping their fingers above the buttons to be used to record responses. Each participant performed a practice block before beginning the experiment to ensure that they were acquainted with the experimental procedures. Each experiment was structured with test blocks interspersed with rest periods; participants were instructed to minimize muscle movement during test blocks, and to maintain fixation in the centre of the screen. No specific instructions were made regarding blinking, and a blink artefact reduction algorithm was performed to minimize the contamination of vertical ocular artefacts to the EEG.

Experiment 1 was performed using a different set of amplifiers from experiments 2 - 5. Differences in data acquisition have no significant consequence for the data that are presented and analyzed in this thesis because analogous signal processing and analysis techniques were performed for all data. For both sets of

General Methods

amplifiers, electro-oculogram (EOG) electrodes were placed above and below the left eye, and on the outer canthi.

In experiment 1, EEG was recorded from 61 silver/silver chloride electrodes embedded in an elasticized cap (Neuromedical Supplies, "QuickCap") connected to a Contact Precision amplifier (Contact Precision). The specific electrodes used were: FP1, FP2, AF3, AF4, AF7, AF8, FZ, F1, F2, F3, F4, F5, F6, F7, F8, FCZ, FC1, FC2, FC3, FC4, FC5, FC6, FT7, FT8, CZ, C1, C2, C3, C4, C5, C6, T7, T8, CPZ, CP1, CP2, CP3, CP4, CP5, CP6, TP7, TP8, PZ, P1, P2, P3, P4, P5, P6, P7, P8, POZ, PO3, PO4, PO5, PO6, PO7, PO8, OZ, O1, O2. Electrode positions were based on the International 10-20 system (Jasper, 1958). All channels were referenced to an electrode placed on the right mastoid process and an additional electrode was placed on the left mastoid. Data were recorded using Scan 4.2 software (Neuromedical Supplies). Impedances were maintained below $5k\Omega$. The data were band pass filtered between 0.01 and 40Hz and digitized at a rate of 125Hz (8ms/point). Data were re-referenced off-line to recreate an average mastoid reference. EEG was segmented into 2112ms epochs, starting 104ms before stimulus onset.

For experiments 2 – 5, EEG was recorded from 62 silver/silver chloride electrodes embedded in an elasticized cap (Neuromedical Supplies, "QuickCap") connected to a SynAmps2 amplifier (Neuromedical Supplies). The electrodes used were as described above, expect that FPZ was included, AF7 and AF8 were omitted, and CB1 and CB2 were included. As above, all electrode positions were based on the International 10-20 system (Jasper, 1958). EEG channels were referenced to an electrode placed between CZ and CPZ; two further electrodes were placed on the

mastoid processes. Data were recorded using Scan 4.3 software (Neuromedical Supplies). Impedances were below $5k\Omega$ at the beginning of acquisition. The data were band pass filtered between 0.1 and 40Hz and digitized at a rate of 250Hz (4ms/point). As described above, data were re-referenced off-line to recreate an average mastoid reference. EEG was segmented into 2100ms epochs, starting 100ms before stimulus onset.

Data were processed using Neuroscan Edit software (Neuromedical Supplies). Ocular artefacts were removed using a regression procedure (Semlitsch et al., 1986), and trials were excluded from grand-average ERPs: (a) if EEG saturated; (b) where drift exceeded $\pm 75\mu$ V (measured by the difference between the first and last data points in the epoch); or, (c) where activity anywhere in the epoch exceeded $\pm 100\mu$ V. Waveforms were smoothed over a 5-point kernel, whereby each sampled data point is modified to represent the average of the two previous and two subsequent data points. To ensure a good signal-to-noise ratio, a minimum of 16 artefact-free trials per condition was set as a criterion before an individual participant's data were included in grand-average ERPs. This criterion was chosen because a reduction in noise is inversely proportional to the root square of the number of samples (Perry, 1966), and follows from a pragmatic concern because a criterion of 25 trials (which represents the value at which the signal-to-noise ratio would have been doubled) would have resulted in a loss of a significant amount of data.

Data analysis

Behavioural data

Behavioural measures included accuracy and response time (RT) data, as well as the proportion of trials supported by recollection and familiarity, as assessed by variants of the Remember/Know procedure. Two-tailed statistical tests were applied. Where data from more than two measures were compared, repeatedmeasures ANOVA were used, and statistical significance was assessed with an alpha of 0.05. Specific factors and levels will be described in individual empirical chapters. Any *post hoc* comparisons were investigated with t-tests, with alpha being Bonferroni-corrected depending on the number of statistical tests applied to the data. Where data from only two measures were compared, t-tests were applied, and statistical significance was assessed with an alpha of 0.05.

ERP data

ERPs were quantified by measuring the mean amplitude (with respect to the mean pre-stimulus baseline) of two consecutive latency periods from 300 – 500ms and 500 – 700ms, in which neural correlates of familiarity and recollection have been observed previously (e.g., Yovel & Paller, 2004). Where appropriate, alternative latency periods were also analyzed to determine whether variability in the timing of effects could explain apparent differences between conditions of interest. As with behavioural data, two-tailed statistical tests were applied; ERP data were analyzed using repeated-measures ANOVA. One problem in using the ANOVA model to analyze ERP data concerns the assumption of sphericity required for the ANOVA model. Sphericity is the requirement that there is homogeneity of

General Methods

co-variance amongst all levels of a factor; ERP data tend to violate this assumption because the co-variance of data from adjacent electrodes is greater than the covariance of data from more distal electrodes. This violation of the sphericity assumption is likely to lead to a type 1 error and so F-ratios are reported with degrees of freedom corrected for non-sphericity (Greenhouse & Geisser, 1959) where appropriate. This correction for non-sphericity represents a more conservative test of statistical significance, and minimizes the chance of spuriously rejecting a null hypothesis. For the ERP data, statistical significance was assessed with an alpha level of 0.05; no Bonferroni-correction was applied for planned subsidiary analyses.

Data from frontal and parietal electrodes were used to analyze ERP data (see Figure 9 below). As described in chapter 3, these scalp locations are where neural correlates of familiarity and recollection have been observed previously (e.g., Rugg et al., 1998) and provide a close fit for the data acquired across all five experiments described in this thesis. Frontal and parietal electrode strings provide two levels of a location factor; left and right hemisphere electrodes provide two levels of a hemisphere factor, while strings of electrodes ranging from superior to inferior provide three levels of a site factor. The specific structure of ANOVA used included the factors of old/new, location (frontal/parietal), hemisphere (left/right) and site (superior/medial/inferior). The specific electrodes included in the analysis were: F1/3/5/2/4/6 and P1/3/5/2/4/6. The focus of the research described in this thesis is on ERP old/new effects, and therefore only main effects and interactions involving the critical old/new factor are reported.



Figure 9: Schematic illustration showing electrodes used for analysis. The figure shows a schematic illustrating the position of electrodes over the scalp. The front of the head is at the top, and the left of the head is on the left. Each circle represents an electrode, and large black circles illustrate the electrodes used for analysis. Electrodes from frontal and parietal locations provided two levels of a location factor; left and right hemisphere electrodes provided two levels of a hemisphere factor; finally, electrodes in each quadrant provided three levels of a site factor, ranging from superior electrodes next to the midline, through medial electrodes, to inferior electrodes.

Magnitude analyses

Magnitude analyses were performed for two reasons: first, to assess whether old/new effects were reliable; and second, to assess whether reliable old/new effects differed in size between conditions. Data from each condition of interest were analyzed separately to assess whether reliable old/new effects were present; if reliable effects or interactions involving the critical old/new factor were observed then planned subsidiary ANOVA were performed separately for different scalp regions to better characterize the pattern of old/new effects. The data were also examined to gauge where the effects achieved their greatest magnitude because the location of the maximal old/new difference provides further information about where the effect is most active. Where appropriate, a second set of magnitude analyses was performed on 'difference waveforms' derived from subtracting the new waveform from the old waveform. This subtraction allows direct comparison of the relative sizes of old/new effects across conditions of interest, and can allow inferences to be drawn about the degree to which cognitive operations are engaged. These magnitude analyses assess whether there are *quantitative* differences between ERP old/new effects associated with different conditions.

Topographic analyses

Topographic analyses assess whether *qualitative* differences in ERPs are present across conditions (as opposed to the quantitative differences assessed by magnitude analyses). Differences in the scalp topography of reliable old/new effects were investigated to gauge whether underlying differences in cognitive operations could be posited across conditions. The difference between old and new waveforms was rescaled using the max/min method (McCarthy & Wood, 1985) to eliminate a confound that exists between ERP data and the ANOVA model. As described in chapter 2. when a dipole changes strength there is a multiplicative effect on the electrical activity detected at the scalp, leading to differential amplitude changes being observed between electrodes. These differential amplitude changes may lead to spurious interactions that would suggest that different scalp distributions are being compared. This type I error is minimized by normalizing difference waveforms. The max/min method calculates the amplitude of the old/new difference at each electrode relative to all other electrodes and maintains the pattern of relative differences while removing gross amplitude differences between electrodes likely to

give rise to spurious interactions. Specifically, the method finds maximum and minimum values in each condition, subtracts the minimum from each datum, and divides by the mid range value. Where analysis reveals topographic differences between old/new effects associated with different experimental conditions, then it is assumed that differences in underlying neural activity, and hence cognitive operations, can be posited.

Chapter 5 – ERP 1: Name/Other Specifics/No Specifics

Introduction

Do you ever find someone familiar without recollecting any specific information such as where or when you know them from? This common experience, summed up by the phrase 'I know your face but I can't remember your name', encapsulates the 'dual-process' view of episodic memory. According to dualprocess models, performance on recognition memory tests can reflect the assessment of stimulus 'familiarity', or 'recollection' of details about a previous episode (Atkinson & Juola, 1974; Mandler, 1980; Tulving, 1985; Yonelinas, 1994). Much evidence for dual-process models originates from recognition tests employing lexical stimuli. By contrast, here we investigate the common experience described above, asking if recollection and familiarity can also be identified in face recognition tests. We describe an experiment using event-related potentials (ERPs) that provides strong evidence for a dual-process view of episodic retrieval, while challenging dominant ideas about the neural correlates of familiarity and recollection.

Various dual-process models exist, each making specific predictions about the exact nature of familiarity and recollection (for a review, see Yonelinas, 2002). Despite some differences, these models converge on the view that familiarity is relatively automatic, occurring early in the processing stream, while recollection is more controlled and occurs later. To be clear, we view familiarity as supporting the conscious experience of knowing that a stimulus has been previously encountered, without the retrieval of contextual information about the prior episode, whereas recollection allows additional contextual information to be reported. Despite the relative parsimony of single-process models (e.g., Donaldson, 1996), which argue that familiarity is simply sub-threshold recollection, a body of evidence indicates that two dissociable processes underpin episodic recognition. Here we briefly review ERP evidence, which has identified neural correlates of familiarity and recollection.

When stimulus-locked ERP waveforms for correctly recognized old items ('hits') are compared to correctly recognized new items ('correct rejections'), the old waveform is more positive going at a number of different scalp locations and at a range of different latencies. This 'ERP old/new effect' reflects the summed activity of multiple subcomponents, providing evidence for the contribution of dissociable cognitive processes to recognition performance (e.g., see Donaldson et al., 2002). Most relevant here, a mid frontal old/new effect (300 - 500ms) has been linked with familiarity (Rugg et al., 1998; Curran, 2000; Curran & Cleary, 2003; Mecklinger, 2000 - although see Tsivilis et al., 2001, for an alternative interpretation), and a left parietal old/new effect (500 - 700ms), varies in a manner consistent with recollection (Wilding & Rugg, 1996; Donaldson & Rugg, 1998; Curran, 2000; see Allan et al., 1998, for a review). Importantly, evidence suggests that the two ERP effects are dissociable on both topographic (e.g., see Rugg et al., 1998) and functional grounds (e.g., see Rhodes & Donaldson, 2007; Greve et al., 2007), providing strong evidence for dual-process accounts.

The majority of the ERP evidence supporting dual-process models comes from paradigms using lexical stimuli. Recently, Yovel and Paller (2004) argued that the use of lexical stimuli introduces a confound because the stimuli possess a preexisting level of familiarity; instead, they attempted to isolate familiarity-based

responding using novel faces as stimuli. Faces of unknown individuals were paired with spoken occupations at study; old and new faces were intermixed and presented alone in the test phase. Participants indicated what type of information was retrieved at test. For all items endorsed as being 'old', a three-way response choice was made: occupation, other specifics, and no specifics. Importantly, Yovel and Paller argued that occupation and other specifics responses required recollection, while a no specifics response was made in the absence of recollection. The no specifics response was assumed to index familiarity for faces, and unlike in studies using lexical stimuli, this is uncontaminated with pre-experimental exposure.

Yovel and Paller found that providing a clear operational definition of familiarity the no specifics old/new effect exhibited a parietal distribution from 500 – 700ms: there was no evidence of the mid frontal effect typically associated with familiarity. The absence of a mid frontal effect was interpreted as resulting from the use of non-nameable stimuli, suggesting that its presence in studies using lexical stimuli reflects 'conceptual priming' rather than familiarity. Thus, Yovel and Paller argued that the parietally distributed old/new effect seen for faces represents a distinct neural correlate of familiarity. The occupation old/new effect also exhibited a parietal distribution during the same latency period, albeit exhibiting an earlier onset, longer duration and wider spread across the scalp. Critically, the distributions of the no specifics and occupation old/new effects were statistically equivalent, leading to the conclusion that common neural generators support both familiarity and recollection.

Yovel and Paller's findings pose two problems for dual-process accounts of recognition memory. First, familiarity and recollection are assumed to be

ERP 1

ERP 1

qualitatively distinct, and should therefore exhibit topographically dissociable neural correlates. In this regard, Yovel and Paller note that the occupation effect did in fact exhibit a more anterior maximum than that of the no specifics effect; thus, it remains possible that a topographic difference between recollection and familiarity was not found due to the relatively low density of scalp electrodes. Second, dualprocess theories posit that familiarity occurs before recollection. According to Yovel and Paller's data, however, the neural correlate of recollection onsets before that of familiarity. Taken together, the timing and distribution of these ERP old/new effects are difficult to reconcile with dual-process theory.

Dual-process theory predicts that familiarity and recollection support recognition of episodes from the past, and the models are agnostic as to the nature of the encoded information. Schloerscheidt and Rugg (2004) have shown that the mid frontal effect is elicited by visually presented test words that were encoded as auditory samples, and therefore that the old/new effect is not modality-specific; these data are consistent with dual-process models. Given that the mid frontal effect has also been reported in studies using words (Rugg et al., 1998), pictures (Curran & Cleary, 2003), object forms (Mecklinger et al., 1998) and faces (Nessler et al., 2005) there is good evidence to suggest that the effect does not show materialspecificity either. In this respect, Yovel and Paller's demonstration that familiarity for faces elicits a parietal old/new effect is controversial.

The present study was conducted to gauge whether familiarity for faces is indeed indexed by a parietal old/new effect. The design of the experiment closely resembled that of Yovel and Paller, but with the following deviations: i) names were paired with faces at study, rather than occupations, to operationalize the experience

ERP 1

of 'I know your face but I can't remember your name'; ii) memory performance for names required the length of study and test blocks to be half the size used by Yovel and Paller; iii) a dense array of 61 electrodes was used to lend topographic analyses greater sensitivity to detect subtle differences in the distribution of old/new effects between conditions. In addition, the faces used were masked of hair, ears and background in a bid to force participants to use facial information alone to support recognition.

If the mid frontal old/new effect provides a generic index of familiarity then it should be elicited by face stimuli; however, if this is not the case, following Yovel and Paller, familiarity should elicit a parietal old/new effect. Either way, from a dual-process perspective, dissociable neural correlates of recollection and familiarity would be expected.

Method

Twenty-four (13 female) participants with a mean age of 23 years (range: 18 -35) took part in the study. Nine participants failed to contribute enough trials to all conditions; data from the remaining 15 participants are presented here.

Data were acquired during 18 study-test blocks. Each block contained 12 unique face-name pairings presented at study, and was followed by the same 12 faces intermixed with 6 new faces at test. Half of the faces were taken from the average face pool while the other half were taken from the distinctive face pool, counterbalanced across participants. All data reported here are collapsed across face morphing conditions: despite the intention to examine the effects of distinctive

versus average faces, in practice there were insufficient trial numbers to examine ERPs for distinctive and average conditions separately.

In the study phase, on each trial a name was presented auditorily at face onset. In the test phase, participants indicated whether they thought each face was 'old' or 'new' by pressing one of two buttons. If a 'new' response was made, the trial terminated. If an 'old' response was made, the blank screen was followed by a prompt indicating three response options: *name, other specifics* and *no specifics*. If a *no specifics* or an *other specifics* response was made, this terminated the trial. Participants were asked to respond *no specifics* if recognition was devoid of contextual retrieval and to respond *other specifics* if they recollected information from the study episode but could not retrieve the name that was paired with the face. Participants were asked to respond *name* if they could recall the name that was paired with the face at study, and were required to report the name. The experimenter pressed a key to terminate the trial having recorded the reported name.

The response options allowed trials to be sorted into recollection and familiarity bins for averaging EEG into ERPs. Recollection was inferred on trials where participants made either a *name* or an *other specifics* response to a studied face. Following Yovel and Paller, where participants failed to supply the correct name for any face then the trial was recoded as *other specifics*. Both *name* and *other specifics* responses require the participant to reinstate aspects of the study episode and therefore require recollection. Familiarity was inferred on trials where participants made a *no specifics* response to a studied face. Participants are assumed to make this response when recognition of a face fails to reinstate any of the context

in which the face was previously encountered, providing an analogue of recognition supported by familiarity.

Grand-average ERPs were formed for 4 conditions: *name*, *other specifics*, *no specifics* and correct rejection. The average number of trials in these conditions was 32, 46, 38 and 69, respectively.

Behavioural Results

Recognition responses averaged 73% (s.d. 11 %) correct for old faces, with 20% (s.d. 10 %) false alarms and 79% (s.d. 10 %) correct rejections for new faces. Figure 10 shows probabilities for hits subsequently assigned to each of the 3 response categories. A one-way repeated-measures ANOVA revealed no significant differences in performance levels across categories. When a name was produced, it was correct 82% of the time (s.d. 16%).



Figure 10: Performance.

The mean response time for correct recognition of old faces ('hits') was 1499ms (s.d. 287ms), and the mean response time for correct rejection of new faces was 1397ms (s.d. 282ms). Figure 11 shows the mean response times for hits

Probabilities of hits subsequently assigned to the three categories are plotted. No differences were observed between the conditions.

assigned to each category. A one-way repeated-measures ANOVA revealed a significant difference in response times [F(2,28) = 11.6; p < 0.001]. Subsidiary t-tests revealed that *name* responses were significantly faster than both *other specifics* [t(14) = 2.9; p < 0.05] and *no specifics* [t(14) = 4.2; p = 0.001] responses.



Figure 11: Response time.

Response times for the initial recognition decision are plotted for the three response categories. Name was faster than both of the other two categories, while there was no difference between other specifics and no specifics.

ERP Results

Figure 12 shows the grand-average ERP waveforms at midline frontal and parietal electrodes for the 3 hit conditions compared to correct rejection. In each case, the hit waveform diverges from the correct rejection waveform between 300 and 350ms post-stimulus. For *name* and *other specifics*, the difference persists for around 400ms and appears largest at the frontal electrode. By contrast, for *no specifics*, the difference persists for around 250ms and appears largest at the parietal electrode. As can be seen in Figure 12, the old/new effects are largest for the *name* condition and smallest for the *no specifics* condition. The topography of the old/new effects is illustrated in Figure 13, which highlights the anterior distribution for *name* and *other specifics*.



Figure 12: Old/new effects.

Old/new effects are shown for all three conditions at midline frontal (FZ) and parietal (PZ) electrodes. For the two recollection conditions (name and other specifics), the difference between old and new waveforms is larger at the frontal location; in contrast, for the familiarity condition (no specifics) the difference between old and new waveforms is larger at the parietal electrode.

Name old/new effect

The analysis of data from 300 - 500ms revealed a main effect of old/new [F(1,14) = 18.1; p = 0.001], along with interactions between old/new and location [F(1,14) = 6.1; p < 0.05] and between old/new and site [F(1.1,15.9) = 5.2; p < 0.05]; these interactions reflect larger effects at the frontal location, and at superior sites. Examination of the data revealed that the effect was maximal at FCZ [t(14) = 4.5; p = 0.001].

For the 500 - 700ms latency period, the analysis revealed a main effect of old/new [F(1,14) = 33.5; p < 0.001] and interactions between: old/new, location and

hemisphere [F(1,14) = 23.8; p < 0.001]; old/new, location and site [F(1.9,26.8) = 7.5; p < 0.05]; and between old/new, location, hemisphere and site [F(1.6,22.8) = 5.7; p < 0.05]. At the frontal location, the effect was bigger at superior sites, and on the right hemisphere; whereas at the parietal location, the effect was marginally bigger on the left hemisphere (p = 0.06). Examination of the data found that the effect was maximal at F2 [t(14) = 5.3; p < 0.001].

Other specifics old/new effect

Analysis of data from the 300 - 500ms latency period revealed a main effect of old/new [F(1,14) = 10.3; p < 0.01] and an interaction between old/new, location and hemisphere [F(1,14) = 5.5; p < 0.05]. At the frontal location, the effect is greater on the right hemisphere, whereas at the parietal location the effect is greater on the left hemisphere (although hemispheric interactions were non-reliable at either location). In addition, the analysis revealed a marginally significant interaction between old/new, hemisphere and site [F(1.5,20.7) = 3.5; p = 0.06]. Additional analyses investigating the initial 3-way interactions examined left and right hemispheres separately at each location. This analysis revealed an interaction between old/new and site at the frontal location on the left hemisphere [F(1.3,18.2) = 5.0; p < 0.05] reflecting smaller effects at inferior sites than superior sites. Examination of the data found that the effect was maximal at FC2 [t(14) = 3.3; p = 0.005].

For the 500 - 700ms latency period, the analysis revealed a main effect of old/new [F(1,14) = 11.1; p = 0.005] and an interaction between old/new, location and hemisphere [F(1,14) = 9.9; p < 0.01]. The effect was greater on the right

hemisphere at the frontal location. Examination of the data found that the effect was maximal at AF4 [t(14) = 3.2; p < 0.01].

No specifics old/new effect

From 300 - 500ms, the analysis revealed a main effect of old/new [F(1,14) = 11.7; p < 0.01]. The effect was only marginally significant at the frontal location (p = 0.065), but was reliable at the parietal location [F(1,14) = 11.9; p < 0.01]. Examination of the data revealed that the effect was maximal at CZ [t(14) = 3.5; p < 0.01].

The analysis of data from 500 - 700ms revealed an interaction between old/new, hemisphere and site [F(1.9,27.1) = 4.7; p < 0.05], reflecting a superior distribution on the left hemisphere relative to an inferior distribution on the right hemisphere. In addition, the analysis revealed marginally significant interactions between old/new and location [F(1,14) = 4.1; p = 0.063] and between old/new and hemisphere [F(1,14) = 3.9; p = 0.069]. The effect was larger at the parietal location, and at inferior sites. Examination of the data revealed that the effect was maximal at P4 [t(14) = 2.6; p < 0.05].

Comparison across conditions

The preceding analyses demonstrate the presence of significant old/new effects for each condition. Difference waveforms were computed for all three conditions, allowing direct comparison of the size of the old/new differences across conditions. Data were submitted to ANOVA with factors of condition (name vs. other specifics/name vs. no specifics/other specifics vs. no specifics), location (frontal/ parietal), hemisphere (left/right) and site (superior/medial/inferior).





The distributions of the old/new difference are plotted for each of the conditions using topographic maps that represent the spread of activity across the scalp. Maps show the front of the head at the top, and are plotted as if looking down onto the scalp from above. Maps are shown for two latency periods: 300 – 500ms and 500 – 700ms. Scale bars show the size of the old/new difference, and differ across conditions. For the two recollection conditions (name and other specifics) the old/new effect has an anterior distribution; in contrast, for the familiarity condition (no specifics) the old/new effect has a posterior distribution.

The analysis of data from 300 - 500ms revealed no significant differences between *name* and *other specifics*. However, when *name* was compared to *no specifics*, the analysis revealed a marginally significant main effect of condition [F(1,14) = 4.2; p = 0.06], and interactions between condition and location [F(1,14) =7.1; p < 0.05], and between condition and hemisphere [F(1,14) = 4.6; p < 0.05]. The *name* effect is larger than the *no specifics* effect, and this difference in magnitude is greater at the frontal location, and on the left hemisphere. Subsidiary analyses revealed a main effect of condition at the frontal location [F(1,14) = 7.9; p < 0.05]but no reliable differences were observed at the parietal location. Finally, when other specifics was compared to *no specifics*, the analysis revealed an interaction between condition, location and hemisphere [F(1,14) = 12.1; p < 0.01] reflecting a larger effect for other specifics at the frontal location on the right hemisphere. In sum, whilst *name* and *other specifics* exhibit no differences during the 300 – 500ms latency period, *name* and *other specifics* exhibit larger old/new effects than *no specifics*.

From 500 - 700ms, when name was compared to other specifics the analysis revealed a main effect of condition [F(1,14) = 5.7; p < 0.05], reflecting a larger effect for name than for other specifics. When name was compared to no specifics, the analysis revealed a main effect of condition [F(1,14) = 13.9; p < 0.01] along with interactions between condition and location [F(1,14) = 12.6; p < 0.01], condition, location and hemisphere [F(1,14) = 11.0; p = 0.005] and between condition, location and site [F(1.4, 19.9) = 7.1; p < 0.01]. In addition, the analysis revealed a marginally significant interaction between condition and site [F(1.1,15.6)]= 4.1; p = 0.056]. The *name* effect is larger than the *no specifics* effect, and the difference in magnitude is greater at the frontal location, and at superior sites. Furthermore, the difference between waveforms at the frontal location is greater on the right hemisphere, and at superior sites, whereas at the parietal location, the difference between the waveforms is greater on the left hemisphere, while no differences were observed across the levels of the site factor. Subsidiary analysis revealed main effects of condition at both frontal [F(1,14) = 17.3; p = 0.001] and parietal [F(1,14) = 4.8; p < 0.05] locations. Finally, when *other specifics* was compared to *no specifics*, the analysis revealed a main effect of condition [F(1,14) =11.8; p < 0.01], reflecting a bigger effect for *other specifics*, and an interaction between condition, location and hemisphere [F(1,14) = 16.8; p = 0.001] reflecting a

larger effect for *other specifics* at the parietal location on the left hemisphere. Main effects of condition were observed at the frontal [F(1,14) = 10.6; p < 0.01] location, but not at the parietal location. In sum, during the 500 – 700ms latency period, the sizes of the old/new effects are graded such that *name* > *other specifics* > *no specifics*.

Topographic analyses

As is clear from Figure 13, the *name* and *other specifics* distributions have an anterior focus while the *no specifics* distribution has a posterior focus. To directly assess whether the apparent differences in distribution are statistically reliable, additional topographic comparisons were carried out. The data were rescaled and submitted to ANOVA with factors of condition (*name* vs. *other specifics/name* vs. *no specifics/other specifics* vs. *no specifics*), location (frontal/parietal), hemisphere (left/right) and site (superior/medial/inferior).

During the 300 - 500ms latency period, no differences were observed between *name* and *other specifics*, and between *name* and *no specifics*. In contrast, when *other specifics* was compared to *no specifics*, the analysis revealed an interaction between condition, location and hemisphere [F(1,14) = 7.1; p < 0.05]. The interaction reflects differences at the frontal location on the right hemisphere, where the *other specifics* effect is more positive-going than *no specifics*.

When data from 500 – 700ms were compared, the analysis failed to reveal any differences between *name* and *other specifics*. Comparison of *name* and *no specifics* revealed interactions between condition and location [F(1,14) = 10.7; p < 0.01], and between condition, hemisphere and site [F(2.0,27.7) = 3.4; p < 0.05]. As is evident from Figure 13, these results reflect two principle differences between the old/new effects: first, the *name* effect exhibits an anterior distribution relative to the posterior distribution of the *no specifics* effect; and second, the *name* effect is larger over superior sites, particularly at right anterior electrodes, but this is not the case for the *no specifics* condition.

Finally, *other specifics* was compared to *no specifics*, revealing an interaction between condition, location and hemisphere [F(1,14) = 15.9; p = 0.001], as well as a marginally significant interaction between condition and location [F(1,14) = 4.2; p = 0.059]. Again, as is evident from Figure 13, the *other specifics* condition is greater at the frontal location, whereas the *no specifics* condition is greater at the parietal location. In addition, the *no specifics* effect is greater on the right hemisphere at the parietal location.

Late right frontal old/new effects

One concern about the neural correlate of recollection reported here is that it may reflect the late right frontal old/new effect often observed in source memory tasks (e.g., Wilding & Rugg, 1996) and thought to reflect post-retrieval monitoring processes. Figure 14 below shows all waveforms at representative superior and right frontal electrodes; as can be seen from the figure, there are apparent differences in both the modulation of the waveforms and in the distribution of the effect throughout the epoch. To investigate this issue, waveforms were analysed in consecutive 200ms latency periods from 300 - 1500ms for the two recollection conditions. Data from the frontal location were submitted to ANOVA with factors of condition (*name/other specifics*), hemisphere (left/right) and site (superior/medial/inferior). The analysis revealed a main effect of condition [F(1,14) = 6.1; p < 0.05] in the 500 – 700ms period, while no differences were observed in any other latency periods.



Figure 14: Dissociation between early and late frontal old/new effects. At the superior frontal electrode (FC2), waveforms for the two recollection conditions (name and other specifics) are differentiated, whereas at the right frontal electrode (AF8) the same waveforms are of equivalent magnitude. Topographic maps show a change in distribution for the name old/new effect across the epoch; from 500 – 700ms, the effect has a superior distribution, whereas from 700ms onwards the distribution becomes more right-lateralised. Thus, the neural correlate of recollection observed at superior frontal electrodes (500 – 700ms) is both functionally and topographically dissociable from the late right frontal old/new effect.

This finding demonstrates that the neural correlate of recollection observed from 500 – 700ms differentiates between the two recollection conditions, with a more positive-going waveform for *name* than for *other specifics*. In contrast, frontal potentials are of equivalent magnitude later in the epoch, suggesting that the late right frontal old/new effect is modulated differently from the neural correlate of recollection. Thus, the neural correlate of recollection observed at the frontal location (500 - 700 ms) is dissociable from the late right frontal old/new effect on functional grounds.

To assess whether different neural generators are active at the frontal location across the epoch, topographic analyses were performed on data from the name condition. Data were submitted to ANOVA with factors of latency (500 -700ms vs. 700 - 900ms/ 500 - 700ms vs. 900 - 1100ms/ 500 - 700ms vs. 1100 -1300ms/ 500 – 700ms vs. 1300 – 1500ms), hemisphere (left/right) and site (superior/medial/inferior) comparing the distribution of the *name* effect (500 – 700ms) with the distributions of the name effects present during each of the subsequent latency periods. The analysis revealed interactions between latency and site for each comparison (500 - 700 ms vs. 700 - 900 ms [F(1.1,15.6) = 8.5; p < 100 ms]0.01]; 500 - 700ms vs. 900 - 1100ms [F(1.1,15.0) = 8.5; p = 0.01]; 500 - 700ms vs. 1100 - 1300ms [F(1.1,15.1) = 8.9; p < 0.01]; 500 - 700ms vs. 1300 - 1500ms [F(1.2,16.5) = 10.9; p < 0.01]. For each comparison, the F-value increases, reflecting the fact that the topography of the *name* effect becomes steadily more inferior throughout the epoch. This pattern of results suggests that the superiorly distributed neural correlate of recollection is generated by a different neural population from that which produces the old/new effects present later in the epoch. Thus, the neural correlate of recollection observed at the frontal location (500 – 700ms) is dissociable from the late right frontal old/new effect on topographic grounds.

Discussion

The experience of 'I know your face but I can't remember your name' is common, but the neural correlates of recollection and familiarity for faces have not

ERP 1

been widely investigated. Here, we separated ERPs according to whether participants could recognize faces with or without the retrieval of contextual information. We provide evidence for a neural correlate of familiarity that exhibits a posterior scalp distribution – quite different from that seen in most recognition memory studies. More importantly, we dissociate recollection and familiarity for faces, providing clear evidence for a neural correlate of recollection that exhibits an anterior maximum. Below we discuss this novel finding in relation to the traditional old/new effects, and in light of dual-process accounts of recognition memory.

Topographic dissociation between familiarity and recollection

Assuming that performance supporting *name* and *other specifics* responses requires recollection, whereas performance supporting *no specifics* responses requires only familiarity, the data presented here show that recollection elicits a frontally focused old/new effect while familiarity elicits a more posterior old/new effect. To be clear, we do not claim a double dissociation between recollection and familiarity, with entirely separate effects in each case. Rather, reliable old/new effects at the frontal location were only found for recollection conditions, whereas old/new effects were identified for both familiarity and recollection conditions at the parietal location.

Although positive going old/new effects are present at the parietal location for all three hit conditions, we are unable to tell whether this reflects the activity of a common set of neural generators. This question is of interest because it speaks to the issue of whether familiarity and recollection co-occur. If the parietal portion of the effect seen for *name* and *other specifics* reflected familiarity alone, then the amplitude of the three hit conditions would be expected to be equivalent. In fact, at

ERP 1

the parietal electrode the pattern was graded, with the *name* condition exhibiting greater positivity than *other specifics*, which was in turn greater than *no specifics* (particularly from 500 – 700ms). Moreover, it seems likely that at least part of the posterior old/new effects seen for *name* and *other specifics* reflects simple propagation of the anterior recollection old/new effect across the scalp. Thus, the present findings leave open the possibility that the neural generators of familiarity are active whenever retrieval is successful. Regardless, our data clearly show that anterior activity accompanying familiarity.

The present findings are broadly consistent with data reported by Paller et al. (2000), in which faces presented without biographical information at study elicited a posterior old/new effect when recognized, whereas faces paired with biographical information at study elicited additional anterior activity when recognized. In their paper, the authors state that "effects at posterior locations (PZ and OZ) were reliable for named and unnamed faces" and "effects at anterior locations (FZ and CZ) were reliable only for named faces" (Paller et al., 2000, p.102). While specific details including electrode montage, analysis strategy and the precise boundaries between effects differ between our data and those of Paller et al., the same underlying anterior/posterior difference is present. Paller et al. argued that the posterior portion of the old/new effect reflects face recognition while the frontal portion reflects access to semantic information. The experiment employed a one-stage old/new decision, and the authors were therefore unable to specify whether familiarity or recollection elicited the posterior activity. In contrast, the present results imply that the posterior portion of the face recognition old/new effect is actually a neural correlate of familiarity.
To our knowledge, unequivocally dissociable neural correlates of familiarity and recollection for faces have not been reported previously. In an attempt to characterize neural correlates of recollection and familiarity for faces, Yovel and Paller (2004) reported that the distribution of effects did not differ topographically. In contrast, our data identify a frontally maximum old/new effect for recollection, which is topographically distinct from the posterior old/new effect associated with familiarity. An obvious question that arises is why a topographic difference was not found by Yovel and Paller. One possibility is that our topographic dissociation reflects greater sensitivity to detect differences due to a denser electrode array. Another factor may be our experimental design, which included names as stimuli, and required relatively short study-test blocks to facilitate a sufficient level of performance to form ERPs. Perhaps more important may be the faces we used, which were masked of ears, hair and background; this difference in stimuli raises the possibility that different strategies were employed by participants across studies (thereby evoking different recollection effects). While the critical factor remains to be determined, our procedures reveal distinct neural correlates of familiarity and recollection.

No mid frontal old/new effect when a face feels familiar

As noted in the introduction, previous studies have identified a mid frontal effect (300 – 500ms) as the neural correlate of familiarity. One interesting feature of the present data concerns the *prima facie* topographic resemblance of the recollection old/new effect to the putative mid frontal index of familiarity, particularly during the 300 – 500ms latency period. We do not equate the two effects for several reasons. First, mid frontal familiarity effects are typically of

equivalent magnitude across conditions where items are thought to be equally familiar (e.g., Curran, 2000), yet in the current data there are clear differences between hit conditions, with significantly larger effects for the *name* and *other specifics* conditions compared to *no specifics* (see Figure 12). Second, there were no reliable effects over frontal electrodes in the one condition where a correlate of familiarity would be most expected – the *no specifics* condition. Third, at a functional level, equating the anterior effect seen here with the typical mid frontal effect has an unpalatable theoretical implication – it implies that recollection during face recognition is primarily supported by familiarity.

Another possibility is that the recollection old/new effect seen here is an early manifestation of the well documented late right frontal old/new effect considered to reflect post-retrieval processing (Wilding & Rugg, 1996). We reexamined our data to consider this possibility and reject it for two reasons: first, from 500 – 700ms the effect observed at superior frontal electrodes is sensitive to the nature of the information recollected (with a bigger effect for name than for other specifics) whereas later right frontal activity is not sensitive to the nature of information recollected; second, the topographies of the two effects differ. Nevertheless, it remains possible that activity from 500 - 700 ms represents a blend of mid frontal and late right frontal old/new effects. Of greatest importance, however, is the finding that familiarity for faces elicits a posterior old/new effect. Regardless of whether the anterior activity associated with recollection reflects the mid frontal effect, the late right frontal effect, a blend of the two, or a less well established correlate of recollection, familiarity was associated with a topographically dissociable posterior effect, which demonstrates that familiarity is not generically associated with the mid frontal old/new effect.

A neural correlate of absolute familiarity?

One motivation for examining face recognition was the possibility that unfamiliar faces allow absolute familiarity to be examined. This view is based upon a distinction between absolute and relative familiarity (see Mandler, 1980; Rugg et al., 1995). In a study-test paradigm, old items are relatively more familiar than new items because they have been encountered recently. If words are used as stimuli then all test items will have a baseline of familiarity because they have been encountered outside the experimental context; assessments of absolute familiarity will not be diagnostic of previous occurrence and so performance must be supported by sensitivity to relative changes in familiarity. In contrast, where previously unencountered stimuli are employed then assessments of absolute familiarity may be diagnostic of previous occurrence. By this view, the mid frontal effect would be considered an index of relative familiarity, whereas the parietal effect seen for faces reflects assessment of absolute familiarity.

Is face recognition special?

The ERP old/new effects presented here differ from those typically found during episodic retrieval, raising the possibility that the processes elicited in recognition tests vary according to the nature of the material that must be remembered. To some extent this is to be expected; for example, recent work using event-related fMRI has revealed clear differences in the regions of sensory cortex that are reactivated during retrieval depending on the modality of the information being retrieved (Wheeler et al., 2000). Nonetheless, attempts to reveal stimulus or modality specific retrieval correlates with ERPs have often proved fruitless (e.g., Schloerscheidt & Rugg, 1997).

ERP 1

One clear difference between word and face recognition is that newly learned faces have not been consolidated into long term memory. By this view, recognition of a stimulus associated with a pre-existing representation may be critical for the engagement of the standard left parietal and mid frontal old/new effects. Evidence against this view comes from Groh-Bordin et al. (2006), who demonstrated a mid frontal effect associated with recognising blobs that do not have pre-existing representations. Of course, it remains possible that representations could be extracted from blobs at study (e.g., based on the similarity of the blobs to items stored in memory) leading to the usual pattern of old/new effects.

Mid frontal effects have also been reported for unknown faces in at least two paradigms (Johansson et al., 2004; Nessler et al., 2005). One way to reconcile the present findings with those of Nessler et al. is to conclude that task demands can promote a reliance on assessments of either relative or absolute familiarity, each of which is associated with a distinct neural correlate. By this view, performance on a continuous recognition paradigm might be associated with assessments of relative familiarity, eliciting a mid frontal effect, whereas traditional study-test paradigms using faces might allow greater reliance on absolute familiarity – possibly due to the greater opportunity for encoding that is available – and elicits a parietal old/new effect associated with familiarity. This interpretation does not, however, account for the findings of the study by Johansson et al. (2004).

Employing a study-test paradigm, Johansson et al. identified topographically dissociable frontal and parietal old/new effects using faces with positive, neutral and negative expressions. The parietal effect was only significant for negative faces, and using corroborative evidence from a control experiment showing that negative faces

ERP 1

were more likely to be 'remembered' than 'known', the authors argued that the parietal activity reflects recollection and that the frontal activity reflects familiarity. As with the Nessler et al. study, the association between components and memory processes is inferred on the basis of previous studies: no task manipulations were employed to isolate familiarity- or recollection-based responding. In the case of Johansson et al., the connection between the parietal activity and recollection was predicated on the fact that negative faces were associated with more 'remember' than 'know' responses. However, this claim is weak given that the same behavioural difference was present for neutral faces, a condition that did not elicit a parietal effect.

Although the present findings and those of Johansson et al. are difficult to reconcile, they both provide evidence for dissociable frontal and parietal effects. In addition, the present findings suggest that the two effects seen for faces are present in the same latency period, unlike the traditional effects seen for words, where the mid frontal effect onsets before the left parietal effect. Not only does the parietal activity observed in the present study occur early, it is also bilaterally distributed, differing from the left parietal effect. Thus, whilst Johansson et al. assume that the effects seen for faces reflect the traditional mid-frontal familiarity and parietal recollection effects, the results presented here urge caution with this interpretation. Specifically, the data strongly suggest that frontal activity reflects recollection and parietal familiarity by task performance. Nonetheless, and perhaps most importantly, across the studies using faces it is now clear that the parietal and frontal effects are dissociable and need not co-occur.

ERP 1

There are, of course, many other possible differences between the experimental paradigms employed using faces as stimuli. Response demands can be confidently ruled out because the *no specifics* and *other specifics* conditions involved the same response requirements, but led to differential patterns of activity, whereas the *other specifics* and *name* conditions involved different response requirements but led to equivalent patterns of activity. Other factors are harder to discount; for example, the characteristics of the stimulus set may be germane. Word stimuli are typically highly controlled (e.g., matched for length, frequency, etc.) whereas equivalent norms are less easy to apply for faces. The face stimuli in our experiment were specifically controlled to be homogenous (with cropped hair, no jewellery, etc.), whereas the examples provided by Nessler et al. (2005) are more heterogeneous. Whether such characteristics play some role in determining the pattern of old/new effects seen across the current set of studies remains to be seen.

Regardless of whether performance in the *no specifics* condition is supported by absolute or relative familiarity, the present data are consistent with a dualprocess account. Not only are topographically dissociable effects elicited by familiarity and recollection, but the effects differ in their time course, with the frontal old/new effect associated with recollection appearing to last longer (see Figure 12). Functionally, face recognition performance can be separated according to whether familiarity or recollection supports retrieval, and at this level face recognition is no different from any other kind of stimulus recognition in providing evidence for dual-process theory. At a neural level, however, a different pattern of activity seems to support face recognition than is typically characteristic of episodic retrieval – at least under the conditions employed here. Whether features such as the particular structure of the paradigm or the characteristics of the stimuli employed

determine the pattern of effects remains to be seen. Regardless, if dual-process theories are to explain recognition memory at both functional and neural levels of analysis then they need to accommodate the differences between the old/new effects elicited in the present paradigm and those more commonly associated with familiarity and recollection. To our knowledge, no current dual-process model distinguishes between the retrieval processes engaged by different types of paradigm or stimulus.

Conclusion

The present study examined the neural correlates associated with the experience of 'I know your face but I can't remember your name', identifying topographically dissociable ERP old/new effects associated with recollection and familiarity. The current data are suggestive of the material specificity of the ERP old/new effect: the effects seen here for faces do not match those typically seen in studies of word recognition. Any claims of material specificity are premature, of course, and must await evidence from paradigms directly comparing stimulus materials. Regardless, the present finding raises the possibility that there may be more than one route to the feeling of familiarity engendered by a stimulus, depending on whether assessment of relative or absolute familiarity is diagnostic of previous occurrence. Further research investigating the differences between various types of stimuli on the neural correlates of recognition memory promises to aid in elucidating the functional characteristics of ERP old/new effects, and in assessing the generalisability of dual-process models of recognition memory. Fundamentally, these new data provide clear evidence that the ERP old/new effect does not provide a generic index of retrieval processing under all circumstances.

ERP 1

Chapter 6 – ERP 2: Manipulating Face Familiarity

Introduction

Experiment 1 (reported by MacKenzie & Donaldson, 2007) identified neural correlates of familiarity and recollection that are largely inconsistent with previous literature. Familiarity was associated with a posterior old/new effect (300 – 500ms) and recollection was associated with an anterior old/new effect that was present during the same latency period as the posterior effect. Importantly, a topographic difference between the two effects is consistent with dual-process theories of episodic memory in that it supports the inference that different cognitive operations support familiarity- and recollection-based recognition. Given that the effects observed in Experiment 1 differ from the typical mid frontal and left parietal effects that are widely considered to provide indices of familiarity and recollection, respectively (Rugg & Curran, 2007), one of the aims of Experiment 2 was to replicate the neural correlates observed in Experiment 1. While the posterior old/new effect associated with familiarity has been previously reported by Yovel and Paller (2004), the anterior effect associated with recollection, and reported by MacKenzie and Donaldson (2007), is a novel finding and would therefore benefit from replication.

Experiment 1 included a manipulation of face shape, with distinctive and average versions of each face being used as stimuli. However, there was an insufficient number of trials to examine ERPs for distinctive and average faces separately, and so Experiment 2 was designed to allow for the investigation of the issue of whether manipulating face shape modulates the neural correlate of familiarity and/or the neural correlate of recollection. The hypothesis that

manipulating face shape might modulate the neural correlate of familiarity is derived from the observation that average faces are rated as being more familiar, and lead to more false alarms, than distinctive faces (see Pilot Experiment below). If false alarms arise because of stimulus familiarity, then it follows that average faces might recruit familiarity to a greater extent than distinctive faces, and that this differential recruitment of familiarity might be manifest in the old/new effect.

Given that there was no qualitative difference between the two recollection conditions in Experiment 1, only one recollection condition was chosen for Experiment 2 to boost statistical power; a variant of the remember/know procedure (Tulving, 1985) was adopted. In Experiment 1, frontally distributed old/new effects that were maximal at superior sites correlated with recollection, and the magnitude of the effect was greater when names were retrieved than when other specific information was retrieved. In the name condition, participants correctly supplied the name that was paired with the face at study; whereas in the other specifics condition, participants were only required to indicate that they had recollected specific details from the study episode. Because there was no qualitative difference between the old/new effects associated with these two conditions, it appears that the recall of accurate contextual details is not necessary for the effect to be observed. Therefore, participants in Experiment 2 were not required to report the contextual information that they recollected; rather, a remember response was required whenever a face was recognized and episodic contextual information was additionally retrieved, and a *familiar* response was required whenever a face was simply recognized (i.e., and no contextual information was retrieved).

Based on the results of Experiment 1, it was predicted that the old/new effects associated with *remember* responses would have an anterior distribution and that the effects associated with *familiar* responses would have a posterior distribution, with both effects being observed within the 300 – 700ms latency period. Importantly, topographic dissociations should be observed between the *remember* and *familiar* old/new effects, replicating the results of Experiment 1, and supporting a dual-process view of recognition memory. Experiment 2 also included a manipulation of face shape, with distinctive and average faces being used as stimuli. Given that morphing faces towards average shape increases perceived familiarity (see below), it was expected that average faces would be associated with a larger neural correlate of familiarity than distinctive faces.

Pilot Experiment

Pilot Introduction

Donaldson, MacKenzie and Davis (2004) showed a series of faces to participants and asked them to rate how familiar each face was on a five-point scale ranging from 'not at all familiar' to 'very familiar'. Faces were systematically manipulated to vary from original, distinctive faces towards average face shape. Higher familiarity ratings were observed the closer a face was to average shape. Donaldson, MacKenzie and Davis demonstrated that manipulating face shape in this way varies perceived ratings of familiarity, and therefore the same manipulation of face shape was used to assess the impact on recognition performance. If the face shape manipulation varies the amount of familiarity associated with the stimuli

during a recognition memory test then it would be expected that false alarms should show an effect, with a greater probability of false alarms for average faces⁴.

Pilot Methodology

Eight participants (4 males) with a mean age of 41 (range: 24 - 56) studied a series of faces, and rated how familiar each face felt on a five-point scale ranging from 'not at all familiar' to 'very familiar'. Faces were either unmorphed, or were morphed 25%, 50% or 75% towards average shape. Allocation of faces to morph levels was counterbalanced across participants. In the test phase, all studied faces were shown again, along with an equal number of unstudied faces. Unstudied faces were drawn in equal proportion from the four levels of morph. Test faces were shown for 1000ms, and participants made an old/new discrimination for each face.

Pilot Results

Figure 15 shows mean familiarity ratings for each level of morph; as can be seen, perceived familiarity increases as face shape becomes closer to average. Mean familiarity rating data were submitted to ANOVA, and the analysis revealed a significant linear trend [F(1,7) = 12.3; p = 0.01], which suggests that there is increasing perceived familiarity attributed to faces depending on how close to average shape the faces are, at least within the confines of a rating experiment. Of greater interest is the test phase data, which allow more direct inferences to be

⁴ While hits also might be expected to show an effect of face shape in the same direction as for false alarms, recollection is more likely to contribute to hit performance than to false alarm performance; the contribution of recollection to hit performance could in theory obfuscate any effect of increased familiarity for average faces.

drawn concerning the amount of familiarity associated with faces at different levels of morph during a recognition memory test.



Figure 15: Familiarity rating.

Figure 16 shows response probabilities for hits and false alarms at each level of morph. There appears to be a greater probability of hits than false alarms over all, and little difference in the hit rate across levels of morph; in contrast, the false alarm rate increases across morph levels. Data were submitted to ANOVA with factors of status (hit/false alarm) and morph (0%/25%/50%/75%). The analysis revealed main effects of status [F(1,7) = 36.2; p = 0.001] and morph [F(3,21) = 4.3; p < 0.05], as well as an interaction between the factors [F(3,21) = 6.9; p < 0.01]. When hits were analysed separately, no differences were observed; when false alarms were analysed separately, a main effect was observed [F(3,21) = 6.9; p < 0.01]. This finding demonstrates that the interaction described above is due to differences in the false alarm rate. Paired-samples t-tests found that false alarms for unmorphed faces (0%) difference from each of the other levels of morph (0% vs. 25% [t(7) = 2.5; p < 0.05];

The figure shows familiarity ratings for four levels of morphed face. Participants rated how familiar faces were on a five-point scale. Faces were either unmorphed (0%) or were morphed 25%, 50% or 75% towards average shape. Mean ratings of familiarity increase as a function of manipulating face shape towards average. Error bars show the standard error of the mean.

0% vs. 50% [t(7) = 3.9; p < 0.01]; 0% vs. 75% [t(7) = 6.1; p = 0.001], while there are no significant differences between 25%, 50% and 75%.



Figure 16: Pilot performance.

The figure shows the probability of hits and false alarms for four levels of morphed face. There is little difference in the hit rate across levels of morph, but there is a trend for increasing false alarms as a function of manipulating face shape towards average. Error bars show the standard error of the mean.

Pilot Discussion

The test phase data show an increase in false alarms as faces move towards average shape. False alarms are usually attributed to familiarity (Dobbins et al., 2000; although false recollection cannot be ruled out, Gallo et al., 2004), and therefore these pilot data suggest that average faces are more familiar than distinctive faces on two independent bases: first, during encoding, average faces are perceived to be more familiar than distinctive faces; and second, during retrieval, average faces are more likely to be falsely recognized than distinctive faces.

The pilot data described here were therefore used as a basis for designing Experiment 2. Unmorphed faces (0%) and faces that were morphed 50% towards

average shape (50%) were chosen to represent distinctive and average faces, respectively, because the greatest difference in perceived familiarity was between these two levels of morph (see Figure 15), and because there was no increase in false alarms between 50% and 75%.

Method

Thirty-five right-handed native-English speakers gave informed consent and took part in the experiment. Eleven data sets were discarded due to poor behavioural performance or contamination of EEG with artefacts, and so data from 24 participants (15 females) are presented here. The mean age of participants was 22 years (range: 17 - 31).

An adaptation of the remember/know procedure was used in which participants made an initial old/new discrimination followed by a *remember* or *familiar* response for each test item receiving an 'old' response. Both *remember* and *familiar* responses terminated the trial sequence, which differs from Experiment 1 in that *name* trials were followed by a recall attempt. As described above, the task requirement to recall information was abandoned because there had been no qualitative difference in the recollection old/new effects in Experiment 1. Apart from these two procedural differences, all other experimental parameters matched those already described for Experiment 1.

Behavioural Results

Performance

Figure 17 shows the probability of hits and false alarms for distinctive and average faces. The hit rate is high while there are relatively few false alarms; there appears to be a greater probability of an 'old' response for average faces, which is manifest in the hit rate but is particularly clear in the false alarm rate.



Figure 17: Performance.

The mean probability of hits and false alarms are plotted for distinctive and average faces. Average faces were associated with a higher hit rate and false alarm rate than distinctive faces. Error bars show the standard error of the mean.

A two-way repeated-measures ANOVA with factors of status (old/new) and face type (distinctive/average) revealed main effects of status [F(1,23) = 414.8; p < 0.001] and face type [F(1,23) = 23.2; p < 0.001] along with an interaction between the factors [F(1,23) = 9.3; p < 0.01]. The interaction appears to reflect a greater difference between the two face types for false alarms than for hits; this interpretation was confirmed by paired-samples t-tests, which found a significant difference in the false alarm rate between distinctive and average faces [t(23) = 6.8; p < 0.001]. There was no reliable difference in the hit rate between face types. The elevated false alarm rate for average faces suggests that guessing contributed more to recognition performance for average faces than for distinctive faces. To correct for the influence of guessing, a measure of discriminability called 'sensitivity' (Snodgrass and Corwin, 1988) was computed by subtracting the probability of committing a false alarm from the probability of making a hit for each face type. Figure 18 shows greater sensitivity to discriminate between old and new test items for distinctive faces than for average faces. A paired-samples t-test found a significant difference in sensitivity between the face types [t(23) = 3.1; p < 0.01], which supports the view that distinctive faces are easier to discriminate than average faces.



Figure 18: Sensitivity.

Mean sensitivity is plotted for distinctive and average faces. This measure was computed by subtracting the probability of false alarms from the probability of hits (Snodgrass and Corwin, 1988). Participants had greater sensitivity to discriminate between studied and unstudied items for distinctive faces than for average faces. Error bars show standard error of the mean.

Response Time

Figure 19 shows response times for hits, false alarms, correct rejections and misses. Average faces are generally associated with longer response times – except for false alarms, where distinctive faces are associated with longer response times.



Figure 19: Response time.

Mean response times for all response categories are plotted for distinctive and average faces. Correct responses to studied faces were faster than all other response categories, while correct rejections were faster for distinctive faces than for average faces. Error bars show standard error of the mean.

A three-way repeated-measures ANOVA with factors of status (old/new), accuracy (correct/incorrect) and face type (distinctive/average) revealed main effects of accuracy [F(1,23) = 50.8; p < 0.001] and face type [F(1,23) = 5.9; p < 0.05] along with an interaction between status and accuracy [F(1,23) = 7.1; p < 0.05], reflecting faster response times for hits than for correct rejections, and slower response times for misses than for false alarms. In addition, the analysis revealed an interaction between status, accuracy and face type [F(1,23) = 8.3; p < 0.01]. Paired-samples t-tests found a significant difference in response times between face types for correct rejections [t(23) = 4.9; p < 0.001] but not for any other response categories. The increased response time for average faces suggests that participants had greater difficulty in deciding that a face was unstudied, and is consistent with the foregoing demonstration of a decreased ability to discriminate old faces from new faces for the average face condition.

Remember/Familiar Responses

For each participant, the probabilities of making *remember* and *familiar* responses were calculated by dividing the number of each response by the total number of old faces shown at test for both face types. These measures reflect the probability of making *remember* and *familiar* responses when presented with an old test item. These raw probabilities underestimate the contribution of familiarity to recognition performance because *familiar* responses are only made when items are not recollected: if an item is familiar and recollected it receives a *remember* response and so in this manner the original remember/know procedure systematically underestimates the contribution of familiarity. Following from this concern, the independent R/K procedure (IRK; Jacoby, Yonelinas & Jennings, 1997) was used to estimate the contributions of familiarity and recollection; this estimate was achieved by dividing the original probability of making a *familiar* response by (1 - pR), which is the probability that an item does not receive a *remember* response.

Figure 20 shows that there is slightly more recollection associated with recognising distinctive faces than average faces, and that there is more familiarity associated with recognising average faces than distinctive faces. A two-way repeated-measures ANOVA with factors of response category (*remember/familiar*) and face type (distinctive/average) revealed a main effect of response category [F(1,23) = 51.1; p < 0.001] and an interaction between response category and face type [F(1,23) = 27.0; p < 0.001]. Paired-samples t-tests found a significant difference in the estimate of familiarity [t(23) = 3.5; p < 0.01] between face types,

and no difference in the estimate of recollection. These results suggest that the face shape manipulation varies familiarity but not recollection.



Figure 20: Estimates of recollection and familiarity. Mean probabilities of the contribution of recollection and familiarity to recognition performance are plotted for distinctive and average faces. The contribution of familiarity was rescaled under the an independence assumption, demonstrating that familiarity played a greater role in performance than recollection. There were no differences in the amount of recollection for each type of face, while average faces were more likely to recruit familiarity than distinctive faces. Error bars show standard error of the mean.

Remember/Familiar Response Times

Figure 21 shows response times for hits subsequently given a *remember* or a *familiar* endorsement. The figure shows that *familiar* responses are associated with longer response times, and that there is little difference in response time across face types A two-way repeated measures ANOVA with factors of response category (*remember/familiar*) and face type (distinctive/average) revealed a main effect of response category [F(1,23) = 95.3; p < 0.001], which reflects longer response times for *familiar* responses than for *remember* responses.





Mean response Times for the initial old/new discrimination are plotted for correctly recognized faces that were subsequently given Remember and Familiar judgments. Faces that were given a Remember response were quicker to be recognized than faces that were given a Familiar response. No differences were observed between distinctive and average faces for either response category. Error bars show standard error of the mean.

In sum, morphing faces towards average shape results in an increased false alarm rate, and a concomitant decrease in sensitivity to discriminate studied items from unstudied items; the manipulation also increases the length of time taken to make correct rejections. The IRK data offer an explanation of these results by suggesting that there is a greater contribution of familiarity involved in recognising average faces than distinctive faces: the elevated familiarity of average faces leads to more false alarms and makes it difficult to discriminate between old and new faces, as demonstrated by decreased sensitivity and longer response times to correctly reject new average faces.

ERP Results

The mean number of trials included in grand-average ERPs was: Distinctive *remember* = 36.9; Average *remember* = 35.8; Distinctive *familiar* = 29.3; Average

familiar = 36.2; Distinctive correct rejection = 38.5; Average correct rejection = 31.6. Figure 22 on page 119 shows *familiar* old/new effects from midline frontal and parietal sites for both distinctive and average faces; as can be seen, from 300 - 700ms the difference between old and new waveforms is greater at the parietal electrode than at the frontal electrode for both face types.



Figure 22: Familiar old/new effects.

Grand average ERPs are shown for correctly identified familiar (old) and new faces. Midline frontal (FZ) and parietal (PZ) sites are shown for both distinctive (left) and average (right) faces. The depicted epoch begins 100ms pre-stimulus onset and ends 1100ms post-stimulus onset. From 300 – 700ms, familiar old/new effects were only reliable at the parietal location. The magnitude of the parietal effect is greater for average faces than for distinctive faces. If the parietal effect indexes familiarity then the larger effect for average faces suggests that average faces recruit more familiarity than distinctive faces. Average Faces: Familiar old/new effects.

Figure 23 on page 122 shows *remember* old/new effects for distinctive and average faces; the difference between old and new waveforms appears to be present at both frontal and parietal sites from 300 – 700ms.

Distinctive Faces: Familiar old/new effects

To examine the pattern of old/new effects, the data were submitted to ANOVA with factors of old/new, location (frontal/parietal), hemisphere (left/right) and site (superior/medial/inferior). The analysis of data from 300 – 500ms revealed an interaction between old/new and location [F(1,23) = 8.3; p < 0.01] reflecting the presence of a reliable main effect of old/new at the parietal location [F(1,23) = 7.5;p < 0.05] but not at the frontal location. Examination of the data found that the old/new effect was maximal at the P4 electrode [t(23) = 3.3; p < 0.01]. The analysis of data from 500 – 700ms revealed an interaction between old/new, location and hemisphere [F(1,23) = 5.2; p < 0.05]. As in the earlier latency period, a main effect of old/new was only present at the parietal location [F(1,23) = 4.7; p < 0.05], while at the frontal location a hemispheric asymmetry was observed, with a new > old negativity being observed on the left hemisphere. Examination of the data found that the old > new effect was maximal at the P3 electrode [t(23) = 2.1; p < 0.05].

Distinctive Faces: Remember old/new effects

The analysis of data from 300 - 500ms revealed a main effect of old/new [F(1,23) = 8.2; p < 0.01]. For consistency across analyses, data from frontal and parietal locations were analysed separately; the old/new effect was reliable at the frontal location [F(1,23) = 5.3; p < 0.05] and only marginally significant at the parietal location [F(1,23) = 4.1; p = 0.056]. Examination of the data found that the effect was maximal at the CZ electrode [t(23) = 2.7; p < 0.05]. The analysis of data from 500 – 700ms revealed a main effect of old/new [F(1,23) = 24.5; p < 0.001] and interactions between: old/new and site [F(1.1,25.2) = 4.9; p < 0.05]; old/new, location, location and hemisphere [F(1,23) = 13.4; p = 0.001]; and between old/new, location,

hemisphere and site [F(1.5,33.8) = 6.1; p = 0.01]. The old/new effect is greater at superior sites than at inferior sites; at the frontal location, the old/new effect is only reliable on the right hemisphere, while on the left hemisphere, the effect is greater at superior and medial sites than at inferior sites. When data from each location were analysed separately, the old/new effects were reliable at both the frontal [F(1,23) = 9.2; p < 0.01] and parietal [F(1,23) = 32.7; p < 0.001] locations. Examination of the data found that the effect was maximal at the CPZ electrode [t(23) = 6.6; p < 0.001].

Average faces: Familiar old/new effects

The analysis of data from 300 - 500ms revealed a main effect of old/new [F(1,23) = 5.8; p < 0.05] and an interaction between old/new and site [F(1.1,25.9) =10.4; p < 0.01] reflecting an effect that is maximal at superior sites. When the frontal and parietal locations were analysed separately, the old/new effect is only reliable at the parietal location [F(1,23) = 9.6; p = 0.005]. Examination of the data found that the effect was maximal at the PZ electrode [t(23) = 3.1; p = 0.005]. The analysis of data from 500 - 700ms revealed interactions between: old/new and location [F(1,23) = 4.9; p < 0.05]; old/new and site [F(1.4,31.7) = 9.0; p < 0.01];and between old/new, location and hemisphere [F(1,23) = 6.4; p < 0.05]. The old/new effect is greater at the parietal location than at the frontal location, and greater at superior sites than at inferior sites; at the frontal location, the old > new pattern can only be observed on the right hemisphere, with a new > old negativity being present on the left hemisphere. As with the earlier latency period, when the frontal and parietal locations were analysed separately, the old/new effect was only reliable at the parietal location [F(1,23) = 4.8; p < 0.05]. Examination of the data found that the effect is maximal at the PZ electrode [t(23) = 2.9; p < 0.01].



Grand average ERPs are shown for correctly identified remember (old) and new response categories. Midline frontal (FZ) and parietal (PZ) sites are shown for both distinctive (left) and average (right) faces. The depicted epoch begins 100ms prestimulus onset and ends 1100ms post-stimulus onset. Remember old/new effects were reliable at both frontal and parietal locations. The magnitude of the frontal effect is greater for distinctive faces than for average faces. If the frontal effect indexes recollection then the larger effect for distinctive faces is consistent with Remember/Familiar data, which showed that distinctive faces recruit more recollection than average faces.

Average faces: Remember old/new effects

The analysis of data from 300 - 500ms revealed a main effect of old/new [F(1,23) = 6.9; p < 0.05] and an interaction between old/new and site [F(1.2,26.9) = 4.3; p < 0.05], reflecting an effect that is maximal at superior sites. When the frontal and parietal locations were analysed separately, the old/new effect was only reliable at the parietal location [F(1,23) = 9.3; p < 0.01]. Examination of the data found that

the effect was maximal at the CP2 electrode [t(23) = 2.7; p < 0.05]. The analysis of data from 500 – 700ms revealed a main effect of old/new [F(1,23) = 26.1; p < 0.001] and interactions between: old/new and location [F(1,23) = 7.1; p < 0.05]; old/new and site [F(1.2,28.6) = 8.7; p < 0.01]; and between old/new, location and hemisphere [F(1,23) = 5.4; p < 0.05]. The old/new effect is larger at the parietal location than at the frontal location, and larger at superior sites than at inferior sites; at the frontal location, the effect is greater on the right hemisphere than on the left. The old/new effects were reliable at both frontal [F(1,23) = 7.6; p < 0.05] and parietal [F(1,23) = 32.3; p < 0.001] locations. Examination of the data found that the effect was maximal at the CP2 electrode [t(23) = 5.8; p < 0.001].

False alarms and correct rejections

It would be a great interest to investigate ERPs for false alarms because it is widely assumed that false alarms are made on the basis of familiarity. Given that average faces led to more false alarms than distinctive faces, then it might be expected that some familiarity-related ERP modulation would be observed in the contrast between false alarms and correct rejections for distinctive and average faces. As a result of the 2:1 weighting of old items to new items at test, which was purposefully held constant across the studies described in this thesis, there was an insufficient number of participants who contributed enough trials to examine ERPs for false alarms.

However, an examination of the contrast between correct rejections for distinctive and average faces might also reveal a familiarity-related modulation. The study phase data from the pilot experiment demonstrate that average faces are rated as being more familiar than distinctive faces, despite not having been encountered

before. The assessment of stimulus familiarity that is theorized to support recognition memory may not depend on having encountered a stimulus before, but rather depends on the comparison of a current stimulus with all similar items stored in memory. Items that fall below a familiarity-strength decision criterion will engender a degree of familiarity, and by this rationale, the contrast between ERPs for correctly rejected distinctive and average faces may reveal a neural correlate of familiarity. Figure 24 shows waveforms for distinctive and average face correct rejections; the distinctive waveform is more positive-going than the average waveform, and the difference between waveforms appears to be greatest at the midline parietal electrode (PZ).



Figure 24: Correct rejection waveforms.

Grand average ERPs for correctly identified new items are plotted for distinctive and average faces at selected frontal and parietal electrode sites. The depicted epoch begins 100ms pre-stimulus onset and ends 1100ms post-stimulus onset. The waveform for distinctive faces is slightly more positive-going than the waveform for average faces from approximately 400ms post-stimulus at electrode PZ, where the difference between waveforms appears to be greatest.

The analysis of data from 300 - 500ms failed to reveal any significant differences between the waveforms. In contrast, the analysis of data from 500 - 700ms revealed an interaction between condition and site [F(1.3,30.7) = 4.2; p < 0.05], reflecting a positive-going deflection for distinctive faces that is greater at

superior sites than at inferior sites. Subsidiary analysis revealed no difference at the frontal location, whereas at the parietal location the analysis revealed an interaction between condition and site [F(1.2,28.3) = 4.7; p < 0.05]. Examination of the data found that the difference was maximal at PZ, although the effect was not reliable at any individual electrode.

Visual inspection of the waveforms in Figure 24 suggests that the difference between waveforms persists beyond 700ms post-stimulus, and therefore further analysis was performed to verify whether the pattern of results seen from 500 – 700ms reflects an accurate characterization of the difference between the correct rejection waveforms. The analysis of data from 700 – 900ms revealed a main effect of condition [F(1,23) = 5.4; p < 0.05] and an interaction between condition and site [F(1.1,25.5) = 4.5; p < 0.05], reflecting the augmentation of the difference between waveforms at superior sites. As with the analysis of data from 500 – 700ms, subsidiary analysis revealed differences at the parietal location only (main effect of condition [F(1,23) = 5.6; p < 0.05] and marginal interaction between condition and site [F(1.1,26.2) = 4.0; p = 0.052]). Examination of the data found that the difference was maximal at electrode PZ [t(19) = 2.3; p < 0.05]. Finally, the analysis of data from 900 – 1100ms failed to reveal any significant differences between the waveforms.

This pattern of results demonstrates that the difference between correct rejection waveforms for distinctive and average faces is a positive-going deflection for distinctive faces, maximal at midline parietal sites. It is important to note that the topographic characteristics of this ERP modulation resembles the neural correlate of familiarity observed in the present study. Figure 25 illustrates the distribution of the difference between correct rejection waveforms: the parietal distribution of this familiarity-related modulation is consistent with the view that parietal potentials reflect familiarity.



Figure 25: Correct rejection contrast topography.

Topographic distributions of the difference between correct rejections for distinctive and average faces. Each cartoon shows the distribution of the difference between correctly rejected new items for distinctive and average faces, averaged across a 200ms time period. The front of the head is at the top of each map, and the left hemisphere is on the left-hand side. Each dot represents a recording electrode. The scale bar indicates the range of activity (in microvolts). The difference between waveforms is reliable at the parietal location from 500 – 900ms post-stimulus, and is greater at midline electrode locations.

Summary

Familiar old/new effects for both face types were only observed at the parietal location, whereas *remember* old/new effects were observed at both frontal and parietal locations from 500 – 700ms. From 300 – 500ms, however, *remember* effects were different for each face type, with distinctive faces being associated with frontal effects and average faces being associated with parietal effects. In addition, correct rejections waveforms were modulated at the parietal location, with distinctive faces being associated with more positive-going potentials from 500 – 900ms.

Amplitude analyses

Difference waveforms were analysed to assess whether distinctive and average faces differ in the magnitude of the old/new effects associated with them. It was predicted that the face shape manipulation would modulate the putative neural correlate of familiarity but not recollection. Figure 26 shows the sizes of the *familiar* effects at the parietal location where the effects were reliable; the average face effect appears to be larger than the distinctive face effect at electrode PZ.



Figure 26: Magnitude of familiar old/new effects, 300 – 500ms. The mean size of the familiar old/new difference (in microvolts) is plotted for distinctive and average faces at selected sites from the parietal location. Error bars show the standard error of the mean. There is a larger effect for average faces than for distinctive faces at superior sites, although the difference between conditions is non-reliable.

The magnitude of the *familiar* old/new effects for both face types was compared: during the 300 - 500ms latency period, the analysis revealed an interaction between face type and site [F(1.1,26.4) = 4.3; p < 0.05], reflecting the superior distribution of the average face effect relative to a more broadly distributed distinctive face effect. The analysis of data from 500 - 700ms also revealed an interaction between face type and site [F(1.2,28.3) = 5.8; p < 0.05], which again reflects the superior distribution. of the average face effect. However, examination of the data found that none of the differences was significant at any individual electrode during either latency period

Figure 27 shows the sizes of the *remember* old/new effects at both frontal and parietal locations (midline sites are shown) from 300 – 500ms. Frontal effects were only reliable for distinctive faces and parietal effects were only reliable for average faces. The magnitudes of the *remember* old/new effects for each face type were compared and no significant differences were observed in either latency period from 300 – 700ms.



Figure 27: Magnitude of remember old/new effects, 300 - 500ms.. The mean size of the remember old/new difference is plotted (in microvolts) for distinctive and average faces at midline frontal (FZ) and parietal (PZ) electrodes. Error bars show the standard error of the mean. Frontal effects were only reliable for distinctive faces and parietal effects were only reliable for average faces. If the frontal effect reflects recollection and the parietal effect reflects familiarity then this pattern of results suggests that recollection is only present for distinctive faces during the 300 - 500ms latency period while familiarity is only present for average faces.

Topographic analyses

The distributions of the old/new difference are plotted below for the *familiar* effects (Figure 28, page 129) and for the *remember* effects (Figure 29, page 130). The *familiar* effects have a clear posterior distribution in both latency periods, while the *remember* effects have more anterior distributions, particularly for distinctive faces.



Figure 28: Familiar topography.

Topographic distributions of the Familiar old/new difference for distinctive and average faces. Each cartoon shows the distribution of the difference between correctly recognized old faces given familiar decisions and correctly rejected new faces, averaged across a 200ms time period. The front of the head is at the top of each map, and the left hemisphere is on the left-hand side. Each dot represents a recording electrode. The scale bar indicates the range of activity (in microvolts). For both face types, the effects have a posterior distribution; the effects are more superiorly focused for average faces than for distinctive faces.

A first topographic analysis was performed to assess whether the

distributions of the familiar and remember old/new effects differ for distinctive

faces: different distributions would provide evidence in support of dual-process theory. The analysis of data from 300 - 500ms revealed an interaction between condition and location [F(1,23) = 5.2; p < 0.05], reflecting the posterior distribution of the *familiar* effect relative to the more anterior distribution of the *remember* effect. The analysis of data from 500 - 700ms failed to reveal any reliable differences.





Topographic distributions of the Remember old/new difference for distinctive and average faces. Each cartoon shows the distribution of the difference between correctly recognized old faces given familiar decisions and correctly rejected new faces, averaged across a 200ms time period. The front of the head is at the top of each map, and the left hemisphere is on the left-hand side. Each dot represents a recording electrode. The scale bar indicates the range of activity (in microvolts). For both face types, there is little activity from 300 – 500ms, while the effects have widespread distributions in the later latency period, with a slightly more anterior distribution for distinctive faces.

A second analysis was performed to assess whether the distributions of the

familiar and remember old/new effects differ for average faces. The analysis of data

from 300 - 500ms failed to reveal any significant differences. The analysis of data from 500 - 700ms revealed an interaction between condition, location and site [F(1.2,27.6) = 5.4; p < 0.05], reflecting differences at the parietal location where the *familiar* effect is focused around the midline and the *remember* effect is more broadly distributed.

A third analysis was performed to assess whether the effects change across the 500ms latency boundary. The analysis of *familiar* effects for distinctive faces revealed an interaction between latency, location and hemisphere [F(1,23) = 7.5; p < 0.05], reflecting differences at the frontal location where the early effect is equivalent across sites and the later effect is greater at inferior sites (marginally significant interaction between latency and site [F(1.2,27.5) = 3.2; p = 0.077). Importantly, no differences in distribution were observed at the parietal location. The analysis of *familiar* effects for average faces failed to reveal any significant differences. Taken together, the lack of a difference in topography for both the distinctive and average *familiar* effects at the parietal location, where the old/new effects were reliable, is consistent with the view that there are no qualitative differences in the *familiar* old/new effects across the 500ms latency boundary.

Finally, the analysis of *remember* effects for distinctive faces revealed an interaction between latency, location and hemisphere [F(1,23) = 4.7; p < 0.05]. At the frontal location, the effects are greater on the right hemisphere in both latency periods, whereas at the parietal location, effect is greater on the right hemisphere from 300 - 500ms while the effect is greater on the left hemisphere from 500 - 700ms. The analysis of *remember* effects for average faces failed to reveal any significant differences.

Discussion

The present experiment was performed to assess three questions: first, are familiarity and recollection associated with posterior and anterior old/new effects, respectively; second, can topographically dissociable neural correlates of familiarity and recollection be observed; and third, does the manipulation of face shape modulate the neural correlates of familiarity and/or recollection? Familiarity was associated with posterior old/new effects and recollection was associated with old/new effects that had more anterior distributions, replicating some of the findings reported for Experiment 1. Importantly, topographically dissociable neural correlates and average faces. Finally, manipulating face shape provided little support for the view that posterior old/new effects vary in a manner consistent with familiarity.

ERP old/new effects

For distinctive faces, recollection was associated with old/new effects that were only reliable at the frontal location from 300 – 500ms, and reliable at both frontal and parietal locations from 500 – 700ms. During the early latency period, the posterior *familiar* effect was found to be topographically dissociable from the anterior *remember* effect, while no topographic differences were observed from 500 – 700ms. It was expected that anterior/posterior topographic differences would be observed in both latency periods, so the lack of such a difference in the 500 – 700ms period is difficult to interpret. One possibility is that a large posterior familiarity signal has blended with an anterior recollection signal, and that the resulting old/new effect is weighted so much in favour of familiarity that it does not difference from the lack of a

topographic dissociation between familiarity and recollection effects from 500 – 700ms, the data from the 300 – 500ms latency period clearly replicate the pattern of results observed in Experiment 1, and stand in support of dual-process accounts of recognition memory.

For average faces, recollection was associated with old/new effects that were only observed at the parietal location from 300 – 500ms, and observed at both the frontal and parietal locations from 500 – 700ms. No topographic difference between *familiar* and *remember* effects was observed from 300 – 500ms, during which time a topographic difference was observed for distinctive faces. This key difference across face types concerns the presence/absence of reliable old/new effects at the frontal location: only distinctive faces were associated with frontal effects from 300 – 500ms, which drives the qualitative difference in ERPs that was observed. If it is assumed that old/new effects at the frontal location reflect recollection, following from the results of Experiment 1, then this pattern of results suggests that average faces do not recruit recollection at a time when distinctive faces do. This interpretation of the data is consistent with behavioural measures indicating a greater involvement of familiarity to average face recognition; by this account, recognition performance may have been supported by relatively more familiarity than recollection – even in cases where participants made *remember* decisions.

Familiarity

The neural correlates of familiarity observed in the present study replicate the findings of Experiment 1. In Experiment 2, familiarity was associated with posterior old/new effects for both distinctive and average faces, and therefore the view that familiarity for facial stimuli has a posterior neural correlate replicates the

controversial findings of both Yovel and Paller (2004) and MacKenzie and Donaldson (2007). As discussed in Experiment 1, the lack of a mid frontal old/new effect associated with familiarity is an important finding because the mid frontal effect is considered by many researchers to provide a generic index of familiaritybased retrieval (Azimian-Faridani & Wilding, 2006; Curran & Cleary, 2003; Rugg et al., 1998). The present observation of a posterior old/new effect associated with familiarity demonstrates that familiarity is not always associated with the mid frontal effect.

Faces of previously unknown individuals were used as stimuli in the present experiment at least in part due to the proposal that the mid frontal effect reflects conceptual priming rather than familiarity (Voss & Paller, 2006; Yovel & Paller, 2004). Faces that have never been encountered before are clearly bereft of preexisting semantic representations, and the observation that such stimuli give rise to posterior old/new effects provides some indirect support for the conceptual priming hypothesis. Some theorists argue that familiarity is a phenomenological experience rather than a process *per se* (Mecklinger, 2000); and it remains possible that different processes support the feeling of familiarity under different circumstances. Where conceptual representations are unavailable, then perhaps perceptual representations are capable of being accessed in order to gauge whether an item has been encountered previously. By this account, the posterior effects observed across Experiments 1 and 2 may reflect perceptually-mediated familiarity.

Recollection

The neural correlates of recollection observed in the present experiment do not replicate the effects observed in Experiment 1 (reported by MacKenzie &
Donaldson, 2007) so clearly. Despite anterior/posterior topographic dissociations between recollection and familiarity (at least in some conditions and latency periods), the distribution of the recollection old/new effects in Experiment 2 was slightly more posterior than in the previous experiment. The reason for the difference in the distribution of the neural correlate of recollection across studies is unclear. One possible reason for this difference may be the temporal overlap between the neural correlates of familiarity and recollection observed for faces; in Experiment 1 it was shown that the neural correlates of familiarity and recollection are both present from 300 - 700 ms. If it is assumed that familiarity contributes a signal during recollection then a blend of posterior familiarity and anterior recollection effects would be expected; if familiarity is more active in the present data than in Experiment 1 then it is conceivable that more posterior recollection effects would be observed. Another possibility concerns response demands: in Experiment 1 participants were required to report the name they recalled on some recollection trials, whereas in Experiment 2 participants simply had to indicate whether recognition was supported by familiarity or recollection. It remains possible that different response demands might have led to different cognitive operations being engaged, which could explain the topographic difference across experiments.

The neural correlates of recollection observed here did not display the typical left parietal distribution commonly reported in recognition memory studies. While a certain degree of left lateralization of the effects were observed at posterior electrodes, it is difficult to argue that left parietal effects are present unless a second anterior effect co-occurs with the left parietal effect. One possibility is that recollection for faces recruits a different retrieval process to recollection for verbal material. In this case, the present results suggest that recollection may be a material

specific process, which is not predicted by dual-process models. However, such a conclusion is highly speculative and requires that recognition memory for faces is directly compared with other types of stimulus. Experiment 3 will test the hypothesis that recollection processing is material specific by comparing old/new effects associated with recollecting faces and names.

Manipulating familiarity

A pilot experiment showed that average faces are rated as being more familiar than distinctive faces, and pilot test phase data showed more false alarms for average faces than for distinctive faces. Together, these findings suggest that there is a greater degree of familiarity inherent in average faces compared to distinctive faces when the faces are encountered for the first time. The pilot experiment included a simple old/new response only, and it is therefore impossible to discern whether there was a greater degree of familiarity attributed to average faces that were encountered for a second time as old items in the test list.

In the ERP experiment, recognition performance was superior for distinctive faces compared to average faces, and the remember/familiar data suggest that this superiority may result from interference caused by the relatively greater familiarity of average faces. It was found that the face shape manipulation varied familiarity but not recollection, and therefore it would be expected that the manipulation might vary the neural correlate of familiarity but not that of recollection.

However, examination of the magnitude of the ERPs revealed that the *familiar* old/new effects were not modulated by manipulating face shape. There did appear to be a trend towards a greater effect for average faces but the difference

between conditions was not statistically reliable. Null results are difficult to interpret: this finding may have arisen for a variety of reasons, including the possibility that the old/new effects associated with *familiar* responses do not isolate familiarity-based retrieval (because the remember/know process is not process pure) or because the ERPs do not have sufficient resolution to demonstrate real differences in underlying neural activity. Future research could probe this issue by collecting data from a large number of participants to increase statistical power; if the modulation of the neural correlate of familiarity by face shape is a genuine phenomenon then it would be expected that increased power would foster a reliable difference in the magnitude of effects to be observed.

Conclusion

Neural correlates of familiarity and recollection for faces differ from those typically reported using verbal material. In Experiments 1 and 2, familiarity was associated with posterior old/new effects and recollection was associated with topographically dissociable anterior effects. Given that the posterior familiarity and anterior recollection effects are not predicted by previous studies using mainly verbal material, Experiment 3 was devised to test whether the particular experimental paradigm employed is the cause of the unorthodox old/new effects that have been observed. Alternatively, by comparing face and name recognition directly, Experiment 3 might discover that characteristics of the facial stimulus set employed lead to the pattern of old/new effects observed in Experiments 1 and 2.

Chapter 7 – ERP 3: Face versus Name Recognition

Introduction

Episodic memory is amongst the highest human cognitive functions, and allows one's past to be re-experienced in the present (Tulving, 1983). The hallmark of episodic memory is recollection, a retrieval process that allows information about personally experienced events to be reinstated in consciousness. In everyday life, recollection can occur spontaneously; for example, when the smell of baking bread brings a childhood visit to a bakery back to mind. In the laboratory, however, recollection is typically described as a relatively slow, effortful process; for example, when you recognize a stimulus as having been studied this may then bring back to mind the colour that it was studied in. Regardless of the exact characterization of recollection as spontaneous or effortful, one fundamental assumption is common to all current memory models: a single recollection process supports episodic memory. In the present article we challenge this assumption on the basis of electrophysiological data that reveal dissociable neural correlates of recollection.

Although recollection lies at the heart of episodic memory, it is not the only basis for making episodic memory judgments. Dual process models of recognition memory (e.g., Atkinson & Juola, 1974; Jacoby & Dallas, 1981; Mandler, 1980; Yonelinas, 1994) describe a second route to episodic retrieval: familiarity is a fastacting, relatively automatic process that provides a conscious feeling of 'oldness'. A wide range of evidence supports the dual process distinction, suggesting that recollection and familiarity operate independently (see Yonelinas, 2002, for a review). For example, task dissociations demonstrate that recollection alone

supports source memory judgments - where specific contextual details must be retrieved. Similarly, recollection and familiarity also elicit distinct phenomenological experiences, which are exploited by the remember/know procedure (Tulving, 1985). By definition, *remember* responses occur when recognition is accompanied by memory for specific details about the study episode (made on the basis of recollection), whereas *know* responses reflect recognition without the retrieval of specific details (made on the basis of familiarity). Perhaps most importantly in the current context, all dual process theories assume that recollection is material independent (i.e., the same process is engaged regardless of the information to be remembered).

One of the strongest bases for dual process models is evidence from eventrelated potentials (ERPs). ERPs are an electrophysiological method that can be used to provide a record of the neural activity evoked during performance of a cognitive task. ERP studies of episodic recognition memory reveal differences in activity between correctly identified old and new stimuli; referred to as ERP old/new effects (see Friedman & Johnson Jr., 2000; Rugg & Curran, 2007 for reviews). In particular, an early (300 – 500ms post stimulus onset) modulation maximal over mid frontal scalp electrodes is associated with familiarity, while a later (500 – 700ms) modulation maximal over left parietal scalp is widely accepted as the neural correlate of recollection. The mid frontal and left parietal old/new effects have been functionally dissociated by a number of task (e.g., Rugg et al., 1998) and stimulus (e.g., Greve et al., 2007) manipulations, providing strong evidence that the effects reflect distinct cognitive processes. The majority of ERP findings to date have been interpreted within a dual process framework. In this light, a wide range of evidence suggests that the left parietal effect provides a material independent index of

recollection – primarily because equivalent ERP effects have been observed for a variety of different stimulus materials (e.g., words – Donaldson & Rugg, 1998; line drawings – Curran & Cleary, 2003; landscape/object compound stimuli – Tsivilis et al., 2001) and for information that changed format between study and test (Schloerscheidt & Rugg, 2004).

Somewhat controversially, in a recent study (MacKenzie & Donaldson, 2007; see Donaldson & Curran, 2007) we reported that recollection for faces was associated with an anteriorly distributed old/new effect, maximal around 400 – 600ms post-stimulus onset. In this experiment participants studied a series of photographs of faces, each presented with an auditory name. At test, old and new faces were presented, and participants made an initial old/new decision, and for faces judged old, were asked to report any contextual information about the study episode that they could recollect. ERPs associated with recollection and familiarity conditions revealed a posterior old/new effect (replicating the findings of Yovel & Paller, 2004). More important for present purposes, ERPs associated with recollection elicited an anterior old/new effect that was larger when recognition was accompanied by retrieval of the associated name compared to when other specific contextual information was retrieved. Although a recollection related anterior old/new effect had not been discussed previously, a comparable neural correlate of recollection appears to be present in previous experiments using non-verbal stimuli (e.g., see Duarte et al., 2004, Fig. 8; Paller et al., 2000, Fig. 4; Yovel & Paller, 2004, Fig. 2), providing support for the idea that under certain circumstances recollection may be material specific.

Given the weight of evidence that the left parietal old/new effect provides a generic index of recollection (Wilding, 2000; Johnson et al., in press), the claim that recollection is associated with material specific neural correlates cannot be accepted easily. For example, it is possible that the specific procedures (stimuli or response options) employed by MacKenzie and Donaldson (2007) could have been responsible for their atypical pattern of effects. In addition, a study by Curran and Hancock (2007) using a very similar paradigm (with pictures of faces paired with visually presented occupations) reported finding the traditional parietal old/new effect for recollection. In this study, however, the report of a parietal effect for recollection was based on an analysis restricted to posterior electrodes (on a priori grounds). Close examination of the data presented by Curran and Hancock suggests that the distribution of the recollection old/new effect has an anterior maximum, and a fuller analysis of the data would therefore have led to a quite different characterization of the old/new effect. By our reading, therefore, the anteriorly distributed old/new effect associated with recollection reported by MacKenzie and Donaldson (2007) is unlikely to be an artefact of the specific stimuli or procedures employed. Thus, one reason for the present study was to replicate the anterior recollection effect, using a similar paradigm, but explicitly comparing recollection cued by different materials.

In the present experiment participants studied a series of compound visual stimuli, each consisting of a face-name pair. Later, at test, a single element from each pair was presented, randomly intermixed with unstudied faces and names. Importantly, each study episode was only ever probed once, with either the face or the name being presented as a retrieval cue. Participants were required to make an old/new discrimination for each test item, and made secondary remember/familiar

decisions for each item that they decided was old. These response options support inferences about the relative contributions of recollection and familiarity to test performance, and allow the identification of trials where recognition was supported by recollection.

This study addresses the question of whether recollection-related ERP old/new effects are material dependent. By holding the encoding episodes constant across face and name test trials, this paradigm rules out differences at encoding as a potential confound. If equivalent neural correlates of recollection are observed for faces and names, then the pervasive view that recollection is a material independent process will be supported. In contrast, if dissociable neural correlates of recollection are observed for faces and names, then the view that recollection is material specific will be supported, and dual process models will have to accommodate this finding.

Method

26 participants (11 female) with a mean age of 20 years (range: 18-28) took part in the study. Data from 2 participants were discarded due to contamination with ocular artefacts. Of the remaining sample, 20 participants contributed enough trials for ERPs to be formed for *remember* responses to correctly recognized faces and names, and therefore data from these 20 participants are presented here.

Faces and names were shown together visually. Names were presented in 18 point bold Courier New font: during the study phase, names were presented immediately below the faces, while during the test phase, names were presented in the centre of the display, subtending a vertical angle of 0.7° and a maximum horizontal angle of 3.9°. Data were acquired during 18 study-test blocks. Each block

contained 12 unique face-name pairings presented at study, and was followed by 6 of the faces and 6 of the names intermixed with 6 new stimuli (3 faces and 3 names) at test. At study, compound face-name stimuli were shown for 2000ms. At test, face or name stimuli were displayed for 500ms. After stimulus offset, participants indicated whether they thought the face was 'old' or 'new'. If a 'new' response was made, the trial terminated. If an 'old' response was made, two response prompts were displayed: *remember* and *familiar*. Participants were asked to respond *familiar* if a face was simply recognized, and to respond *remember* if a face was recognized and contextual information from the study episode was retrieved.

The response options allowed trials where recognition was supported by recollection for both cue types to be sorted for averaging EEG into ERPs. Recollection was inferred on trials where participants made a *remember* response to a studied stimulus, which requires the participant to reinstate aspects of the study episode and should therefore be supported by recollection.

Grand-average ERPs were formed for 4 conditions: face *remember*, face correct rejection, name *remember* and name correct rejection. The average number of trials in these conditions was 45, 32, 51 and 43, respectively. The recollection old/new effects were first characterized for the face and name conditions separately, and then topographic comparisons were made between the conditions.

ERP 3

Behavioural Results

Performance

Mean probabilities for hits and false alarms are plotted for faces and names in Figure 30. There is little difference in the hit rate across cue types, but there is a greater probability of false alarms for faces than for names.



Figure 30: Performance.

The probability data were submitted to ANOVA with factors of cue type (face/name) and status (hit/false alarm), which revealed main effects of cue type [F(1,19) = 26.7; p < 0.001] and status [F(1,19) = 826.4; P < 0.001], along with an interaction between the factors [F(1,19) = 31.4; p < 0.001], reflecting a greater difference in the probability of hits and false alarms for names than for faces. Paired-samples t-tests found a difference in the false alarm rate across cue types [t(19) = 6.5; p < 0.001] but no difference in the hit rate.

Mean probabilities of making 'old' responses are plotted for studied (Hit) and unstudied (False Alarm) test items. Error bars show the standard error of the mean. The hit rate was equivalent across conditions, while there was a greater probability of false alarms for face trials than for name trials.

One interpretation of the elevated false alarm rate is that there were more guesses for faces than for names. To correct for the contribution of guessing to performance, sensitivity was computed by subtracting the probability of false alarms from the probability for hits. Figure 31 shows sensitivity plotted for each cue type. There is greater sensitivity to discriminate old items from new items when the cue is a name than when the cue is a face. This observation was found to be reliable by submitting the sensitivity data to a paired-sample t-test, which found a significant difference between the two cue types [t(19) = 5.6; p < 0.001].





Mean sensitivity (Pr, Snodgrass and Corwin, 1988) is plotted for face and name test items. Error bars show the standard error of the mean. The ability to discriminate studied stimuli from unstudied stimuli was greater for names than for faces.

Response bias was computed by dividing the probability of false alarms by the complement of sensitivity (Snodgrass & Corwin, 1988), i.e. Br = pFA/(1 - Pr). Figure 32 shows a more liberal bias for faces than for names, implying that faces are more likely to be endorsed as 'old' when participants are uncertain how to respond. This observation was confirmed to be reliable by submitting data to a paired-sample t-test, which found a significant difference in response bias between the two cue types [t(19) = 9.0; p < 0.001].







Response times for correct and incorrect responses to old and new items for the two different cue types are plotted in Figure 33. As can be seen, correct responses (i.e., hits and correct rejections) to faces are faster than correct responses to names, while incorrect responses (i.e., false alarms and misses) to faces are slower than incorrect responses to names. The response time data were submitted to ANOVA with factors of cue type (face/name) and response (hit/correct rejection/miss/false alarm). The analysis revealed an interaction between cue type and response [F(1.8,30.6) = 4.9; p < 0.05], reflecting faster response times for correct face responses and slower response times for incorrect face responses. Paired-samples t-tests comparing the two different cue types found significant differences for hits [t(19) = 3.7; p = 0.001] and for misses [t(19) = 4.2; p < 0.001] but not for correct rejections or for false alarms.





When participants recognized a stimulus, they made a *remember/familiar* endorsement to indicate whether they recollected information from the study episode (*remember*), or whether recognition was supported by an assessment of stimulus familiarity alone (*familiar*). The probability of *remember* and *familiar* responses for hits are plotted below (see Figure 34). Names are more likely than faces to be given a *remember* response, while faces are more likely than names to be given a *familiar* response.

The data were submitted to ANOVA with factors of cue type (face/name) and response (*remember/familiar*); the analysis revealed a main effect of response [F(1,19) = 24.9; p < 0.001], reflecting a greater probability of *remember* responses

overall, along with an interaction between the factors [F(1,19) = 9.7; p < 0.01]reflecting more *remember* responses in name recognition than in face recognition, and more *familiar* responses in face recognition than in name recognition. Pairedsamples t-tests found significant differences for all pair-wise comparisons: *remember* responses for faces and names [t(19) = 2.3; p < 0.05]; *familiar* responses for faces and names [t(19) = 3.4; p < 0.01]; *remember* and *familiar* responses for faces [t(19) = 2.8; p < 0.05]; and, *remember* and *familiar* responses for names [t(19) = 6.5; p < 0.001]. In as much as *remember* and *familiar* responses reflect contributions from recollection and familiarity⁵, respectively, this pattern of results indicates that both face and name recognition receive greater input from recollection than familiarity, and that there is a greater contribution of recollection to name recognition than to face recognition, as well as a greater contribution of familiarity to face recognition than to name recognition.

ERP Results

Grand-average waveforms were formed for *remember* responses to correctly recognized faces and names. Waveforms were first quantified into two *a priori* latency periods where episodic retrieval related effects have been observed previously: 300 - 500ms and 500 - 700ms post-stimulus. To assess whether apparent differences in the old/new effects for faces and names result from variations in timing across conditions, two further latency periods were analysed: 100 - 300ms and 700 - 900ms.

⁵ For two reasons, we have not used the independence remember/know (IRK) procedure to rescale the contribution of familiarity to recognition performance. Firstly, because an analogous procedure cannot be performed on the ERP data. Secondly, because the IRK procedure does not change the estimate of the contribution of recollection to recognition performance – which is the primary focus of this paper.



Figure 34: Remember and familiar responses. Mean probabilities of remember and familiar responses are plotted for correctly recognized face and name test items. Error bars show the standard error of the mean. A double dissociation is evident: there are more remember responses for names than for faces, whereas there are more familiar responses for faces than for names.

Face Cues

Figure 35 (top) shows ERPs for face *remember* and face correct rejections at representative sites from across the scalp. As can be seen, the old waveform becomes more positive-going than the new waveform from around 400ms post-stimulus. The old/new divergence persists until roughly 700ms, and appears to be greatest at frontal electrodes.

The analysis of data from 100 - 300ms and from 300 - 500ms failed to reveal any significant differences; however, the analysis of data from 500 - 700ms revealed a main effect of old/new [F(1,19) = 22.8; p < 0.001] and a marginally significant interaction between old/new, location and hemisphere [F(1,19) = 3.9; p = 0.06], reflecting a bigger effect on the right hemisphere at the frontal location. Examination of the data found that the effect is maximal at F2 [t(19) = 4.4; p < 0.001]. Finally, the analysis of data from 700 - 900ms failed to reveal any significant differences. This pattern of results demonstrates that face recollection is associated with an anterior old/new effect (500 - 700ms).

Name cues

Figure 35 (bottom) shows waveforms for correctly recognized old names given *remember* responses with correct rejections for names at representative sites from across the scalp. The old waveform is more positive-going from around 300 – 700ms post-stimulus onset. The difference between waveforms appears to be biggest at the left parietal electrode.

The analysis of data from 100 - 300ms revealed a main effect of old/new [F(1,19) = 4.5; p < 0.05], and examination of the data revealed that the effect is maximal at FC1 [t(19) = 2.4; p < 0.05]. The analysis of data from 300 - 500ms revealed a main effect of old/new [F(1,19) = 10.2; p = 0.05] and interactions between old/new and hemisphere [F(1,19) = 9.7; p < 0.01], old/new, location and site [F(1.4,25.9) = 7.5; p < 0.01] and between old/new, location, hemisphere and site [F(1.7,32.8) = 11.3; p < 0.001]. The effect is bigger on the left hemisphere than on the right. Subsidiary analyses revealed a main effect of old/new [F(1,19) = 9.4; p < 0.01] at the frontal location, along with an interaction between old/new and site [F(1.4,26.2) = 7.6; p < 0.01], reflecting a bigger effect at superior sites. The analysis of parietal sites revealed a main effect of old/new [F(1,19) = 5.8; p < 0.05], and interactions between old/new and hemisphere [F(1,19) = 26.3; p < 0.001] and between old/new, hemisphere and site [F(1.2,22.2) = 7.1; p < 0.05]. The effect is only present on the left hemisphere, where it is bigger at inferior sites. Examination

Face **P**3 Name P3 10 10 μv μv Old 500 -5 300 500 -5 New ms

of the data found that the effect is maximal at FC1 [t(19) = 4.2; p = 0.001], suggesting that name recollection is associated with a mid frontal old/new effect.

Figure 35: Remember old/new effects for face and name cues. Grand average ERP waveforms are shown for face and name conditions at representative frontal and parietal electrodes. ERPs are shown for recollection responses (old) plotted along with correct rejections (new). The depicted epoch begins 100ms pre-stimulus onset and ends 900ms post-stimulus onset. Scale bars indicate the magnitude of activity (in microvolts) and the time course of activity (in milliseconds). The top of the figure shows the old/new effect for faces: the old waveform is more positive-going than the new waveform from roughly 400 – 700ms post-stimulus onset, and the difference between waveforms is greatest at the frontal location. The bottom of the figure shows the old/new effect for names: the old waveform is more positive-going than the new waveform from roughly 300 – 700ms post-stimulus onset, and the difference between waveform from roughly 300 – 700ms post-stimulus onset, and the difference between waveform from roughly 300 – 700ms

The analysis of data from 500 - 700ms revealed a main effect of old/new [F(1,19) = 22.6; p < 0.001] and interactions between old/new, location and hemisphere [F(1,19) = 8.3; p < 0.01] and between old/new, location, hemisphere and site [F(1.6,29.7) = 8.2; p < 0.01]. Subsidiary analyses revealed a main effect of old/new [F(1,19) = 6.5; p < 0.05] at the frontal location and a main effect of old/new

[F(1,19) = 27.0; p < 0.001] and an interaction between old/new and hemisphere [F(1,19) = 9.9; p = 0.005] at the parietal location, reflecting a bigger effect on the left hemisphere. Examination of the data found that the effect is maximal at P3 [t(19) = 6.6; p < 0.001], suggesting that name recollection is associated with a left parietal old/new effect.

The analysis of data from 700 – 900ms revealed a main effect of old/new [F(1,19) = 5.6; p < 0.05] and interactions between old/new and site [F(1.1,21.4) = 6.1; p < 0.05] and between old/new, location and site [F(1.1,21.8) = 6.4; p < 0.05]. These interactions reflect a new > old negativity that is reliable at the parietal location but not at the frontal location; this negativity is bigger at superior sites than at inferior sites. Examination of the data revealed that the effect is maximal at PZ [t(19) = 4.7; p < 0.001].

This pattern of results suggests that name recollection is associated with a mid frontal effect (maximal from 300 - 500ms) along with a left parietal effect (maximal from 500 - 700ms). From 700 - 900ms, old > new effects can no longer be observed, while a late posterior negativity (LPN) is present over parietal electrodes.

Topographic analysis

Figure 36 shows the distributions of the face recollection and name recollection effects. There appears to be little activity associated with face recollection until 500ms post-stimulus; in contrast, a mid frontal effect and the early onset of a left parietal effect appear to be present in the name recollection condition from 300 – 500ms. From 500 – 700ms, a clear difference in distribution is evident,

with face recollection being associated with an anterior effect and name recollection being associated with a left parietal effect. Finally, the topography of the face effect appears to shift from a superior frontal distribution (500 - 700 ms) to an inferior frontal distribution (700 - 900 ms).

Face



Figure 36: Topography of face and name remember old/new effects. Each cartoon shows the difference between old and new waveforms averaged across a 200ms latency period; four consecutive latency periods from 100 - 900ms post-stimulus onset are shown. The scale bar indicates the range of activity (in microvolts). For faces, the effect present from 300 - 700ms has an anterior focus, whereas for names, the effect is associated with mid frontal (300 - 500ms) and left parietal (500 - 700ms) distributions.

Topographic analyses of rescaled difference waveforms were performed to assess several questions. The first analysis was performed to see if the effects present from 500 – 700ms for faces and for names have the same distribution; a difference in distribution would provide evidence that different cognitive operations are engaged between the two conditions. Data were submitted to ANOVA with

factors of cue type (face/name), location (frontal/parietal), hemisphere (left/right) and site (superior/medial/inferior). The analysis revealed an interaction between condition, location, hemisphere and site [F(1.7,33.1) = 7.5; p < 0.01], reflecting a face recollection effect that is bigger on the right hemisphere at superior, frontal sites, compared to a name recollection effect that is bigger on the left hemisphere at medial, parietal sites. This topographic dissociation implies that different neural generators are active for face recollection and name recollection, consistent with the view that different cognitive operations are engaged when the two cue types are recollected.

A second analysis was performed to assess whether the distribution of the face recollection effect (500 – 700ms) differs from the distribution of the name recollection effect present in the early latency period (300 – 500ms). Although these two effects were present in different latency periods, both were maximal at anterior sites and so it is conceivable that the face recollection effect represents a delayed manifestation of the early mid frontal effect seen for names. The analysis was restricted to data from the frontal location, with ANOVA being performed with factors of condition (face 500 – 700ms/name 300 – 500ms), hemisphere (left/right) and site (superior/medial/inferior). The analysis revealed an interaction between condition and site [F(1,19) = 4.9; p < 0.05]. The face recollection effect is bigger on the right hemisphere while the name recollection effect is bigger on the left hemisphere. This topographic dissociation between the mid frontal effect for names (300 – 500ms) and the anterior effect for faces (500 – 700ms) suggests that the anterior effect observed for faces cannot simply be explained as a delayed manifestation of the mid frontal effect observed for names.

A third analysis was performed to assess whether the anterior effect for faces (500 - 700 ms) differs from the late right frontal effect that emerges during the next latency period (700 - 900 ms). The analysis was restricted to data from the frontal location, with ANOVA being performed with factors of latency (500 - 700 ms/700 - 900 ms), hemisphere (left/right) and site (superior/medial/inferior). The analysis revealed an interaction between latency and site [F(1.1,20.3) = 6.7; p < 0.05] reflecting a superior distribution from 500 – 700 ms which differs from the inferior distribution of the effect observed from 700 – 900 ms. This pattern of results suggests that the anterior effect observed for faces cannot simply be explained as the late right frontal effect.

Summary

Statistical analyses identified qualitative differences between the old/new effects associated with recollection elicited by face and name retrieval cues. Face recollection was associated with an anterior effect (500 - 700ms) whereas name recollection was associated with mid frontal (300 - 500ms) and left-parietal effects (500 - 700ms). Topographic analyses demonstrate a difference in the pattern of neural generators responsible for the face recollection effect (500 - 700ms) when compared to the mid frontal (300 - 500ms) and left parietal (500 - 700ms) effects observed for name recollection, and when compared to the late right frontal (700 - 900ms) effect seen for faces. Overall, this pattern of results demonstrates that face recollection and name recollection are associated with different cognitive operations.

Discussion

Here we present dissociable neural correlates of recollection for faces and names, observed in a paradigm designed to keep encoding conditions constant across cue types. During the critical 500 – 700ms latency period, recollection for faces was associated with an anterior old/new effect, whereas recollection for names was associated with a left parietal old/new effect. The old/new effects observed for faces and names were topographically dissociable, providing strong evidence for the involvement of different cognitive operations when faces and names are recollected. This finding is important because it suggests that the ERP old/new effect is material specific, a proposition that has long been considered (Schloerscheidt & Rugg, 1997) but never convincingly demonstrated. At their strongest, the data suggest that recollection for faces and names elicit different recollection processes. Below, we discuss potential confounds in our study, and also consider the veracity of existing claims that faces do in fact give rise to the typical pattern of old/new effects. We then discuss how best to conceive of differences in recollection processing, considering whether the left parietal effect plus an additional process is engaged for faces, or whether separate recollection processes exist for faces and words.

First, however, we highlight the striking nature of the topographic dissociation seen here for faces and words. Given the nature of our paradigm, and based on participants' behavioural performance, we are confident that the stimuli were recollected. Our behavioural data provide equivalent estimates of the involvement of recollection across conditions, but behavioural data are essentially mute with regard to the underlying processes supporting remember judgments for faces and names. By contrast, the ERP data shown in Figure 36 reveal quite distinct

patterns of neural activity across conditions. Evidently, the anterior distribution of the face recollection effect replicates the findings observed for face recognition associated with the retrieval of names and other specific information by MacKenzie and Donaldson (2007). As noted in the introduction, we believe that this anterior effect can be observed in previous studies, but has largely been ignored; the current data strongly suggest that it is real.

An important aspect of our study was the direct comparison of faces and names. Despite using equivalent definitions of recollection, and common encoding episodes, names elicited a different neural response to faces. As would be expected on the basis of previous findings, recollection for names was associated with a left parietal old/new effect (500 – 700ms). In addition, an earlier mid frontal effect (300 – 500ms) was also observed; this effect is believed to reflect familiarity (Rugg et al., 1998; Curran, 2000; Curran & Cleary, 2003; Azimian-Faridani & Wilding, 2006) although conceptual priming (Yovel & Paller, 2004) and novelty detection (Tsivilis et al., 2001) have also been proposed. Although the pattern of ERP effects seen for names is typical of what has been reported in the literature, our findings appear to challenge the wide consensus that the left parietal effect provides a generic index of recollection (Wilding & Rugg, 1996; Allan et al., 1998; Donaldson & Rugg, 1998; Johansson et al., 2004; Johnson et al., in press) and it is in the context of this dominant view that the data presented here will be discussed.

The role of familiarity in recollection

Given the potential implication of our data for how recollection is conceptualized, possible confounds must be considered. Perhaps the most obvious issue is the differential false alarm rate that was evident across conditions. We

carefully matched the paradigm employed for faces and names to rule out procedural differences as a confound. Unfortunately, this design feature led in turn to a greater probability that new items would be wrongly endorsed as 'old' for faces than for names. The elevated false alarm rate observed for faces leads to poorer sensitivity (i.e., discrimination between old and new items); a more liberal response bias; and a greater contribution of familiarity to recognition performance. In theory, any of these features could account for differences in processing for faces and names, and we therefore consider each issue in turn.

First, we view poorer sensitivity as an unlikely source of qualitatively distinct neural correlates of recollection. The recollection ERPs presented here were, of course, formed exclusively from items that were correctly discriminated and had received *remember* responses – regardless of overall differences in discriminability. Even so, for any given retrieval process operating within the normal bounds of performance⁶, we would expect a change in discriminability to produce quantitative rather than qualitative changes in the engagement of that retrieval process; this is not what we found. Nonetheless, it might be argued that any direct comparison across conditions *requires* matched performance, to rule out the possibility that different strategies are being engaged across conditions (which would give rise to qualitative changes in the ERP record). Whilst logically reasonable, this formulation ignores the opposite problem; if we had matched performance across tasks this would have required us to manipulate some other feature of the experiment (e.g., list length, stimulus duration, study task, etc), and this itself would have become a confound. Moreover, matching performance in this

⁶ Here we only consider changes in mid-range performance. Changes at the very bottom or top of the range may indeed elicit qualitative changes in processing, for example, when memory is so poor that participants employ different strategies. For a variety of reasons, however, such floor or ceiling effects should be avoided when examining memory and we do not consider these scenarios further.

way cannot guarantee that differences in strategy will be avoided – participants could still achieve equivalent performance using different strategies. Future studies need to examine the impact of equating discriminability on the comparison of neural correlates of face and name recollection. However, we examined ERPs for highand low-discriminability groups and failed to observe any qualitative change in the distribution of the face recollection effects. Taken together, it seems unlikely that the differential false alarm rate for faces and names in the present study could satisfactorily account for qualitative differences in recollection.

Second, a more liberal response bias is unlikely to influence the recollection old/new effect because response bias operates through familiarity rather than recollection (Yonelinas, 2002). Although response bias has been linked with changes in the amplitude of ERPs at frontal sites, it is the mid frontal effect that has been modulated (Windmann et al., 2002; Azimian-Faridani & Wilding, 2006), or bias related changes have been restricted to ERPs for new items only (Johansson et al., 2004). Furthermore, whilst the impact of response bias cannot be entirely ignored, we again stress that recollection waveforms were based solely on correctly discriminated items, reducing the impact of bias (see Greve et al., 2007, for further discussion of this issue). In short, in the present study frontally distributed effects observed for faces were topographically dissociable from the mid frontal effect seen for names, and it is unlikely that differences in response bias alone could account for the topographic dissociation between the face and name recollection effects.

Of greater concern in interpreting the data is the relatively greater contribution of familiarity to recognition performance for faces than for names. The averaging of ERPs based on *remember* decisions may have failed to exclusively

ERP 3

isolate recollection because familiarity is likely to have contributed to at least some of the *remember* trials. If it is assumed that the mid frontal effect reflects familiarity, then the observation of a mid frontal effect for name recollection during the 300 – 500ms latency period suggests that familiarity was engaged for the *remember* trials. Given that there was a greater contribution of familiarity to face recognition than to name recognition then it is likely that the old/new effect seen for face recollection may also receive a contribution from familiarity and naïvely this could account for the anterior face effect. However, the mid frontal effect was both topographically and temporally dissociable from the anterior old/new effect seen for face recollection; this finding minimizes the possibility that the putative recollection effect seen for faces is simply a reflection of the neural correlate of familiarity typically observed for words (see MacKenzie & Donaldson, 2007).

Despite the foregoing discussion of the potential role of familiarity, we were unable to examine the neural correlates of familiarity-based responses here. The present study focused on recollection, and the behavioural paradigm was therefore designed to elicit enough recollection trials for ERPs to be formed – at the expense of examining familiarity. However, in our previous study (MacKenzie & Donaldson, 2007, see also Yovel & Paller, 2004) we demonstrated that the neural correlates of familiarity and recollection for faces temporally overlap, with both signals being manifest from 300 – 700ms. Critically, the recollection and familiarity effects were topographically dissociable. Familiarity based responses were associated with posterior ERP old/new effects; recollection based responses were associated with posterior activity and additional anterior effects. The present findings show a similar pattern for recollection; although the effect was maximal over anterior electrodes, significant old/new differences were also present across

posterior sites. Based on previous findings, we interpret the posterior activity as a manifestation of the contribution of familiarity to recollection based responses. As we discuss below, this aspect of the data leaves open a disarming alternative – 'the left parietal plus' view. First, however, we consider evidence that faces elicit the standard ERP old/new effect.

Previous reports of standard old/new effects for faces

One problem with asserting that the neural correlate of recollection for faces differs from the neural correlate observed for names is that the literature contains several reports of the typical old/new effects for faces. In fact, when viewed critically, we are unaware of any unambiguous demonstrations of a left parietal old/new effect for faces. Parietal old/new effects have certainly been reported for faces (Münte et al., 1997; Johansson et al., 2004; Curran & Hancock, 2007), but these effects were not left-lateralized in any case. The absence of a hemispheric asymmetry could, of course, reflect a lack of statistical power; alternatively, it could genuinely reflect the engagement of different neural generators to those associated with the left parietal effect. We believe that a clear demonstration of the left parietal old/new effect in the context of recognition memory for faces would be significant. Here we highlight the difficulty in characterising the neural correlates of face recognition in several recent studies.

In a study using faces with positive, neutral and negative expressions, Johansson et al. (2004) observed a parietal old/new effect for negative faces. Using corroborative evidence from a control experiment showing that negative faces were more likely to be 'Remembered' than 'Known', the authors argued that their parietal activity reflected recollection. Whilst plausible in principle, this claim is weakened

by the fact that neutral faces were also more likely to be 'Remembered' than 'Known', yet they did not elicit any parietal activity. Thus, given recent demonstrations that familiarity for faces is associated with activity over posterior scalp electrodes (Yovel & Paller, 2004; Mackenzie & Donaldson, 2007) it remains possible that the parietal effects observed by Johansson et al. (2004) actually reflected familiarity rather than recollection.

An analogous problem exists in interpreting the report of frontally distributed old/new effects by Nessler et al. (2005). In this case, frontal effects found in a continuous recognition paradigm using faces were interpreted as reflecting the traditional mid frontal familiarity effect. This interpretation was not, however, supported by any direct stimulus or response manipulations designed to isolate familiarity-based responding; rather, it relied on visual comparison with effects reported in the wider literature at that time. Given the present demonstration of frontally distributed neural correlates of recollection for faces, it may be that the frontal effects observed by Nessler et al. reflected recollection rather than familiarity. Clearly, data from studies using faces as stimuli should be interpreted more cautiously than was once the case.

It is inherently difficult to identify any individual ERP component (see Luck, 2005), and isolating the posterior activity as the left parietal effect (or not) is far from trivial in practice. Nonetheless, given the growing evidence that faces do indeed elicit different patterns of activity for familiarity and recollection than have traditionally been reported, some caution is needed. For example, Curran and Hancock (2007) used faces in a recognition memory paradigm, and reported a left parietal effect for recollection. As discussed in the introduction, however, the

distribution of the recollection effect appeared to have a frontal maximum (see Curran & Hancock, 2007, Fig. 4). Had data from frontal electrodes been examined in their recollection condition, a different conclusion may well have been drawn. In light of current findings, therefore, it seems imperative that both frontal and parietal sites are routinely analyzed when attempting to characterize recollection related old/new effects for faces.

Material specific recollection processing for faces and names?

The presence of a qualitative difference in the ERP correlates of recollection for faces and names generates two competing interpretations. Our preferred account, the "material specific recollection" view, states that faces and names engage two different recollection processes *per se*. The alternative "left parietal plus" view holds that one common recollection process operates in all cases, but additional material specific processes can also be engaged in some circumstances. We consider each of these views in turn.

Can our data be reconciled with the traditional view of a single recollection process, indexed by the left parietal old/new effect? By the 'left parietal plus' view, our data can be reinterpreted as providing evidence that the left parietal effect is observed for name recollection, whereas for face recollection an anterior effect is observed, but this sits on top of a (weaker) left parietal effect. According to this view, previous reports of posterior activity during recollection of faces, whilst not asymmetrically larger over left than right hemisphere, would nonetheless be viewed as reflecting the left parietal effect. And, as a result, the apparent anterior focus of the face effects reflects some form of additional processing elicited by the use of faces, rather than reflecting a material specific recollection process *per se*. Further

studies will be required to determine whether the left parietal plus view is tenable; of particular importance will be studies that demonstrate further functional differences between ERP effects, or model the underlying sources of activity.

The alternative view is that there are two material specific recollection processes that are selectively engaged depending on the type of information being recollected. By this view, the left parietal effect reflects one form of recollection and the anterior effect reflects another, which raises the question of what function these material specific processes perform? One possibility is that the contexts to be recollected differ for faces and names: given common encoding episodes across cue types, when a face is presented as an item to be recollected the context consists of a name and a rating judgment, whereas when a name serves as the item the context consists of a face and a judgment. While this suggestion is highly speculative, it provides a ready interpretation of the qualitatively different neural correlates of recollection presented here. If true, this finding challenges traditional dual-process accounts of recognition memory; to our knowledge no dual-process model predicts dissociable forms of recollection. However, recently some material specific neural correlates of recollection have been observed for words studied in two different contexts (Johnson et al, in press). In sum, dual-process models may need to be fractionated further if they are to account for both behavioural and neural data.

Of course, quite what is meant by the term 'recollection process' is not usually well delineated. In recognition memory tests, recollection is typically thought to involve a chain of events beginning with the perception of a stimulus cue, which activates representations in the brain, which in turn reactivate representations of information associated with the encoding context, leading to the

phenomenological experience of recollection. The ERP correlates reported during recognition memory tests could in principle reflect changes that occur at any or all of these stages of processing. Thus, a clear challenge for future studies is to more effectively isolate the specific stage of processing that is reflected in the ERPs, decomposing recollection into its constituent parts.

Finally, we note the importance of asking whether the dissociation presented here is inherent to names versus faces, or whether it is simply a manifestation of wider categories of stimuli that engage distinct recollection processes. Whilst the range of stimuli employed in ERP studies is not particularly broad, one possibility is that the left parietal effect reflects the retrieval of verbally-mediated material and that, by contrast, the anterior effect reflects the retrieval of pictorially-mediated material. Consistent with this view is the observation that line drawings of simple objects were associated with a left parietal effect (Curran & Cleary, 2003), whereas photographic images of objects gave rise to a left parietal effect and an additional anterior effect (Duarte et al., 2004). Of course, this proposition must await further empirical evidence demonstrating the systematic manipulation of these two recollection effects.

Conclusion

Face and name recognition were compared and neural correlates of recollection were identified. Face recollection was associated with an anterior effect while name recollection was associated with temporally and topographically dissociable mid frontal and left parietal effects. These findings suggest that neural correlates of recollection elicited by faces and names are qualitatively distinct, demonstrating that dissociable cognitive operations support recollection for faces and names. Whether this turns out to reflect the operation of material specific recollection processes *per se*, or a core recollection process that is supported by an additional recollection processes, remains to be seen. Either way, these novel data are consistent with the view that recollection is material specific in some sense: recollection selectively engages cognitive operations depending on the type of information that is presented as a retrieval cue. Current dual process theories cannot account for this material specific nature of recollection.

Chapter 8 – ERP 4: Famous Face Recognition

Introduction

Are the cognitive processes that support recognition of the face of someone you know the same as the processes that support recognition of a face that you have only seen once before? In theory, recognition of a known face should be supported by the semantic memory system, while recognition of a face that has only been encountered once before should be supported by the episodic memory system (Tulving, 2002). However, recent research suggests that the semantic and episodic memory systems have an interactive relationship, for example with the organisation of semantic memory influencing the likelihood of episodic retrieval (Greve at al., 2007). With the interactive nature of the semantic and episodic memory systems in mind, it seems plausible that episodic memory could support recognition of known faces. In concrete terms, it may be the case that when a known face is recognized, previous episodes involving the person are accessed in order to retrieve information associated with them.

Declarative memory consists of two separate systems: episodic memory and semantic memory (Tulving, 1972). Episodic memories are anchored around a particular event in the past, while semantic memories are devoid of such personal and temporal detail. Episodic memories involve the reinstatement of a past event, whereas semantic memories are experienced as information that is simply known, and importantly, the context in which knowledge was acquired is not retrieved.

The first two experiments described in this thesis established qualitatively distinct anterior and posterior old/new effects in association with recollection and

familiarity, respectively. Experiment 3 further demonstrated that the anterior recollection effect is observed for face recollection but not for name recollection. There are many differences between faces and names that might explain why different neural correlates of recollection were observed in Experiment 3; for example, the two stimulus types differ in physical characteristics including pictorial richness, size and colour. Such physical differences are, however, most likely to influence the early P1 and N2 ERP deflections, which relate to perceptual processing, rather than modulation of waveforms at longer durations after stimulus onset (e.g., 300 – 700ms). There are other differences between the two classes of stimulus that are more likely to be responsible for the qualitatively different old/new effects associated with recollection, including the degree of inter-stimulus homogeneity (Curran & Hancock, 2007), and the degree to which the stimuli are associated with semantic representations.

Names refer to discrete entities with far fewer overlapping features than faces; as such, names represent a more heterogeneous set of stimuli than faces. Curran and Hancock (2007) argued that the unorthodox pattern of old/new effects reported by Yovel and Paller (2004) for faces may result from the use of a homogeneous stimulus set which engenders poorer discriminability (i.e., distinguishing between old and new items). According to this argument, a mid frontal effect will only be observed for familiarity when discriminability is above some threshold value. While this argument remains an empirical question, it fails to explain why the neural correlate of recollection observed for faces differs from the left parietal effect typically observed when lexical stimuli are used to investigate memory. Recollection is most often modelled as a threshold process (Yonelinas, 1994), whereby information is either recollected or not. Even in cases where the

degree of inter-stimulus homogeneity leads to poor discriminability, recollection should in theory be associated with one common neural correlate if recollection is a material independent process, as described by dual-process theories (Atkinson & Juola, 1974; Jacoby & Dallas, 1981; Mandler, 1980; Yonelinas, 1994). In Experiment 3, however, qualitatively distinct neural correlates of recollection were observed for faces and names, which suggests that recollection processing differs for the two types of stimulus. If physical differences between the stimuli are ruled out as potential causes of the different neural correlates of recollection for faces and names, and the inter-stimulus homogeneity hypothesis fails to explain the differences, then one key difference remains: the presence or absence of preexisting semantic representations. Faces that are encountered for the first time in a study list in the laboratory are not associated with pre-existing representations stored in long term memory in the way that names are. Although it could be argued that semantic representations may be extracted from faces on first viewing them, the semantic representations that could be extracted from names or other lexical stimuli have already been consolidated into long term storage in semantic memory.

One motivation for the present study was to investigate whether the difference in neural correlates of recollection observed for faces and names in Experiment 3 reflects the presence/absence of pre-existing representations. Experiment 4 was designed to assess whether the anterior old/new effect associated with recollection is face-specific by establishing neural correlates of retrieval in a task using famous faces, where semantic representations are expected to be activated.

The study-test paradigm was designed to eliminate the influence of semantic memory on recognition performance. If an item has only been encountered once then both episodic and semantic representations are likely to be extracted from the item. The study-test paradigm usually uses words as stimuli, and as such semantic representations already exist for the stimuli; the paradigm requires participants to decide whether items have been encountered earlier in the context of a study list, which is an episodic task, rather than to decide whether items have ever been encountered before, which would represent a semantic retrieval task. The present experimental paradigm requires participants to decide whether faces have ever been encountered before, and if so, to indicate whether or not face recognition is accompanied by the retrieval of person-specific semantic information, such as the person's name or occupation.

Three possible outcomes are predicted. First, if the neural correlates of semantic retrieval have a different distribution from the neural correlates of retrieval observed in episodic memory tests, then it can be concluded that separate retrieval processes support the two declarative memory systems. Second, if the neural correlates of retrieval observed in Experiments 1 - 3 for faces are also observed here (i.e., an anterior effect for retrieval of specific information and a posterior effect for strength-based retrieval) then the hypothesis that there are material specific retrieval processes will be supported. Third, if the neural correlates of retrieval identified for names in Experiment 4 are observed here (i.e., mid frontal and left parietal effects), then differences in the underlying neural representation of the stimuli will be highlighted. If the neural correlates of retrieval for famous faces resemble the correlates observed for names in Experiment 3, then factors such as pictorial richness, size and colour will be unlikely to explain why qualitatively
distinct effects were observed for faces and names, leaving the role of pre-existing representations stored in long term memory as a candidate determinant of the particular retrieval processes engaged in the service of recognition memory.

Method

Twenty-eight participants performed the memory test. Twelve sets of data were discarded either due to poor behavioural performance or the contamination of EEG with artefacts, and so data from 16 participants (11 females) with a mean age of 21 years (range: 18 - 31) are presented here.

The design of the present experiment represents a departure from the previous experiments described in this thesis because the study-test paradigm was replaced by a test-only paradigm. In the test-only paradigm, a series of 200 faces (4) blocks of 50) was presented for 500ms and followed by a blank screen during which participants made one of three responses to each face: can identify, familiar, or don't recognize. Participants were instructed to make a can identify response if they recognized a face and could retrieve person-specific information about the person; a familiar response was required if a face was recognized but the participant could not retrieve any information associated with the face; finally, a don't recognize response was required in cases where a face was not recognized. Following a *can identify* response, participants were prompted to report either the name of the person whose face had been shown, or some other information associated with them, such as their occupation. Familiar and don't recognize responses terminated the trial sequence. The *can identify* and *familiar* response options are intended to provide an analogue of the Remember/Familiar procedure used in Experiments 2 and 3. A *can identify* response was required when recognition of a face was accompanied by the retrieval

of associated information, while a *familiar* response was required when face recognition was not accompanied by the retrieval of associated information; as such, these response options parallel the Remember/Familiar decision criteria.

If the contrast between the *can identify* and *don't recognize* waveforms replicates the neural correlate of recollection observed in Experiments 1 - 3 then this result would support the inference that the anterior old/new effect is a recollection component observed for faces; whereas, if the contrast reveals a difference at left parietal sites then the role of semantic representations in determining the pattern of old/new effects associated with recollection will be highlighted. If the contrast between *familiar* and *don't recognize* waveforms replicates the neural correlate of familiarity observed in Experiments 1 and 2 then this result would support the view that the posterior old/new effect reflects a familiarity component observed for faces; whereas, if the contrast reveals a difference at mid frontal sites then the role of semantic representations in determining the pattern of old/new effects associated with recollection will be be this result would support the view that the posterior old/new effect reflects a familiarity component observed for faces; whereas, if the contrast reveals a difference at mid frontal sites then the role of semantic representations in determining the pattern of old/new effects associated with familiarity will be supported.

Behavioural Results

Figure 37 shows the probabilities of each of the three response categories; as can be seen, there are fewer *familiar* responses than *can identify* or *don't recognize* responses. The data were submitted to ANOVA with a factor of response category (*can identify/familiar/don't recognize*), which revealed a main effect [F(2,30) = 3.4; p < 0.05]. Subsidiary paired-samples t-tests found a difference between the means for the *familiar* and *don't recognize* categories [t(15) = 2.6; p < 0.05], while all other comparisons were non-reliable.



Figure 37: Performance.

Mean response probabilities are plotted for the can identify, familiar and don't recognize conditions. Error bars show the standard error of the mean. Familiar responses were less likely than either of the other two responses.

Response times are plotted in Figure 38. As can be seen from the figure,

familiar responses take longer than either can identify or don't recognize responses.





Response times for all three conditions are plotted. Error bars show the standard error of the mean. Response times in the Familiar condition were slower than response times in the other two conditions.

The data were submitted to ANOVA with a factor of response category (*can identify/familiar/don't recognize*), revealing a main effect [F(2,30) = 23; p < 0.001].

ERP 4

Paired-samples t-tests revealed that the mean response time for the *familiar* category was significantly slower than both the *can identify* [familiar v. can identify: t(15) = 5.4; p < 0.001] and the *don't recognize* [familiar v. don't recognize: t(15) = 5.4; p < 0.001] categories.

ERP Results

Grand-average ERPs were formed for three conditions. The mean number of trials contributed from each participant to each condition was: *can identify* = 47; *familiar* = 37; *don't recognize* = 61. The presence of reliable ERP old/new effects will be assessed separately for the *can identify* and *familiar* conditions. Data will be submitted to ANOVA with factors of condition (*can identify* vs. *don't recognize*/ *familiar* vs. *don't recognize*), location (frontal/parietal), hemisphere (left/right) and site (superior/medial/inferior).

Figure 39 shows waveforms for the two critical contrasts. At the top of the figure, waveforms for *can identify* (old) and *don't recognize* (new) are shown; as can be seen, the difference between waveforms appears to be greatest at the mid frontal electrode (FZ) and additionally at the left parietal electrode (P3). The lower panel of Figure 39 also shows the contrast between *familiar* and *don't recognize* waveforms; there is very little differentiation between the waveforms, with any difference being restricted to an early latency region at the left frontal electrode.

Can identify versus don't recognize effects

The analysis of data from 300 - 500ms failed to reveal any significant differences between the waveforms. However, the analysis of data from 500 -

700ms revealed a main effect of old/new [F(1,15) = 12.1; p < 0.01] and an interaction between old/new and site [F(1.1,16.5) = 7.2; p < 0.05]. The *can identify* waveform is more positive-going than the *don't recognize* waveform, and this difference is greater at superior sites. Examination of the data found that the difference between waveforms is maximal at CP3 [t(15) = 3.6; p < 0.01] - a left centro-parietal electrode. The analysis of data from 700 – 1100ms failed to reveal any significant differences between the waveforms.

A. Can Identify **P**3 **B.** Familiar FΖ P3 PZ 10 10 old μV 0 μV 0 - new 700 1400 ms 0 700 1400 ms 0 -10 -10

Figure 39: Selected waveforms for can identify and familiar responses. Grand average ERPs are shown for recognized (old) faces and faces that were not recognized (new) at selected frontal and parietal electrode sites. The depicted epoch begins 100ms pre-stimulus onset and ends 1400ms post-stimulus onset. Panel A shows waveforms for can identify and don't recognize conditions; the waveforms begin to diverge around 400ms post-stimulus, with can identify being more positivegoing than don't recognize. The difference between the waveforms appears to be largest at the FZ electrode while there is a relatively more sustained positivity at the left parietal electrode (P3). Panel B shows waveforms for familiar and don't recognize; the waveforms show little differentiation, with any apparent difference restricted to the F3 electrode.

Familiar versus don't recognize effects

The analysis of data from 300 - 1100ms failed to reveal any significant differences between the waveforms.



Can Identify



Topography

Figure 40 shows the distribution of the old/new difference for the *can identify* and *familiar* conditions. The *can identify* effect appears to have a left

parietal distribution from 500 – 900ms, while the *familiar* effect was not reliable.

Despite being non-reliable, it is clear from the figure that the *familiar* effect does not have a left parietal distribution, which suggests that different neural generators are active on *can identify* and *familiar* trials. The lack of a reliable old/new effect for *familiar* responses means that a topographic analysis is unwarranted.

Discussion

The present study was designed to assess whether the remember/know procedure (Tulving, 1985) could be adapted for use in a test-only paradigm designed to foster retrieval from the semantic memory system. Participants viewed a series of famous faces and indicated for each face whether they could retrieve associated information (can identify), whether they could recognize the face in the absence of retrieval of associated information (familiar), or whether they could not recognize the face (don't recognize). A substantial amount of data were discarded (N = 10) because several participants made too few *familiar* responses, which suggests that the feeling of familiarity required for know responses in the typical remember/know paradigm was less common when attempting to retrieve information from the semantic memory system. In fact, for the sample of participants analysed here, *familiar* responses were less frequent than the other two response categories. Consistent with Experiments 1 - 3, however, *familiar* responses were associated with longer response times than *can identify* responses. This typical finding is counterintuitive, however, because dual-process models portray familiarity as being a relatively more fast acting process than recollection. However, shorter response times for remember decisions than for know decisions are reliably observed (e.g., Dewhurst et al., 2006), and may reflect a greater amount

of information available to make a mnemonic response following recollection compared to following familiarity.

Retrieval of semantic information associated with famous faces

A reliable ERP old/new effect was observed for the *can identify* condition but not for the *familiar* condition. The *can identify* effect took the form of a positive-going deflection for the *can identify* waveform compared to the *don't recognize* waveform that was maximal over left parietal scalp (500 – 700ms). The resemblance of this effect to the left parietal old/new effect observed in episodic memory tests (e.g., Curran, 1999; Rugg et al., 1998) is striking, and one interpretation is that the existence of semantic representations associated with famous faces is sufficient for the left parietal effect to be observed. However, it is important to note that one important caveat to this interpretation concerns the lack of a correct rejection baseline condition, which renders comparison of the present effect with the left parietal effect difficult.

The left parietal effect was once interpreted as reflecting cognitive processes that are involved with assembling a representation of retrieved episodic information (Curran, 2004). If this account is valid, then the interpretation of the effect must be broadened to include the assembly of a representation of retrieved semantic information. On the other hand, some accounts stress that the left parietal effect reflects processes involved in the orientation of attention to the products of retrieval (Wagner et al., 2005). The present data rest more comfortably within the latter framework, but again the idea that the left parietal effect only reflects processes uniquely involved in episodic retrieval must be challenged.

ERP 4

While it is theoretically possible that individual episodes are accessed when retrieving information about famous people, this seems to be an unlikely scenario for two reasons. First, at a phenomenological level, retrieving the name associated with a famous face does not typically involve conscious processing of individual episodes. Second, at a theoretical level, a cognitive system that assesses multiple episodic representations when one single semantic representation would be sufficient to perform a task is inefficient. Based on these considerations, it seems most plausible that the left parietal effect reflects the retrieval of information from declarative memory most broadly, which includes the semantic memory system in addition to the episodic memory system. Of course, this interpretation remains tentative; further research investigating the retrieval of information from semantic memory using a wide array of stimuli will help to interpret the present effects.

Famous face familiarity

In contrast to the *can identify* condition, no reliable ERP effect was observed for the *familiar* condition. As discussed in Chapter 3, however, interpretation of null results is problematic in ERP research because the lack of a reliable effect may result from several different factors. It may be the case that the neural population whose activity supports familiar judgments for famous faces is organised into a closed field, which cannot produce a dipole capable of projecting an electrical field potential to the scalp. Another reason may be that the activity detected at the scalp is small and that the amount of data collected lacks the necessary resolution to allow differences in ERPs to be observed. Either way, the lack of an effect for *familiar* responses is problematic for a straightforward interpretation of these data. One aim of Experiment 5 described in the following chapter is to collect data from a larger

sample to assess whether the effect is simply small and requires greater resolution to be observed.

Process purity

A note on the issue of process purity is important at this stage. The present paradigm was designed to foster retrieval from semantic memory storage, yet an old/new effect typically associated with episodic retrieval was observed. As discussed above, episodic representations may have been accessed when performing this semantic retrieval task, which highlights the possibility that the task used is not process pure. One way of assessing whether participants retrieved information about individual episodes rather than semantic information would be to require a recall effort proving details of the retrieved information. This task requirement will be incorporated into the design of Experiment 5 described in the following chapter.

However, an alternative interpretation of the present data leads to a critique of the typical view that the left parietal old/new effect reflects episodic retrieval processes. The left parietal effect is usually observed in recognition memory tests using words as stimuli: the effect is observed when waveforms time locked to the onset of a word are analyzed. Given the present demonstration of a left parietal effect in a semantic retrieval task, then it remains possible that it reflects the retrieval of semantic representations associated with test stimuli. Clearly, the process purity issue must be considered carefully when interpreting old/new effects.

Conclusion

The remember/know procedure was adapted for use in a test-only paradigm designed to foster retrieval from semantic memory using famous faces. Although famous faces were more likely to be recognized accompanied by the retrieval of associated semantic information than in its absence, the responses appear to be suited to a semantic retrieval task. An ERP old/new effect associated with the retrieval of associated semantic information had a left parietal distribution, which suggests a degree of overlap in the retrieval processes supporting semantic and episodic memory. These data suggest that the left parietal effect is observed when the stimuli that elicit the retrieval of associated information are represented in semantic memory, and that the left parietal old/new effect reflects the retrieval of information from declarative memory, which includes semantic representations.

Chapter 9 – ERP 5: Studied versus Famous Face Recognition

Introduction

Experiment 5 was devised to assess whether the same cognitive operations are engaged when retrieving information about well known faces compared to retrieving information about faces that have only been encountered once before. In Experiments 1 - 3, an anterior old/new effect was shown to correlate with recollection for recently studied faces that had only been encountered once before. In Experiment 3, however, the anterior effect was absent for recently studied names (which were associated with a left parietal effect). One interpretation of this finding is that the anterior effect is specific to faces, while another account stresses that the presence or absence of pre-existing semantic representations associated with faces leads to the differential recruitment of retrieval processes. It was demonstrated in Experiment 4 that recollection for famous faces was associated with a left parietal effect; therefore, left parietal effects were associated with the retrieval of contextual/associated information for two classes of stimuli associated with preexisting semantic representations – names and famous faces. This pattern of results was interpreted as suggesting that the presence of pre-existing semantic representations may determine whether an anterior or a left parietal effect is observed when associated information is retrieved.

The present study was designed to directly compare recollection of recently studied and previously learned faces, to assess whether face recollection is necessarily associated with an anterior old/new effect, or whether this effect is only observed for faces that are not associated with semantic representations stored in

long term memory. If an anterior effect is observed for recently studied faces but not for famous faces, then the view that semantic representations determine the retrieval processes that support recognition will be supported. If a left parietal effect is observed for famous faces but not for recently studied faces, then again the view that semantic representations determine the retrieval processes that support recognition will be supported. If, however, left parietal and/or anterior effects are observed for both face types, then the alternative view that semantic representations do not determine the retrieval processes that support ecognition will be supported.

Method

Thirty-two participants took part in the experiment. Eight data sets were discarded due to poor behavioural performance or contamination of EEG with artefacts, and so data from 24 participants (12 females) with a mean age of 20 years (range: 18 - 29) are presented here.

The adapted remember/know procedure used in Experiments 2 and 3 was used once more. Participants studied previously unknown faces paired with unique auditorily presented names; later, studied faces were presented again as test items, intermixed with previously unknown unstudied faces and famous faces. Stimulus presentation was sub-divided into 9 study-test cycles. In each cycle, 12 face-name stimuli were studied; at test, 12 studied faces were presented along with 6 unstudied faces and 12 famous faces. Study phase parameters matched those already described for Experiments 1 - 3. At test, participants were instructed to make an old/new judgment as soon as they had decided if they recognized a face. When participants indicated that they recognized a face they were prompted to make a secondary *remember/familiar* judgment; a remember judgment was followed by a prompt

ERP 5

asking the participant to say aloud what they remembered about seeing the face before. Participants were encouraged to make the same *remember* judgment whether they remembered something from a recent study episode for a studied face, or whether they could provide some identifying information about a famous face such as the person's name or occupation. In this manner, *remember* responses were used to isolate trials in which test stimuli initiated the retrieval of associated information, conforming to standard definitions of recollection in the case of studied faces. For famous faces, however, a *remember* response was used to isolate trials in which test stimuli initiated the retrieval of associated trials in which test stimuli initiated the retrieval of associated trials in which test

Behavioural Results

Response probabilities based on the initial old/new discrimination are shown in Figure 41; as can be seen, there is a greater probability of recognizing a studied face than a famous face, and an intermediate probability of correctly rejecting an unstudied face. The performance data were submitted to ANOVA with a factor of condition (famous/CR/studied), which revealed a main effect [F(2,46) = 3.5; p < 0.05]. Paired-samples t-tests identified a significant difference between the famous and studied hit conditions [t(23) = 2.8; p < 0.05] while all other comparisons were non-reliable.

Following 'old' decisions, participants made a *remember/familiar* judgment. The probability of *remember* and *familiar* judgments for correctly recognized studied and famous faces is shown in Figure 42; as can be seen, there is equivalent probability of a *remember* judgment, while there are more *familiar* judgments for studied faces.





Mean probabilities of correctly identified famous, unstudied (CR) and studied faces are plotted. Error bars show the standard error of the mean. Studied faces were more likely to be recognized than famous faces.



Figure 42: Remember and familiar responses.

Mean probabilities of remember and familiar responses for famous and studied faces judged to be old are plotted. Error bars show the standard error of the mean. There were more remember judgments than familiar judgments overall, while there was no difference in the probability of a remember judgment across face types. There were more familiar judgments for studied faces than for famous faces.

The *remember/familiar* data were submitted to ANOVA with factors of face (famous/studied) and response (remember/familiar), revealing a main effect of face [F(1,23) = 7.8; p = 0.01], reflecting the greater performance for studied faces than famous faces, and a main effect of response [F(1,23) = 24.1; p < 0.001], reflecting a greater probability of remember judgments than familiar judgments. The analysis failed to reveal an interaction between the factors (p = 0.09). This pattern of results

suggests that familiarity had a greater influence on performance for studied faces than famous faces.

Response Time data for the initial old/new discrimination are plotted in Figure 43, which shows that the famous hit condition was associated with quicker response times than all other conditions, and that the famous don't recognize condition was associated with longer response times than all other conditions.



Figure 43: Response time.

Mean response times are plotted for all four conditions used to form ERPs. Error bars show the standard error of the mean. Response times for studied hit and correct rejection conditions were equivalent. For famous faces, however, hits were associated with quicker response times than don't recognize responses.

The response time data were submitted to ANOVA with factors of face (famous/studied) and response (old/new). The analysis revealed an interaction between the factors [F(1,23) = 4.5; p < 0.05], reflecting the slower response times for famous don't recognize than for famous hit faces, compared to no difference in response time between the studied hit and correct rejection conditions. Paired-samples t-tests found a significant difference between the means for the famous hit

and famous don't recognize conditions [t(23) = 2.3; p < 0.05] while all other comparisons were non-significant.

ERP Results

The primary aim of this study was to compare old/new effects associated with *remember* responses for studied and famous faces. A sample of 22 participants contributed a sufficient number of trials for the salient ERPs to be examined. The mean number of trials included in grand-average ERPs was: famous remember = 40; famous don't recognize = 41; studied remember = 42; correct rejection = 34. The ERP analysis was designed to first characterize old/new effects for famous and studied faces before comparing the relative size and topography of those effects.

One problem inherent in comparing old/new effects for famous and studied faces is the lack of a common baseline across conditions. The old/new effect typically uses a correct rejection baseline, but the baseline used in the famous face condition comprises trials where famous faces were not recognized. It is unknown whether participants previously encountered the people represented by the famous faces or not, and therefore it is unknown whether the don't recognize baseline should be considered analogous to a miss or a correct rejection baseline, or some blend of the two. It has been shown previously that ERPs for misses can differ from ERPs for correct rejections; for example, Rugg et al. (1998) observed a difference between correct rejection and miss waveforms over posterior scalp from 300 – 500ms that was interpreted as a neural correlate of implicit memory. While this neural correlate of implicit memory has not been replicated to date, for present purposes it is important to determine whether correct rejection and miss waveforms differ. This assessment is important because if the correct rejection and miss

baselines differ then any comparison between the famous and studied face effects would be impossible to interpret.

Fifteen participants contributed enough trials to examine ERPs for correct rejections and misses. Figure 44 shows waveforms for correct rejections and misses at selected frontal and parietal sites. The figure shows that there is very little difference between the ERPs associated with the two response categories; however, the correct rejection waveform appears to be more positive-going than the miss waveform approximately 350ms post-stimulus for a brief period at the parietal electrodes, and the miss waveform appears to be more positive-going than the correct rejection waveform appears to be more positive-going than the



Figure 44: Correct rejection and miss waveforms.

Grand-average ERPs are shown for correct rejections and misses at selected frontal and parietal electrode sites. The depicted epoch begins 100ms pre-stimulus onset and ends 1100ms post-stimulus onset. Scale bars indicate the size of the effects (in microvolts). The waveforms are largely indistinguishable from one another, although some differences are apparent: at the parietal location, the waveform for correct rejections is more positive-going than the waveform for misses for a short duration approximately 300ms post-stimulus; in addition, the miss waveform is more positive-going than the correct rejection waveform at electrode F3 from approximately 700ms post-stimulus.

The analysis of data from four consecutive 200ms latency periods running

from 300 - 1100ms post-stimulus failed to identify any differences between the

waveforms. This result suggests that there is no evidence from the present study that the brain differentiates between studied faces that were not recognized and genuinely new faces that were correctly identified. More importantly, this finding validates the use of different baseline conditions in the following analyses, and allows inferences to be drawn from the comparison of famous and studied face effects.

Famous remember effects

For famous faces, *remember* waveforms were formed for recognized faces for which associated semantic information was correctly supplied, and new waveforms were formed for famous faces that were not recognized. Figure 45 shows waveforms for famous remember faces plotted along with new famous faces. An early negative-going deflection for the remember waveform is apparent at the frontal location, before a positive-going deflection begins at approximately 500ms post-stimulus onset; the difference between conditions appears to be largest on the left hemisphere at the parietal location, where the positivity is sustained throughout the depicted epoch.

The analysis of data from 300 - 500ms revealed an interaction between old/new, location and site [F(1.1,24.1) = 6.0; p < 0.05], reflecting the superior distribution of the effect at the parietal location (main effect of old/new [F(1,21) = 33.8; p < 0.001] and interaction between old/new and site [F(1.2,26.1) = 16.0; p < 0.001]) compared to an effect that is not reliable at the frontal location. Examination of the data revealed that the effect was maximal at PZ, although the old/new difference was not significant at this electrode.



Figure 45: Famous face remember old/new effects. Grand-average ERPs are shown for famous remember (old) and famous don't know (new) conditions at selected frontal and parietal electrode sites. The depicted epoch begins 100ms pre-stimulus onset and ends 1100ms post-stimulus onset. Scale bars indicate the size of the effects (in microvolts). The waveforms begin to diverge approximately 400ms post-stimulus onset, with the old waveform more positive-going than the new waveform; at the left parietal electrode (P3), this positive-going deflection is sustained until the end of the depicted epoch. Two differences between the waveforms are apparent; there is a frontal modulation (500 - 700ms) followed by a left parietal modulation (900 - 1100ms).

The analysis of data from 500 - 700ms revealed a main effect of old/new [F(1,21) = 10.9; p < 0.01] and an interaction between old/new and site [F(1.3,26.9) = 16.3; p < 0.001], reflecting the superior distribution of the effect. Examination of the data revealed that the effect was maximal at FZ [t(21) = 2.9; p < 0.01].

The analysis of data from 700 - 900ms revealed a marginally significant interaction between old/new and hemisphere [F(1,21) = 3.7; p = 0.07], reflecting a bigger effect on the left hemisphere than on the right. Examination of the data revealed that the effect was maximal at the P3 electrode [t(21) = 2.5; p < 0.05].

The analysis of data from 900 - 1100ms revealed an interaction between old/new, location and site [F(1.6,33.2) = 3.7; p < 0.05]: at the frontal location, a negative-going deflection for the remember waveform was greater at the superior sites, whereas at the parietal location, a positive-going deflection for the remember waveform was greater at superior sites. In addition, the analysis revealed a

marginally significant interaction between old/new and location [F(1,21) = 3.8; p = 0.065], which reflects the polarity reversal between the two locations. Examination of the data revealed that the effect was maximal at the P3 electrode [t(21) = 2.4; p < 0.05].

In sum, the *remember* responses for famous faces were associated with an anterior effect (500 - 700ms) and a parietal effect that was initially superiorly distributed (300 - 700ms) and then maximal on the left hemisphere (700 - 1100ms).

Studied remember effects

For studied faces, *remember* waveforms were formed for hits that were subsequently given *remember* responses, and new waveforms were formed for correctly rejected unstudied faces. Figure 46 shows *remember* and new waveforms plotted at selected frontal and parietal electrodes. The waveforms diverge around 300ms post-stimulus, with a positive-going deflection for the *remember* waveform, and the difference between conditions appears to be largest at the frontal location.

The analysis of data from 300 - 500ms revealed a main effect of old/new [F(1,21) = 9.1; p < 0.01] and an interaction between old/new and site [F(1.3,27.1) = 6.0; p < 0.05], which reflects the superior distribution of the effect. Subsidiary analysis of each location separately revealed no differences at the parietal location; however, a main effect of old/new [F(1,21) = 11.1; p < 0.01] and an interaction between old/new and site [F(1.5,30.5) = 7.8; p < 0.01] were observed at the frontal location. Examination of the data revealed that the effect was maximal at FZ [t(21) = 3.7; p = 0.001].



Figure 46: Studied face remember old/new effects. Grand-average ERPs are shown for studied remember (old) and correct rejection (new) conditions at selected frontal and parietal electrode sites. The depicted epoch begins 100ms pre-stimulus onset and ends 1100ms post-stimulus onset. Scale bars indicate the size of the effects (in microvolts). The waveforms begin to diverge approximately 300ms post-stimulus onset, with the old waveform more positivegoing than the new waveform until approximately 800ms post-stimulus; the difference between waveforms is greater at the frontal location than at the parietal location.

The analysis of data from 500 - 700ms revealed a main effect of old/new [F(1,21) = 16.7; p = 0.001] along with interactions between old/new and site [F(1.1,24.4) = 9.3; p < 0.01] and between old/new, location and site [F(1.5,31.5) = 7.8; p < 0.01]. In addition, the analysis revealed a marginally significant interaction between old/new and location [F(1,21) = 3.7; p = 0.07], reflecting a larger effect at the frontal location than at the parietal location. Subsidiary analyses were performed on data from each location separately, and revealed an effect with a superior distribution at the frontal location (main effect of old/new [F(1,21) = 17.7; p < 0.001] and interaction between old/new and site [F(1.3,27.4) = 12.6; p = 0.001]) compared to an effect that was invariant across the levels of the site factor at the parietal location (main effect of old/new [F(1,21) = 8.0; p = 0.01]). Examination of the data revealed that the effect was maximal at F1 [t(21) = 4.5; p < 0.001]. The analysis of data from 700 – 900ms and from 900 – 1100ms failed to reveal any significant differences.

In sum, the remember responses for studied faces were associated with an anterior old/new effect (300 - 700ms). The old/new effect was reliable at the parietal location during the 500 - 700ms latency period, but there was no evidence of lateralization and the effect was maximal at the frontal location.

The *remember* effect for studied faces appears to have a different distribution from the effect observed for famous faces. The *remember* effect for famous faces was also associated with an anterior effect from 500 - 700ms, but in contrast to the effect observed for studied faces, the anterior effect was followed by a left lateralised parietal effect (700 - 1100ms). Although the anterior effect appears to be common to both famous and studied faces, the left parietal effect was only observed for famous faces, during a period in which no effects were observed for studied faces.

Magnitude comparisons

Magnitude comparisons were performed to assess several questions: first, do the famous and studied remember effects vary in size during the latency periods in which they are present; second, do the anterior effects observed for both face types from 500 - 700ms vary in size; and third, do the parietal effects observed for both face types from 500 - 700ms vary in size?

Parietal effects were observed in the famous face condition in all four latency periods. Establishing when the parietal effect is largest is important in characterizing the effect. The magnitudes of the effects were compared; data from the parietal location were submitted to ANOVA with factors of latency (300 - 500ms/500 - 700ms/700 - 900ms/900 - 1100ms), hemisphere (left/right) and site

(superior/medial/inferior). The analysis revealed a main effect of latency [F(1.5,32.5) = 4.1; p < 0.05] and an interaction between latency and site [F(1.4,30.0)]= 6.5; p < 0.01], reflecting the superior distribution of the effect in the first two latency periods from 300 – 700ms compared to the inferior distribution in the last two latency periods from 700 - 1100 ms). Pair-wise comparisons revealed main effects of latency when the magnitude of the effect observed from 700 - 900 ms was compared to all other latencies (300 - 500 ms vs, 700 - 900 ms - [F(1,21) = 7.8; p < 100 ms)0.05]; 500 - 700ms vs. 700 - 900ms - [F(1,21) = 16.1; p = 0.001]; 700 - 900ms vs. 900 - 1100ms - [F(1,21) = 17.6; p < 0.001]), reflecting a larger effect from 700 -900ms than in any other latency. In addition, the subsidiary analyses revealed interactions between latency and site (300 - 500vs. 900 - 1100ms - [F(1.1,22.4) =7.7; p = 0.01]; 500 - 700 vs. 700 - 900ms - [F(1.1,22.4) = 4.5; p < 0.05]; 500 -700ms vs. 900 - 1100ms - [F(1.1,22.9) = 8.9; p < 0.01]; 700 - 900ms vs. 900 - 900 - 900ms vs. 900 -1100ms – [F(1.1,22.7) = 8.0; p < 0.01]), which principally reflect the superior distribution of the effects in the first two latency periods (300 - 700 ms) compared to the inferior distribution of the effects in the last two latency periods (700 – 1100ms). The interaction between the effects present in the last two latency periods reflects the fact that the inferior distribution is not as great from 700 – 900ms as it is from 900 – 1100ms. Together, this pattern of results demonstrates that the famous face effect is maximal from 700 – 900ms, and suggests changes in the distribution of the effect throughout the epoch that will be examined further in the topographic analysis section below.



Figure 47: Magnitude of anterior old/new effects, 500 - 700ms. The magnitude of the mean old/new difference is plotted for famous and studied remember conditions at frontal electrode sites. Error bars show the standard error of the mean. The effect is larger for studied faces than for famous faces, although the difference in size is not reliable.

Anterior effects were observed in the studied remember condition in both the 300 - 500ms and 500 - 700ms latency periods. The magnitude of the effects were compared; data from the frontal location were submitted to ANOVA with factors of latency (300 - 500ms/500 - 700ms), hemisphere (left/right) and site (superior/medial/inferior), and the analysis revealed a marginally significant main effect of latency [F(1,21) = 4.1; p = 0.056], reflecting a larger effect during the 500 – 700ms latency period. This suggests that remember responses for studied faces were associated with an anterior effect that is present from 300 - 700ms and maximal from 500 - 700ms.

Anterior and parietal old/new effects were observed for *remember* responses for both famous and studied faces during one common latency period (500 – 700ms). Difference waveforms were analyzed to investigate the relative sizes of these effects, first at the frontal location, and then at the parietal location. Figure 47 illustrates the magnitude of the anterior old/new effect from 500 – 700ms. The effect is larger for studied than for famous faces; however, when data from the frontal location were submitted to ANOVA with factors of condition (famous/studied), hemisphere (left/right) and site (superior/medial/inferior), no significant differences were observed.



Figure 48: Magnitude of parietal old/new effects, 500 - 700ms. The magnitude of the mean old/new difference is plotted for famous and studied remember conditions at parietal electrode sites. Error bars show the standard error of the mean. The effect is larger for studied faces than for famous faces, but a difference in distribution is evident: the effect for famous faces appears to be greater on the left hemisphere than on the right, whereas the effect for studied faces appears to be less asymmetric.

The magnitude of the parietal old/new difference (500 – 700ms) is illustrated in Figure 48 for famous and studied remember conditions. The effect for studied faces is larger than the effect for famous faces, but a difference in the distribution of the effects is apparent, with a greater left-lateralization for the famous face effect. Data from the parietal location were, however, submitted to ANOVA, and the analysis failed to reveal any significant differences in the magnitude of the old/new effects.

Topographic analysis

Topographic analyses were performed to assess several questions: first, do the famous and studied remember effects change distribution across the latency periods in which they are present; second, do the anterior effects observed for both face types from 500 - 700ms change distribution; and third, do the parietal effects observed for both face types from 500 - 700ms change distribution?

Famous Remember



Figure 49: Recollection topography.

The distributions of the old/new difference are plotted for the famous and studied remember conditions using topographic maps representing the spread of activity across the scalp. Maps show the front of the head at the top, and the left is on the left-hand side. Scale bars indicate the range of activity (in microvolts). Maps show the average activity in four consecutive 200ms latency periods. The distribution of the famous face effect is initially anterior (500 - 700ms) and then left parietal (700 - 1100ms); in contrast, the distribution of the studied face effect is anterior (300 - 700ms).

Figure 49 shows the distribution of the old/new difference averaged across

four consecutive 200ms latency periods. Famous face recollection appears to be

associated with an anterior effect and a later parietal effect from 500 - 700ms. Importantly, the parietal effect does not appear to be present for the studied face condition late in the epoch (700 - 1100ms) when it remains present for famous face recollection. Studied face recollection appears to be associated with the same anterior effect during the first two latency periods (300 - 700ms).

The first topographic analysis was performed to assess whether there is a change in the distribution of the parietal effects observed in the famous face condition. Magnitude analyses suggested that the effects present from 300 - 700ms had a superior distribution, while the effects present from 700 - 1100ms had an inferior distribution. Rescaled difference waveforms were quantified, and data from the parietal location were submitted to ANOVA with factors of latency (300 - 500ms/500 - 700ms/700 - 900ms/900 - 1100ms), hemisphere (left/right) and site (superior/medial/inferior). The analysis revealed interactions between latency and hemisphere [F(2.1,44.3) = 3.8; p < 0.05], reflecting the right-lateralization of the effect from 300 - 500ms compared to the left-lateralization of the effect during each of the three later latency periods, and between latency and site [F(2.3,47.8) = 4.3; p < 0.05], reflecting a superior distribution from 300 - 500ms that is more marked than in any of the subsequent latency periods.

Given the significant change in distribution over time, subsidiary analyses comparing pairs of latency periods were also performed. The analyses revealed that the 300 – 500ms distribution differs from each of the subsequent distributions by having a right-hemispheric asymmetry which differs from the left-hemispheric asymmetry of the effect from 500ms to 900ms (interactions between latency and hemisphere: 300 - 500ms vs. 500 - 700ms [F(1,21) = 5.1; p < 0.05]; 300 - 500ms

vs. 700 - 900ms [F(1,21) = 7.3; p < 0.05]). In addition, the 300 - 500ms distribution has a much greater superior focus than the effects present from 700 - 1100ms (interactions between latency and site: 300 - 500ms vs. 700 - 900ms [F(1.1,23.1) = 6.8; p < 0.05]; 300 - 500ms vs. 900 - 1100ms [F(1.1,23.0 = 5.8; p < 0.05]). The 500 - 700ms distribution has a greater superior focus than the 700 - 900ms distribution (interaction between latency and site [F(1.1,23.8) = 4.5; p < 0.05]) but does not differ from the 900 - 1100ms distribution.

Finally, subsidiary topographic analyses failed to identify any differences between the distributions present from 700 - 900ms and 900 - 1100ms. This pattern of results suggests that the early parietal effects (300 - 700ms) differ from the later parietal effects (700 - 1100ms), but most importantly, the effects present from 700- 900ms do not differ. In sum, *remember* responses for famous faces are associated with a stable neural correlate of retrieval over left parietal scalp from 700 - 1100ms that is maximal from 700 - 900ms post-stimulus onset. Importantly, this neural correlate is present when no reliable effects are observed in the studied face condition.

Topographic analyses were also performed to assess whether the anterior effects present in the studied face condition maintained a stable distribution across the two early latency periods. Rescaled subtraction data from the frontal location were submitted to ANOVA with factors of latency (300 – 500ms/500 – 700ms), hemisphere (left/right) and site (superior/medial/inferior). The analysis failed to reveal any significant differences, which suggests that the distribution of the frontal effects seen in both latency periods is the same. Although it is difficult to interpret null results, which simply imply that there is no evidence of a difference rather than

<u>ERP 5</u>

that no difference is present, evidence from both the magnitude analyses presented in the previous section and the topographic analysis performed here suggest that the anterior effect remains stable during the 300 - 500ms and 500 - 700ms latency periods, with the effect in the later latency period being slightly larger.

A third analysis was performed to assess whether the anterior effects present in the famous face condition differ qualitatively from those observed in the studied face condition. Data from the frontal location (500 – 700ms) were submitted to ANOVA with factors of condition (studied/famous), hemisphere (left/right) and site (superior/medial/inferior). The analysis failed to reveal any significant differences; this result fails to provide any evidence to suggest that the distributions of the frontal effects seen in both the studied and the famous face conditions differ.

Finally, the distributions of the parietal effects present from 500 - 700ms for both famous and studied faces were compared. Data from the parietal location were submitted to ANOVA; despite the famous face distribution having a superior focus and the studied face distribution not changing across the levels of the site factor, the analysis failed to reveal any reliable differences (although the interaction between condition and site approached significance, p = 0.073). Based on the results of this analysis it is difficult to decide whether the same pattern of parietal effects is present for famous and studied faces in this latency period. More importantly, the pattern of parietal activity observed in the studied face condition does not lateralize to the left hemisphere, as would be expected if studied face recollection were associated with the standard left parietal index of recollection typically observed in studies of word recognition. Furthermore, left parietal effect is present for famous faces when it is absent for studied faces later in the epoch from 700 - 1100ms.

Studied Face Remember and Familiar Effects

As a consequence of a high number of familiar responses to studied faces, it also proved possible to examine ERPs for remember and familiar responses to studied faces for a subset of participants (N = 20). An additional set of analyses will therefore investigate the dual-process distinction between recollection and familiarity for faces⁷ by seeking to replicate the topographically dissociable anterior (recollection) and posterior (familiarity) old/new effects observed in Experiments 1 and 2. To be clear, based on the previous results, familiarity should elicit a posterior old/new effect (300 – 700ms). The mean number of trials included in grand-average ERPs was: Studied Remember = 38; Studied Familiar = 36; Correct Rejection = 35.

Figure 50 shows waveforms for familiar hits plotted along with correct rejections. The waveforms begin to diverge around 300ms post-stimulus. At the frontal location the positive-going deflection of the old waveform persists until roughly 600ms post-stimulus, and is followed by a negative-going deflection. At the parietal location, a positive-going deflection of the old waveform is only evident on the right hemisphere from roughly 300 – 400ms post-stimulus.

Data were submitted to ANOVA with factors of old/new, location (frontal/parietal), hemisphere (left/right) and site (superior/medial/inferior). The analysis of data from 300 - 500ms revealed an interaction between old/new, location and site [F(1.3,24.8) = 6.0; p < 0.05]. Subsidiary analysis revealed a marginally significant interaction between old/new, hemisphere and site at the parietal location [F(1.5,28.1) = 3.2; p = 0.07], reflecting a larger difference at

⁷ A small number of participants (N = 12) additionally contributed enough trials to form ERPs for familiar responses to famous faces, but as in Experiment 4 the old/new effect was not reliable and therefore this effect is not considered any further.

inferior sites on the right hemisphere. Examination of the data found that the effect was maximal at the CP6 electrode (but a t-test revealed that the effect was not reliable at this electrode). The analysis of data from 500 - 700ms failed to identify any significant differences.



Figure 50: Studied familiar old/new effects.

Grand-average ERPs for studied familiar (old) and correct rejection (new) conditions at selected frontal and parietal electrode sites. The depicted epoch begins 100ms pre-stimulus onset and ends 1100ms post-stimulus onset. Scale bars indicate the size of the effects (in microvolts). There is little difference between the waveforms during the critical 300 - 700ms latency period; at the parietal location, however, the old waveform is more positive-going than the new waveform from approximately 300 - 400ms post-stimulus onset.

While the preceding analysis provides little evidence of a significant familiarity-related old/new effect, the result was based on *a priori* latency periods. Visual inspection of the waveforms, however, suggested that the right-parietal familiarity old/new effect would be quantified more accurately using a 300 – 400ms latency period. Analysis of data from 300 – 400ms revealed an interaction between old/new, location and site [F(1.4,25.8) = 5.2; p < 0.05], reflecting the presence of effects at the parietal location only. Subsidiary analysis of data from the parietal location revealed an interaction between old/new and hemisphere [F(1,19) = 4.6; p < 0.05], reflecting the right hemispheric lateralisation of the effect, and an interaction between old/new, hemisphere and site [F(1.6,29.7) = 5.2; p < 0.05],

ERP 5

reflecting the inferior distribution of the effect on the right hemisphere. Examination of the data found that the effect was maximal at the CP6 electrode [t(19) = 2.1; p < 0.05].

Magnitude comparison

The neural correlate of familiarity described above for studied faces was based on data from 20 participants who contributed a sufficient number of trials for ERPs to be formed for familiar hits. To compare the size and topography of the neural correlates of recollection and familiarity, therefore, data from the same subsample of participants were used. Difference waveforms were analyzed to assess whether the sizes of the remember and familiar old/new effects present from 300 -500ms differed. Data were submitted to ANOVA with factors of condition (remember/familiar), location (frontal/parietal), hemisphere (left/right) and site (superior/medial/inferior). The analysis revealed marginally significant interactions between condition, hemisphere and site [F(1.3,24.9) = 3.7; p = 0.054], and between condition and site [F(1.1,20.3) = 3.7; p = 0.065]. Subsidiary analysis of data from the frontal location failed to reveal any differences between conditions; however, the analysis of data from the parietal location (see Figure 51) revealed an interaction between condition, hemisphere and site [F(1.4,26.8) = 3.9; p < 0.05], reflecting an interaction between condition and site on the right hemisphere [F(1.1,20.6) = 7.7; p]= 0.01] but not on the left. As can be seen in Figure 51, the remember effect is bigger at the superior site on the right hemisphere while the familiar effect is bigger at the inferior site, although these differences are not reliable at any individual parietal electrode. Additionally, the analysis revealed an interaction between

condition and site [F(1.1,20.2) = 5.1; p < 0.05], reflecting the superior distribution of the remember effect relative to the inferior distribution of the familiar effect.



Figure 51: Magnitude of studied remember and familiar effects. The mean old/new difference is plotted for the studied remember and familiar effects at electrodes from the parietal location. Error bars show the standard error of the mean. The remember effects have a superior distribution, whereas the familiar effects are larger at inferior electrodes than at superior electrodes. The difference in size of the effects is most pronounced on the right hemisphere, where the familiar effect is maximal at inferior sites.

Topographic analysis

Figure 52 shows the distributions of the studied remember and familiar effects. Consistent with the analysis presented above, the familiar effect appears to have a right parietal distribution (300 - 500 ms), which differs from the anterior distribution seen for the remember effect during the same latency period.

Studied Remember



Figure 52: Studied remember and familiar topography.

The distributions of the old/new difference are plotted for the studied remember and familiar conditions using topographic maps representing the spread of activity across the scalp. Maps show the front of the head at the top, and the left is on the left-hand side. Scale bars indicate the range of activity (in microvolts). Maps show the average activity in four consecutive 200ms latency periods. The distribution of the remember effect has an anterior focus (300 - 700ms), whereas the distribution of the familiar effect is maximal at right parietal electrodes from 300 - 500ms poststimulus.

A neural correlate of familiarity?

Figure 53 shows waveforms for remember and familiar judgments to studied hits along with correct rejections at P6 - an inferior electrode on the right hemisphere. The familiar old/new effect was maximal at right inferior sites, and therefore a candidate neural correlate of familiarity is represented in the figure. As can be seen, the remember and familiar waveforms begin to diverge from correct rejections around 300ms post-stimulus, and this divergence persists for approximately 150ms. Studied faces given remember and familiar judgments are likely to be equally familiar, and therefore a demonstration that the remember and familiar old/new effects are of equal magnitude with respect to the parietal activity would support the claim that right inferior component of the old/new effect provides an index of familiarity. As can be seen in Figure 53, the remember and familiar waveforms appear to be equivalent during the 300 - 400ms period. Subtraction data were compared through the use of paired-samples t-tests and no differences were observed at right inferior electrodes from 300 - 500ms. This finding suggests that the effects shown in Figure 53 may be a neural correlate of familiarity for faces.





Grand-average ERPs are shown for studied remember and familiar conditions along with correct rejections at the P6 electrode. The depicted epoch begins 100ms pre-stimulus onset and ends 1100ms post-stimulus onset. Scale bars indicate the size of the effects (in microvolts). Remember and familiar effects were of equivalent magnitude over right inferior parietal electrodes from 300 – 500ms. This finding is consistent with the view that this modulation of the old/new effect represents a neural correlate of familiarity for faces.

Discussion

The present study was designed to allow for the comparison of old/new

effects associated with remember responses for faces that were encountered before
ERP 5

beginning the experiment (famous faces) and faces that have only been encountered once before in a study phase of the experimental context (studied faces). *Remember* responses for studied faces were assumed to be supported by recollection (or a combination of recollection and familiarity) and for operational purposes the process supporting *remember* responses for famous faces will also be referred to as recollection (although the question of whether a putative episodic retrieval process is active in a semantic face recognition task is discussed below). Participants studied a series of face-name compound stimuli and later made old/new discriminations to studied, unstudied and famous faces; a remember/familiar decision was subsequently made for each face endorsed as 'old', and a verbal report of the information that was remembered was required following each remember response.

Behaviourally, more studied faces were recognized than famous faces; the two face types were equally likely to receive *remember* responses, but there were more *familiar* responses for studied faces than for famous faces. The finding that studied and famous faces were equally likely to receive *remember* responses is important because the comparison of ERPs for *remember* responses is not confounded by differences in performance.

Neural correlates of recollection

The neural correlate of recollection associated with famous faces differed from the neural correlate of recollection associated with studied faces. While an anterior old/new effect (500 - 700ms) was observed for both famous and studied faces, a left parietal modulation (700 - 1100ms) was exclusively present for famous faces. The presence of left parietal activity correlating with the retrieval of information about famous faces replicates the finding of Experiment 4, although the

<u>ERP 5</u>

left parietal activity in the present experiment is somewhat delayed compared to the activity observed in Experiment 4. The demands of the present experiment differed in one key regard to those of Experiment 4: in the present experiment famous faces were intermixed with studied and unstudied faces and therefore it is conceivable that participants had to first identify whether any given face was famous or not, and then for faces identified as being famous, associated information had to be retrieved. In Experiment 4, however, all faces were famous and so participants were only required to attempt to retrieve information associated with the images of famous faces; the relatively simpler task demands in Experiment 4 may explain the differences in timing between the left parietal effects observed across studies.

The present experiment was designed to assess whether the anterior old/new effect shown to correlate with recollection in Experiments 1 - 3 would be observed exclusively for studied faces, a finding which would highlight the role of preexisting representations in determining whether the anterior effect is observed. However, anterior effects were observed for both studied and famous faces. These data are problematic because an anterior effect was not predicted for famous faces. Given that familiarity may be active during recollection (as appears to be the case for name recollection effects in ERP 3) the anterior effect observed for famous faces may either represent a neural correlate of familiarity or a neural correlate of recollection. Topographic analysis failed to identify a difference between the anterior effects observed for studied and famous faces, providing no evidence that the effects differ. Despite the difficulties inherent in interpreting such null results, on balance the result is more easily interpreted as evidence that the same anterior effect is present for famous faces and studied faces, and as such this result fails to support the prediction that stimuli that are not associated with pre-existing

ERP 5

representations give rise to an anterior correlate of recollection. Rather, it would seem that the anterior effect reflects a cognitive operation associated with retrieving contextual information common to facial stimuli. More importantly, the finding that famous faces, and not studied faces, were associated with a left parietal effect (700 – 1100ms) provides some support for the view that the presence of pre-existing semantic representations determines whether a left parietal effect will be observed during retrieval.

Neural correlates of familiarity

The validity of dual-process theories of recognition memory receives some support from the present experimental results. Based on data from a subset of the participants, a neural correlate of familiarity for studied faces was identified. A right inferior posterior old/new effect (300 – 500ms) was observed for familiarity, and the magnitude of this effect was equivalent for *remember* and *familiar* conditions, as would be predicted for a neural correlate of familiarity (c.f. Rugg et al., 1998); however, this observation does not replicate the findings of either Experiments 1 or 2. Given that the neural correlate of recollection for studied faces had an anterior focus, the apparent difference in topography between the anterior recollection effect and the posterior familiarity effect corresponds⁸ with the topographic dissociation found in Experiments 1 and 2, and reported by MacKenzie and Donaldson (2007). The qualitative difference in distribution apparent between the neural correlates of recollection and familiarity reported in the present experiment receives statistical support through topographic analysis, which identified differences in the

⁸ Although anterior/posterior topographic differences between recollection and familiarity effects have been observed across three studies, it should be noted that the old/new effect associated with familiarity here had a right-parietal distribution, whereas in Experiments 1 and 2 the distributions of the familiarity effects were not right-lateralized.

distributions of the two effects. These data therefore support the view that the ERP old/new effect contains dissociable neural markers for recollection and familiarity, as predicted by dual-process theory.

A neural correlate of familiarity for famous faces was not observed in the present experiment, which conforms to the finding of Experiment 4, in which no reliable familiarity effect was identified. At a behavioural level, participants reported feelings of familiarity for famous faces when unable to retrieve contextual information about the faces; however, across two studies presented in this thesis ERPs seem unable to identify a neural correlate of this phenomenon, at least within the confines of the experimental procedures used here.

Semantic recollection?

The view that remember responses derived from the remember/know paradigm or its variants isolate recollection-based responding is well established in the episodic memory literature (Yonelinas, 2002). However, the nature of the process (or processes) sub-serving remember responses for famous faces is unclear. In the present paradigm, participants reported semantic information that was associated with each face on *remember* trials. The information provided included names and occupations, but in practice there is no clear (valid or reliable) basis for deciding whether the information was retrieved from either the semantic memory or the episodic memory system. The study-test paradigm is considered to isolate episodic memory because items must be recognized as having been encountered before in the specific context of the study list. In contrast, the present paradigm did not include a study list and so participants could in theory have retrieved information about the famous faces from particular events in their past or from their

general knowledge base; these two sources of information reflect the episodic and semantic memory systems, respectively. Most theorists would likely agree that the present task does not require episodic retrieval in the case of the famous face condition, however, and that semantic retrieval is most likely to have supported performance on famous remember trials.

One interpretation of the observation of a left parietal effect could be that the episodic memory system supported retrieval of information associated with remember responses for famous face recognition. If it is assumed that the left parietal effect indexes recollection, which is an episodic memory retrieval process, then it is tempting to conclude that the presence of the left parietal effect necessarily implies that recollection of information has occurred. However, the functional significance of the left parietal effect is still unclear (Rugg & Curran, 2007). If the left parietal effect does indeed reflect the retrieval of contextual information, then the present demonstration of left parietal effects for famous faces implies that the retrieved contextual information does not necessarily have to be episodic in nature. Rather, by this account, the retrieval of information from declarative memory is sufficient for the left parietal effect to be observed. Furthermore, the one condition where purely episodic representations would be expected – the studied face condition - was not associated with a left parietal effect. One interpretation of this finding would therefore be that the left parietal effect reflects the retrieval of contextual information associated with pre-existing semantic representations.

An alternative account might stress that individual episodes are accessed when retrieving semantic information about famous faces, and that the left parietal effect reflects such episodic retrieval. While this interpretation has the benefit of

ERP 5

honouring the typical functional significance of the left parietal effect as an index of recollection, it seems unlikely that the cognitive system would have to access individual episodes in order to retrieve information that exists in a semantic store. On this basis, the view that the left parietal effect reflects the retrieval of contextual information from declarative memory as a whole is favoured.

Conclusion

The present study compared the retrieval of information about faces that are associated with episodic representations (studied faces) and faces that are associated with semantic representations (famous faces). An investigation of the ERP old/new effects associated with these two conditions revealed a common anterior effect (500 - 700ms) and a left parietal effect (700 - 1100ms) that was selectively observed for famous faces. The functional significance of the anterior effect remains unclear, although the fact that it is elicited by both famous and recently studied faces suggests that it reflects the processing of representations common to both semantic and episodic memory systems. The left parietal effect appears to reflect the retrieval of information associated with pre-existing semantic representations. This finding is important because it implies that episodic representations do not uniquely engage the neural generators responsible for the left parietal effect, and suggests that the left parietal effect reflects retrieval from declarative memory.

Finally, support for dual-process theory was provided through the observation of topographically dissociable anterior and posterior old/new effects correlating with recollection and familiarity, respectively. This dissociation broadly replicates the findings reported by MacKenzie and Donaldson (2007; Experiment 1) and the result of Experiment 2 described in this thesis.

Chapter 10 – General Discussion

This chapter is divided into two sections: first, the results of the five studies presented in this thesis are summarized; and second, the results are integrated with evidence from the wider literature. The research presented in this thesis used event-related potentials (ERPs) to test dual-process accounts of recognition memory: namely, that recollection and familiarity are dissociable retrieval processes (ERP 1 & 2). The functional significance of the observed neural correlate of familiarity was probed by contrasting ERPs for distinctive and average faces, following from the observation that average faces are perceived to be more familiar than distinctive faces (ERP 2). Furthermore, the hypothesis that recollection and familiarity are material independent processes was tested by contrasting face and name recognition (ERP 3). The role of pre-existing semantic representations in determining the pattern of neural activity observed during retrieval was investigated with famous faces (ERP 4 & 5); these studies also raised questions concerning whether common retrieval processes access both episodic and semantic memories.

Summary of results

Examination of stimulus-locked event-related potentials (ERPs) across a series of recognition memory tests using faces identified topographically dissociable neural correlates of recollection and familiarity. An anterior old/new effect (300 - 700ms) was associated with recollection in Experiments 1 - 3 and 5; this effect was observed for correctly recognized faces which attracted *remember* responses, as opposed to *familiar* responses. Most importantly, the anterior effect was larger when names (which had been paired with faces at study) were successfully retrieved than

when other specific contextual information was retrieved (Experiment 1). This modulation of the anterior effect demonstrates that the effect varies in a manner consistent with recollection, providing evidence that the effect can be considered to be a neural correlate of recollection.

A posterior old/new effect was associated with familiarity in Experiments 1, 2 and 5. In Experiments 1 and 2, this effect was observed from 300 – 700ms, whereas in Experiment 5 the posterior effect was only observed from 300 – 500ms. In Experiment 2, the magnitude of the posterior familiarity effect was marginally greater for average faces than for distinctive faces, providing tentative support for the view that the posterior portion of the old/new effect varies in a manner consistent with familiarity. In Experiment 5, the *familiar* and *remember* effects for studied faces were of equivalent magnitude at inferior parietal electrode sites on the right hemisphere; given that faces given both *remember* and *familiar* responses should in theory be equally familiar after a single exposure, this finding provides a second strand of evidence that the posterior effect is modulated as if it were a neural correlate of familiarity. However, a similar modulation of the parietal effect was not observed in any of the other studies, and so the evidence from Experiment 5 may simply reflect sampling error. Nevertheless, the presence of posterior effects

Topographic dissociations between the anterior and posterior effects were observed in Experiments 1, 2 and 5. These qualitative differences between the old/new effects associated with recollection and familiarity demonstrate that at least partially non-overlapping neural populations generate the two effects, and therefore it can be assumed that the two effects reflect the activity of distinct cognitive

operations. This finding indicates that discrete cognitive operations are engaged when episodic information about faces is remembered as opposed to when faces are judged to be familiar. If it is assumed that *remember* and *familiar* responses isolate recollection and familiarity, respectively, then the finding that discrete cognitive operations are engaged across conditions is consistent with dual-process models of recognition memory, which propose that recollection and familiarity are two sources of mnemonic information. It should be noted, however, that the precise pattern of neural activity observed in the present studies for neural correlates of recollection and familiarity differs from the old/new effects typically reported, and possible reasons for this discrepancy will be explored below.

In contrast to the old/new effects observed for the recollection of information elicited by recently studied faces, a left parietal effect was observed across two studies that required retrieval of information about well-known famous faces in experiments designed to foster retrieval from semantic memory (Experiments 4 and 5). Most importantly, a left parietal effect (700 – 1100ms) was observed when information associated with famous faces was retrieved, while studied face recollection was associated with an earlier anterior effect (300 – 700ms) only. However, an anterior effect was also observed for famous faces from 500 – 700ms, and there was no evidence of a topographic difference between the anterior effects observed for famous and studied faces. This pattern of results suggests that while the anterior effect may be common to both types of face, only the retrieval of information associated with famous faces elicits the left parietal effect. The functional significance of the left parietal effect, and the potential importance of pre-existing semantic representations in determining the processes supporting retrieval from declarative memory, are discussed below.

Theoretical implications

The results of the studies described in this thesis have several important theoretical implications. Most importantly, the results support a dual-process view of episodic retrieval (Atkinson & Juola, 1974; Jacoby & Dallas, 1981; Mandler, 1980; Tulving, 1985; Yonelinas, 1994), while also providing new information about the identification and validation of neural correlates of recollection and familiarity. The question of the extent to which the ERP old/new effect is material independent or material specific (Johnson et al., in press) will be discussed; the conceptual priming hypothesis (Yovel & Paller, 2004) of the mid frontal ERP old/new effect will also be considered. The present results also have implications for the relationship between the semantic and episodic memory systems, and in particular for the question of whether common retrieval processes act upon information stored in these systems.

The neural correlate of recollection

The present results represent an important qualification to the view that recollection is generically indexed by a left parietal old/new effect. In a recent study, material dependent recollection-related old/new effects were observed for words studied under two different encoding conditions, yet left parietal effects were common to both conditions, supporting the conclusion that the left parietal effect reflects generic recollection processing (Johnson et al., in press). As Figure 54 shows, in the studies described in the present thesis, left parietal old/new effects were only observed for stimuli that were associated with pre-existing semantic representations (i.e., names and famous faces), while anterior old/new effects were observed for faces, whether they were associated with pre-existing semantic

representations (famous faces) and not (studied faces). This finding implies that a pre-existing semantic code is necessary for the left parietal effect to be observed, whereas the presence/absence of semantic representations has no bearing on whether the anterior effect is observed. Recent data showing that a left parietal effect is exclusively observed for stimuli associated with pre-existing representations⁹ (Cycowicz & Friedman, 2007) conforms with the view that an underlying semantic code is required for the left parietal index of recollection to be observed. It therefore seems to be the case that recollection processing differs as a function of the way that the information to be retrieved from memory is represented in the brain.

The prevailing view that the left parietal effect reflects generic recollection processing (Johnson et al., in press) appears to crucially depend upon the use of words or other previously learned information to be used as stimuli. Consistent with this view, frontally distributed old/new effects were observed in a recognition memory study using meaningless blobs, while there was no evidence of a left parietal effect (Groh-Bordin et al., 2006). A central conclusion of this thesis is that the view that the left parietal effect reflects generic recollection processing must be restricted to cases where the stimuli used are associated with pre-existing semantic representations. This conclusion remains tentative, however, because there may be other differences across stimulus categories which may have greater explanatory power that the presence/absence of pre-existing representations, including the

⁹ In the Cycowicz & Friedman (2007) study, a left parietal effect was observed for items that were not associated with a pre-existing semantic representation following explicit encoding instructions, but following incidental encoding instructions the same items did not elicit a left parietal effect. These data provide partial support for the view that pre-existing representations are necessary for the left parietal effect to be observed, and suggest that attending to novel items is sufficient to extract semantic representations from those items.



number of times an item has been encountered previously, and differences in discriminability that might entrain different strategies to support recollection.

Figure 54: Retrieval of contextual/associated information. Schematic depiction of ERP old/new effects observed across the studies described in this thesis. A – when a studied face was presented as a retrieval cue and episodic information was retrieved, at anterior (500 – 700ms) effect was observed. B – when a famous face was presented as a retrieval cue and associated information was retrieved, both anterior (500 – 700ms) and left parietal (700 – 1100ms) effects were observed. C – when a studied name was presented as a retrieval cue and episodic information was retrieved, a left parietal (500 – 700ms) effect was observed.

The comparison of previously unknown faces with words and famous faces in the studies presented here was based on theoretical accounts of the potential role of conceptual representations in recognition performance (Yovel & Paller, 2004; Voss & Paller, 2006). According to this hypothesis, faces of unknown individuals are devoid of conceptual representations prior to being studied in a recognition memory test; given the unorthodox patterns of old/new effects observed when using faces of unknown individuals in Experiments 1 and 2, both names and famous faces were specifically chosen as stimuli for subsequent experiments on the grounds the stimuli are associated with pre-existing conceptual representations. While other differences between the stimulus types may determine whether the left parietal effect is observed, any conclusion based on these differences would be *post hoc*. The possible role of pre-existing representations in determining the particular neural correlate of recollection that is observed is hypothesis-driven; while further research is required to fully endorse this view, it nevertheless represents a tentative conclusion derived form the research presented in this thesis.

The resemblance of the anterior old/new effect to the mid frontal effect typically interpreted as an index of familiarity-based retrieval is striking. In the interests of parsimony, it is tempting to conclude that the anterior effect reflects familiarity rather than recollection; however, the anterior effect observed for faces was dissociated from the mid frontal old/new effect observed for names on topographic grounds, and so an account of the anterior effect in terms of familiarity is not supported by the data. Furthermore, in Experiment 1 the anterior effect was modulated by the quality of information that was retrieved, and therefore it appears to function as if it indexes recollection rather than familiarity. Frontal effects are typically observed in source memory tests, but these frontal effects tend to have an inferior distribution on the right hemisphere (e.g., Wilding & Rugg, 1996), while the anterior effect identified across the present studies was maximal at superior sites. In Experiment 1, the anterior effect was dissociated from the late right frontal effect on both functional and topographic grounds.

The finding that faces (including famous faces), but not names, gave rise to an anterior neural correlate of recollection is consistent with the view that the ERP

old/new effect is material specific, at least under certain circumstances. Faces alone were associated with the anterior effect, which may suggest that the effect is specific to faces, or that some other feature of the facial stimuli determines the precise pattern of old/new effects that is observed. Recognition of faces has been associated with anterior old/new effects previously (Paller et al., 2001; Nessler et al., 2005); and more broadly, many researchers who investigate face processing argue that there are dedicated pathways for face processing (e.g., Kanwisher & Yovel, 2006). Based on these considerations, it may be the case that faces are treated separately in declarative memory from other types of information. Thus, there may be a specialized recollection process for faces, and that the activity of this face specific recollection process is indexed by the anterior old/new effect.

While the conclusion that there may be face specific processing in episodic memory is of great potential significance, there is some existing evidence that cautions against this view. A frontal effect was reported for recollection of pictorial stimuli (Schloerscheidt & Rugg, 1997); while it is unclear from the report whether this frontal activity reflects the mid frontal or late right frontal effects, or whether the activity resembles the anterior effect observed here, in this study the authors argued that the rich pictorial content of photographic images gives rise to differential recollection processing. In support of this view, an anterior effect that bears close resemblance to the effects described here for faces was identified in a study using photographs of objects where recollection was operationalised as the difference between remember and know waveforms (Duarte et al., 2004)¹⁰. Given

¹⁰Citing evidence from Duarte et al. (2004) as supporting evidence is problematic for two reasons: first, the authors did not discuss this anterior effect after reporting it; second, and more importantly, operationalising recollection as the difference between remember and know waveforms differs markedly from the standard correct rejection baseline typically used in the field. It is important that researchers are able to compare data and the use of non-standard operationalisations such as this poses serious problems for comparison of data sets.

that line drawings of objects were associated with a left parietal effect (Curran & Cleary, 2003), and photographic images of objects were associated with a left parietal effect and an additional anterior effect (Duarte et al., 2004), it remains possible that photographic images are recollected differently from less pictorially rich stimuli such as line drawings. The anterior effect observed here may therefore reflect recollection processing that acts upon visually rich stimuli. Whether the anterior effect is considered to be a face-specific or a pictorial-specific effect, the data presented here conform to the view that the ERP old/new effect is not material independent. These data are preliminary, however, and further experimentation manipulating stimulus materials is clearly required to help adjudicate between these two competing views.

One final possibility to be considered is the proposal outlined in Experiment 3 that the anterior effect observed for recollection contains the summation of the left parietal effect and an additional anterior effect. This proposal is an attempt to interpret the data within the framework of the typical old/new effects reported in recognition memory studies. By this account, when previously unknown faces elicit recollection two signals are observed at the scalp; the left parietal signal may reflect core recollection processing while the anterior signal reflects additional processing of pictorial content. While this "left parietal plus" view is attractive in its attempt at parsimony, it represents a somewhat convoluted account of the data. If the posterior portion of the old/new effect observed for recollection reflects a weak recollection signal, then it would be tempting to interpret the neural correlates of familiarity for faces observed here as reflecting recollection rather than familiarity. Rather, given that recollection and familiarity are most often modeled as having an independent relationship, it seems more plausible to interpret posterior activity as reflecting

familiarity that occurs during recollection rather than weak recollection. On this basis, the material specific account of the left parietal and anterior old/new effects is preferred.

The neural correlate of familiarity

Familiarity for faces was associated with posterior old/new effects in three of the studies described in this thesis. Importantly, the observed effects did not share the mid frontal distribution observed for names; rather, the familiarity effects had a posterior scalp distribution. The mid frontal effect is widely considered to be the neural correlate of familiarity because it has been shown to be equivalent after deep and shallow encoding (Rugg et al., 1998), and because it is observed for items thought to be recognized on the basis of familiarity, such as plurality-reversed lures and mirror-reversed line drawings of objects (Curran, 1999; Curran & Cleary, 2003). The mid frontal effect is considered to provide a generic index of familiarity because it has been observed for different types of stimuli such as words and pictures. Demonstrations of posteriorly distributed old/new effects associated with familiarity are therefore rather controversial (MacKenzie & Donaldson, 2007; Voss & Paller, 2006; Yovel & Paller, 2004;).

The reason why the face familiarity effect does not share the mid frontal distribution of the putative neural correlate of familiarity remains unclear. One possibility is that familiarity for faces is computed in a different way from familiarity for names, or stimuli associated with pre-existing representations more generally. Familiarity may result from different computations, including conceptual priming and perceptual priming (Jacoby, 1991). Given that previously unencountered faces cannot by definition be associated with pre-existing semantic

General Discussion

representations, then perhaps perceptual priming generates familiarity for stimuli that do not have semantic representations.

While the present results do not contribute to the debate concerning the conceptual priming hypothesis of the mid frontal effect directly (Voss & Paller, 2006), it is noteworthy that the mid frontal effect was only observed for names. Names are likely to be associated with semantic representations whereas faces that have only been encountered once before in the study phase of a recognition memory experiment are not associated with pre-existing representations. It seems likely that the existence of semantic representations is necessary for the classic mid frontal effect to be observed, although one caveat to this view concerns reports of mid frontal effects for blobs (Groh-Bordin et al., 2006) and faces (Nessler et al., 2005).

Despite the preceding consideration of the role of conceptual representations in determining whether the mid frontal effect is observed, other factors must be considered. Familiarity may only be available to support recognition performance in cases where there is sufficient inter-stimulus heterogeneity to provide a sufficiently high level of discriminability (Curran & Hancock, 2007). If this proposition is valid, then the question arises as to what process supports familiar responses when discriminability is low? In Experiments 1, 2 and 5 presented in this thesis, posterior effects were observed to correlate with familiarity, and these posterior effects appear to share the scalp distribution of a neural correlate of implicit memory (Rugg et al., 1998). Although a common distribution is insufficient evidence to posit common underlying cognitive operations, it may nevertheless be the case that, when discriminability is low, implicit memory processes must by engaged to support familiarity judgments. This proposal is unsatisfactory, however, because of the lack

of specification given to the implicit memory processing in question. An alternative view is that recollection supports familiarity-based judgments. By this logic, the left parietal effect reflects recollection and therefore any parietal effect observed must also be supported by recollection.

The preceding argument is undermined by the finding that posterior effects associated with familiarity-based judgments have never been demonstrated to be lateralized to the left hemisphere, as would be expected if the effects reflected the same underlying processing as recollection. According to the assumptions behind the topographic analysis of ERP data, a difference in distribution reflects the operation of distinct cognitive operations (Luck, 2005). Therefore, it is unlikely that the parietal effects observed for familiarity are due to recollection processing. Rather, some computation of familiarity based upon non-conceptual representations is the most likely generator of familiarity for faces. In the absence of conceptual representations, one tenable possibility is that perceptual representations are accessed to support familiarity, although of course this conclusion remains an open empirical question.

While recently studied faces were associated with a posterior old/new effect, no neural correlate of familiarity was observed for famous faces. The failure to observe a neural correlate of familiarity for famous faces may be a result of several different factors, including the fact that the activity of the neural population engaged when famous faces are familiar may not be detectable at the scalp, or that the effect was too small to be observed. One further possibility is simply that familiarity is only capable of retrieving information from episodic memory. By this account, there

may not be two independent bases for semantic retrieval, as is proposed for episodic retrieval according to dual-process models.

Relationship between episodic and semantic memory systems

The final two experiments described in this thesis allowed for the investigation of the question of whether common retrieval processes access episodic and semantic memories. In support of this view, left parietal effects were associated with the retrieval of information associated with names and with famous faces. To date, the left parietal effect has been exclusively reported in tests of episodic recognition memory, and therefore the demonstration of left parietal effects in tests designed to foster retrieval from semantic memory represents an important step in current understanding of memory retrieval. The left parietal effect is thought to reflect the orientation of attention to recollected information (Rugg & Curran, 2007), but this definition now appears to be too narrow. The data presented in this thesis suggest that the left parietal effect should be considered as reflecting the retrieval of information from declarative memory itself, including both the episodic and the semantic memory systems.

However, the possibility remains that individual episodes are accessed when information associated with famous faces is retrieved. If this is the case then the left parietal effect might simply reflect the retrieval of episodic information rather than retrieval from declarative retrieval more broadly. This scenario appears to be unlikely because episodic information is not typically available at a phenomenological level when identifying famous people. Rather, identifying famous people is accompanied by a general sense of knowing who the famous people are. In addition, at a theoretical level of analysis it is not parsimonious to

access individual episodic representations to perform a task that accessing one stable semantic representation might be capable of supporting. It therefore seems more likely that the left parietal effect reflects the retrieval of information from declarative memory rather than simply from episodic memory.

However, this conclusion raises the question of why familiarity is not considered to be associated with the left parietal effect. If familiarity also reflects the retrieval of information from declarative memory, then it would be expected that left parietal effects would be observed for familiarity in addition to recollection. One possibility is that the left parietal effect reflects the retrieval of qualitative information, whereas the mid frontal effect reflects the retrieval of quantitative information; this distinction stems from the Yonelinas (1994) dual-process model, where recollection and familiarity are characterized as being the processes supporting the retrieval of qualitative versus quantitative information, respectively. However, to reconcile this model of episodic retrieval with the observation of a left parietal effect for famous faces then the interpretation of the processing underlying the left parietal effect must be broadened to include the retrieval of qualitative information from both the semantic and episodic memory systems.

Future directions

The research presented in this thesis suggests that the ERP old/new effect may be material specific under certain circumstances. It appears that the presence or absence of pre-existing representations associated with the stimuli used to probe memory determines the pattern of old/new effects that is observed. However, in the absence of supporting data from closely related paradigms this conclusion is speculative. Future research investigating the generalisability of this conclusion is

clearly warranted. One strand to this research might query whether the anterior effect observed here as a neural correlate of recollection is specific to faces. In a similar vein, further studies designed to foster retrieval from semantic memory using stimuli other than famous faces might help to decide whether the left parietal effect is routinely observed when qualitative or contextual information is retrieved from declarative memory.

The hypothesis that familiarity can only serve as a basis for recognition when discriminability is sufficiently high (Curran & Hancock, 2007) requires rigorous testing. This hypothesis is readily testable by systematically varying test parameters to foster discriminability of certain levels across conditions. An ERP investigation of this issue might shed light on the proposition that the mid frontal effect is only observed when discriminability is high, and also whether posterior effects are observed when discriminability is low.

Another important direction would allow for a comparison of neural correlates of implicit memory (operationalized as the difference between miss and correct rejection waveforms, following Rugg et al., 1998) and familiarity. One problem with the posterior neural correlate of implicit memory, as it is currently proposed, is that studied items that are missed are likely to include items that are familiar but that fall below a decision criterion as well as items that are not familiar at all. It remains possible, therefore, that the neural correlate of implicit memory observed by Rugg et al. (1998) reflects perceptually-mediated familiarity rather than implicit memory. In addition, for reasons outlined above, the computations that underlie the vague concept of 'implicit memory' require to be carefully delineated for this research topic to progress further.

Conclusion

The retrieval of information from episodic memory is supported by multiple cognitive operations, each of which are engaged under different circumstances. Dual-process theories of recognition memory propose that recollection and familiarity are independent bases for making recognition judgments, but evidence from the study of event-related potentials (ERPs) suggests that neither recollection nor familiarity are functionally homogenous. Recollection may be associated with a left parietal old/new effect when the information to be retrieved from memory is associated with pre-existing semantic representations, and be associated with an anterior old/new effect when the information to be retrieved from memory has rich pictorial content. Most importantly, however, and regardless of the precise explanation of why multiple recollection signals are observed, the data presented here are inconsistent with single-process accounts of recognition memory.

Familiarity may also be computed by distinct cognitive operations under different circumstances. Mid frontal effects are observed for familiarity when the information to be retrieved from memory is associated with semantic or conceptual representations. In the absence of such conceptual representations the perceptual code associated with the information to be retrieved from memory may be diagnostic of previous occurrence, and leads to a posterior old/new effect being observed. This proposal rests upon the assumption that perceptual representations are formed before conceptual representations are consolidated into storage in semantic memory.

While the distinction between semantic and episodic memory systems is not challenged here, it appears that at least one common retrieval process accesses both

semantic and episodic memories. This finding is novel and must be considered speculative at present; nonetheless it generates more questions than definitive conclusions. The left parietal old/new effect, rather than reflecting the recollection of information from episodic memory, appears to reflect retrieval from declarative memory more broadly, including both semantic and episodic memories.

Finally, the predominant view that recollection and familiarity are material independent retrieval processes is clearly at odds with the data presented here. On the whole, the research described in this thesis may be considered to be consistent with dual-process models of recognition memory. However, based on the analysis of neural data, it would appear that dual-process models of recognition memory are outmoded. The studies presented here indicate that the dual-process constructs of recollection and familiarity may actually only have explanatory power at a cognitive level of analysis. At a neural level, neither recollection not familiarity appear to be homogenous processes. While cognitive models that were devised before the burgeoning popularity of brain imaging methods may be able to explain a wide variety of mnemonic phenomena, they do so without constraining theorizing with neural data. The current challenge for mnemonic theorists is to integrate behavioural and neural data to provide useful information about how memory functions and is organized. The unitary phenomenon of memory has been steadily fractionated since the time of patient H.M. (Scoville & Milner, 1957), and this present thesis offers further fractionation of the retrieval processes that support recognition memory.

References

Aggleton, J.P. & Brown, M.W. (1999). Episodic memory, amnesia and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences*, **22**, 425-444.

Allan, K., Wilding, E.L. & Rugg, M.D. (1998). Electrophysiological
evidence for dissociable processes contributing to recollection. *Acta Psychologica*,
98, 231-252.

Allison, T., Wood, C.C. & McCarthy, G. (1986). The central nervous system. In Coles, M.G.H., Donchin, E. & Porges, S.W. (eds.) *Psychophysiology: Systems, Processes and Applications*. London: Guildford Press, pp5-26.

Atkinson, R.C. & Juola, J.F. (1974). Search and Decision Processes in Recognition Memory. In Krantz, D.H., Atkinson, R.C., Luce, R.D. (eds.) *Contemporary Developments in Mathematical Psychology Volume 1: Learning, Memory and Thinking*. San Francisco: Freeman, pp. 243-293.

Azimian-Faridani, N. & Wilding, E.L. (2004). An event-related potential study of the revelation effect. *Psychonomic Bulletin & Review*, **11**, 926-931.

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

Baddeley, A. (2003). Double dissociations: Not magic but still useful. *Cortex*, **39**, 129-131.

Bruce, V. & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*, **77**, 305-327.

Cary, M. & Reder, L.M. (2003). A dual-process account of the list-length and strength-based mirror effects in recognition. *Journal of Memory & Language*, **49**, 231-248.

Coles, M.G.H. & Rugg, M.D. (1995). Event-related brain potentials: an introduction. In Coles, M.G.H. & Rugg, M.D. (eds.) *Electrophysiology of Mind: Event-Related Brain Potentials and Cognition*. London: Oxford University Press, pp1-26.

Coltheart, M. & Davies, M. (2003). Inference and explanation in cognitive neuropsychology. *Cortex*, **39**, 188-191.

Contact Precision, http://www.psylab.com.

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

Corley, M., MacGregor, L.J. & Donaldson, D.I. (2007). It's the way that you, er, say it: Hesitations in speech affect language comprehension. *Cognition*, **105**, 658-668.

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

Curran, T. (1999). The electrophysiology of incidental and intentional retrieval: ERP old/new effects in lexical decision and recognition memory. *Neuropsychologia*, **37**, 771-785.

Curran, T. (2000). Brain potentials of recollection and familiarity. *Memory* & *Cognition*, **28**, 923-938.

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

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

Curran, T. & Dien, J. (2003). Differentiating amodal familiarity from modality-specific memory processes: An ERP study. *Psychophysiology*, **40**, 979-988.

Curran, T. & Hancock, J. (2007). The FN400 indexes familiarity-based recognition of faces. *NeuroImage*, **36**, 464-471.

Cycowicz, Y.M. & Friedman, D. (2007). Visual novel stimuli in an ERP novelty oddball paradigm: Effects of familiarity on repetition and recognition memory. *Psychophysiology*, **44**, 11-29.

De Renzi, E., Liotti, M. & Nichelli, N. (1987). Semantic amnesia with preservation of autobiographical memory: A case report. *Cortex*, **3**, 194-216.

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

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

Dobbins, I.G., Khoe, W., Yonelinas, A.P. & Kroll, N.E.A. (2000). Predicting individual false alarm rates and signal detection theory: A role for remembering. *Memory & Cognition*, **28**, 1347-1356.

Donaldson, D.I., Allan, K. & Wilding, E.L. (2002). Fractionating episodic memory retrieval using event-related potentials. In: Parker, A., Wilding, E.L., Bussey, T. (eds.) *The Cognitive Neuroscience of Memory: Encoding and Retrieval*. Psychology Press, Hove, pp 39-58.

Donaldson, D.I. & Curran, T. (2007). Letter to the editor. *NeuroImage*, **36**, 488-489.

Donaldson, D.I., MacKenzie, G. & Davis, A. (2004). Your Face Looks Really Familiar and I Still Can't Remember Your Name! Poster presented at the 45th Annual Meeting of the Psychonomic Society, Toronto, Canada.

Donaldson, D.I., Petersen, S.E. & Buckner, R.L. (2001). Dissociating memory retrieval processes using fMRI: Evidence that priming does not support recognition memory. *Neuron*, **31**, 1047-1059.

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

Donaldson, D.I. & Rugg, M.D. (1999). Event-related potential studies of associative recognition and recall: Electrophysiological evidence for context dependent retrieval processes. *Cognitive Brain Research*, **8**, 1-16.

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

Donders, F.C. (1868). Over de snelheid van psychishe processen. *Onderzoe-Kingen Gedaan in Het Physiologisch Laboratorium Der Utrechtsche Hoogeschool, 1868-1869, Tweede Reeks*, II, 412-431. Translated by Koster, W.G. (1969). *Acta Psychologia*, **30**, 412-231.

Duarte, A., Ranganath, C., Winward, L., Hayward, D. & Knight, R. T. (2004). Dissociable neural correlates for familiarity and recollection during the encoding and retrieval of pictures. *Cognitive Brain Research*, **18**, 255-272.

Dunn, J.C. & Kirsner, K. (2003). What can we infer from double dissociations? *Cortex*, **39**, 1-7.

Düzel, E., Vargha-Khadem, F., Heinze, H.J. & Mishkin, M. (2001). Brain activity evidence for recognition without recollection after early hippocampal damage. Proceedings of the National Academy of Science, **98**, 8101-8106.

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

Dzulkifli, M.A. & Wilding, E.L. (2005). Electrophysiological indices of strategic episodic retrieval processing. *Neuropsychologia*, **43**, 1152-1162.

Eichenbaum, H., Otto, T. & Cohen, N.J. (1994). Two functional components of the hippocampal memory system. *Behavioural Brain Sciences*, **17**, 449-518.

Fortin, N.J., Wright, S.P. & Eichenbaum, H. (2004). Recollection-like memory retrieval in rats is dependent on the hippocampus. *Nature*, **431**, 188-191.

Fraser, C.S., Bridson, N.C. & Wilding, E.L. (2007). Controlled retrieval processing in recognition memory exclusion tasks. *Brain Research*, **1150**, 131-142.

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

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

Gabrieli, J.D.E., Vaidya, C.J., Stone, M., Francis, W.S., Thompson-Schill, S.L., Fleischman, D.A., Tinklenberg, J.R., Yesavage, J.A. & Wilson, R.S. (1999). Convergent behavioural and neuropsychological evidence for a distinction between identification and production forms of repetition priming. *Journal of Experimental Psychology: General*, **128**, 479-498.

Gallo, D.A., Weiss, J.A. & Schacter, D.L. (2004) Reducing false recognition with criterial recollection tests: Distinctiveness heuristic versus criterion shifts. *Journal of Memory & Language*, **51**, 473-493.

Gardiner, J.M., Ramponi, C. & Richardson-Klavehn, A. (2002). Recognition memory and decision processes: A meta analysis of remember, know, and guess responses. *Memory*, **10**, 83-98. Geng, H., Qi, Y., Li, Y., Fan, S., Wu, Y. & Zhu, Y. (2007).

Neurophysiological correlates of memory illusion in both encoding and retrieval phases. *Brain Research*, **1136**, 154-168.

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

Glanzer, M. & Adams, J.K. (1985). The mirror effect in recognition memory. *Memory & Cognition*, **13**, 8-20.

Glaser, E.M. & Ruchkin, D.S. (1976). *Principles of Neurobiological Signal Analysis*. New York: Academic Press.

Gratton, G. (1998). Dealing with artifacts: the EOG contamination of the event- related brain potential. *Behavior Research Methods Instruments & Computers*, **30**, 44-53.

Green, D.M. & Swets, J.A. (1966). Signal Detection Theory and *Psychophysics*. New York: Wiley.

Greenhouse, S.W. & Geisser, S. (1959). On the methods in the analysis of profile data. *Psychometrika*, **24**, 95-112.

Greve, A, Van Rossum, M.C.W. & Donaldson, D.I. (2007). Investigating the functional interaction between semantic and episodic memory: Convergent behavioural and electrophysiological evidence for the role of familiarity. *NeuroImage*, **34**, 801-814.

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

Haig, A.R., Gordon, E. & Hook, S. (1997). To scale or not to scale: McCarthy and Wood revisited. *Electroencephalography & Clinical Neurophysiology*, **103**, 323-325.

Handy, T.C. (2005). Basic principles of ERP quantification. In Handy, T.C. (ed.) *Event-Related Potentials: A Methods Handbook*. Cambridge, MA: MIT Press, pp33-55.

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

Hintzman, D.L., Caulton, D.A. & Levitin, D.J. (1998). Retrieval dynamics in recognition and list discrimination: further evidence of separate processes of familiarity and recall. *Memory & Cognition*, **26**, 449-462.

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

Huddy, V., Schweinberger, S.R., Jentzsch, I. & Burton, A.M. (2003). Matching faces for semantic information and names: An event-related brain potentials study. *Cognitive Brain Research*, **17**, 314-326. Huppert, F.A. & Piercy, M. (1978). The role of trace strength in recency and frequency judgements by amnesic and control subjects. *Quarterly Journal of Experimental Psychology*, **30**, 347-354.

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

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

Jacoby, L.L. & Kelley, C. (1991). Unconscious influences of memory: dissociations and automaticity. In Milner, A.D. & Rugg, M.D. (eds.) *The Neuropsychology of Consciousness*. London: Academic Press, pp201-233.

Jacoby, L.L., Yonelinas, A.P. & Jennings, J.M. (1997). The relation between conscious and unconscious (automatic) influences: A declaration of independence. In Cohen, J.D., Schooler, J.W. (eds). *Scientific approaches to the question of consciousness*. Hillsdale, NJ: Erlbaum. pp. 13–47.

Jasper, H.A. (1958). The ten-twenty system of the international federation. *Electroencephalography & Clinical Neurophysiology*, **10**, 371-375.

Johansson, M., Mecklinger, A. & Treese, A.C. (2004). Recognition memory for emotional and neutral faces: An event-related potential study. *Journal of Cognitive Neuroscience*, **16**, 1840-1853. Johnson, J.D., Minton, B.R. & Rugg M.D. (in press). Content-dependence of the electrophysiological correlates of recollection. *NeuroImage*.

Joordens, S. & Merikle, P.M. (1993). Independence or redundancy? Two models of conscious and unconscious influences. *Journal of Experimental Psychology: General*, **122**, 462-467.

Kanwisher, N. & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London B*, **361**, 2109-2218.

Katznelson, R.D. (1981). EEG recording, electrode placement, and aspects of generator localization. In Nunez, P. (ed.) *Electrical Fields of the Brain: The Neurophysics of EEG*. New York: Oxford University Press, pp176-213.

Knowlton, B.J. (1998). The relationship between remembering and knowing: A cognitive neuroscience perspective. *Acta Psychologica*, **98**, 253-265.

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

Kutas, M. & Dale, A. (1997). Electrical and magnetic readings of mental functions. In Rugg, M.D. (ed.) *Cognitive Neuroscience Studies in Cognition*. Cambridge, MA: MIT Press, pp197-241.

Kutas, M. & Hillyard, S.A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, **207**, 203-205.

Lorente de Nó, R. (1947). Analysis of the distribution of action currents of nerve in volume conductors. *Studies of the Rockefeller Institute of Medical Research*, **132**, 384-477.

Luck, S.J. (2005). An introduction to the event-related potential technique. Cambridge, MA.: MIT Press.

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

Macmillan, M.A. & Creelman, C.D. (1991). *Detection theory: A user's guide*. Cambridge University Press: Cambridge.

Mandler, G. (1980). Recognizing: The judgement of previous occurrence. *Psychological Review*, **87**, 252 – 271.

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

Mayes, A.R. (1992). Automatic memory processes in amnesia: how are they mediated? In Milner, A.D. & Rugg, M.D. (eds.) *The Neuropsychology of Consciousness. Foundations of Neuropsychology.* San Diego, CA: Academic Press, pp235-261.

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

McCarthy, G. & Wood, C.C. (1985). Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. *Clinical Neurophysiology*, **62**, 203-208.

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

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

Miller, G.A., Lutzenberger, W. & Elbert, T. (1991). The linked-reference issue in EEG and ERP recording. *Journal of Psychophysiology*, **5**, 273-276.

Münte, T.F., Brack, M., Grootheer, O., Wieringa, B.M., Matzke, M. & Johannes, S. (1997). Event-related brain potentials to unfamiliar faces in explicit and implicit memory tasks. *Neuroscience Research*, **28**, 223-233.

Murdock, B.B. (1997). Context and mediators in a theory of distributed associative memory (TODAM2). *Psychological Review*, **104**, 839-862.

Naveh-Benjamin, M., Guez, J. & Sorek, S. (2007). The effects of divided attention on encoding processes in memory: Mapping the locus of interference. *Canadian Journal of Experimental Psychology*, **61**, 1-12.

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

Nessler, D., Mecklinger, A. & Penney, T. B. (2005). Perceptual fluency, semantic familiarity and recognition-related familiarity: An electrophysiological exploration. *Cognitive Brain Research*, **22**, 265-288.

Neuromedical Supplies, http://www.neuro.com.

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

Otten, L.J. & Rugg, M.D. (2005). Interpreting event-related brain potentials. In Handy, T.C. (ed.) *Event-Related Potentials: A Methods Handbook*. Cambridge, MA: MIT Press, pp3-16.

Paller, K.A., Gonsalves, B., Grabowecky, M., Bozic, V.S. & Yamada, S. (2000). Electrophysiological correlates of recollecting faces of known and unknown individuals. *NeuroImage*, **11**, 98-110.

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

Perry, N.W. (1966). Signal versus noise in evoked potential. *Science*, **153**, 1022.

Picton, T.W., Bentin, S., Berg, P., Donchin, E., Hillyard, S.A., Johnson, R.,
Miller, G.A., Ritter, W., Ruchkin, D.S., Rugg, M.D. & Taylor, M.J. (2000).
Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiology*, **37**, 127-152.
Picton, T.W., Lins, O.G. & Scherg, M. (1994). The recording and analysis of event-related potentials. In Boller, F. & Grafman, J. (eds.) *Handbook of Neuropsychology*. Amsterdam: Elsevier, pp429-499.

Price, C.J. & Friston, K.J. (1997). Cognitive conjunction: a new approach to brain activation experiments. *NeuroImage*, **5**, 261-270.

Reed, A.V. (1973). Speed-accuracy trade-off in recognition memory. *Science*, **181**, 574-576.

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

Rhodes, S.M. & Donaldson, D.I. (in press). Association and not semantic relationships elicit the N400 effect: electrophysiological evidence from an explicit language comprehension task. *Psychophysiology*.

Richardson-Klavehn, A. & Bjork, R.A. (1988). Measures of memory. Annual Review of Psychology, **39**, 475-543.

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

Rotello, C.M. & Heit, E. (2000). Associative recognition: a case of recall-toreject processing. *Memory & Cognition*, **28**, 907-922. Ruchkin, D.S. (1988). Measurement of event-related potentials: signal extraction. In Picton, T.W. (ed.) *Handbook of Electroencephalography and Clinical Neurophysiology: Vol. 3. Human Event-Related Potentials*. Amsterdam: Elsevier, pp7-43.

Ruchkin, D.S., Johnson, R. & Friedman, D. (1999). Scaling is necessary when making comparisons between shapes of event-related potential topographies: a reply to Haig et al. *Psychophysiology*, **36**, 832-834.

Rugg, M.D. (1995). Event-related potential studies of human memory. In Gazzaniga, M.S. (ed.) *The Cognitive Neurosciences*. Cambridge, MA: The MIT Press.

Rugg, M.D. & Coles, M.G.H. (1995). The ERP and cognitive psychology. In Coles, M.G.H. & Rugg, M.D. (eds.) *Electrophysiology of Mind: Event-related potentials and cognition*. New York: Oxford University Press.

Rugg, M.D., Cox, C.J.C., Doyle, M.C. & Wells, T. (1995). Event-related potentials and the recollection of low and high frequency words. *Neuropsychologia*, **33**, 471-484.

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

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

Rugg, M.D., Roberts, R.C., Potter, D.D., Pickles, C.D. & Nagy, M.E.

(1991). Event-related potentials related to recognition memory: effects of unilateral temporal lobectomy and temporal lobe epilepsy. *Brain*, **114**, 2313-2332.

Rugg, M. D. & Yonelinas, A. P. (2003). Human recognition memory: A cognitive neuroscience perspective. *Trends in Cognitive Sciences*, **7**, 313-319.

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

Schloerscheidt, A.M. & Rugg, M.D. (1997). Recognition memory for words and pictures: an event-related potential study. *Neuroreport*, **8**, 3281-3285.

Schloerscheidt, A.M. & Rugg, M.D. (2004). The impact of change in stimulus format on the electrophysiological indices of recognition. *Neuropsychologia*, **42**, 451-466.

Semlitsch, H.V., Anderer, P., Schuster, P. & Presslich, O. (1986). A solution for reliable and valid reduction of ocular artefacts applied to the P300 ERP. *Psychophysiology*, **23**, 695–703.

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

Shallice, T. & Warrington, E.K. (1970). Independent functioning of verbal memory stores: a neuropsychological study. *Quarterly Journal of Experimental Psychology*, **22**, 261-273.

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

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

Spencer, K.M. (2005). Averaging, detection, and classification of single-trial ERPs. In Handy, T.C. (ed.) *Event-Related Potentials: A Methods Handbook*. Cambridge, MA: MIT Press, pp209-227.

Squire, L.R. & Zola, S.M. (1998). Episodic memory, semantic memory, and amnesia. *Hippocampus*, **8**, 205-211.

Srinivasan, R., Tucker, D.M. & Murias, M. (1998). Estimating the spatial nyquist of the human EEG. *Behavior Research Methods Instruments & Computers*, **30**, 8-19.

Sternberg, S. (1969). The discovery of processing stages: extensions of Donders' method. *Acta Psychologica*, **30**, 276-315.

Sternberg, S. (2001). Separate modifiability, mental modules, and the use of pure and composite measures to reveal them. *Acta Psychologica*, **106**, 147-246.

Strong Jr., E.K. (1912). The effect of length of series upon recognition memory. *Psychological Review*, **19**, 447–462.

Tendolkar, I., Schoenfeld, A., Golz, G., Fernández, G., Kühl, K. P., Ferszt, R. & Heinze, H. J. (1999). Neural correlates of recognition memory with and without recollection in patients with Alzheimer's disease and healthy controls. *Neuroscience Letters*, **263**, 45-48.

Tiddeman, B., Burt, D.M. & Perrett, D. (2001). Computer graphics in facial perception research. *IEEE Computer Graphics and Applications*, **21**, 42-50.

Trenner, M.U., Schweinberger, S.R., Jentzsch, I. & Sommer, W. (2004). Face repetition effects in implicit and explicit tasks: An event-related brain potentials study. *Cognitive Brain Research*, **21**, 388-400.

Tsivilis, D., Otten, L.J. & Rugg, M.D. (2001). Context effects on the neural correlates of recognition memory: An electrophysiological study. *Neuron*, **31**, 497-505.

Tucker, D.M. (1993). Spatial sampling of head electrical fields: the geodesic sensor net. *Electroencephalography & Clinical Neurophysiology*, **87**, 154-163.

Tulving, E. (1972). Episodic and semantic memory. In Tulving, E. & Donaldson, W. (eds.) *Organization of Memory*. New York: Academic Press, pp381-403.

Tulving, E. (1983). *Elements of Episodic Memory*. Oxford: Oxford University Press.

Tulving, E. (1985). How many memory systems are there? *American Psychologist*, **40**, 385-398.

Tulving, E. (2002). Episodic memory: from mind to brain. *Annual Review of Psychology*, **53**, 1-25.

Tulving, E., Hayman, C.A.G. & MacDonald, C.A. (1991). Long-lasting perceptual priming and semantic learning in amnesia: A case experiment. *Journal of Experimental Psychology: Learning, Memory & Cognition*, **17**, 595-617.

Urbach, T.P. & Kutas, M. (2002). The intractability of scaling scalp distributions to infer neuroelectric sources. *Psychophysiology*, **39**, 791-808.

US Social Security Records (2004). Taken from the internet on 12th October 2004: <u>www.ssa.gov/OACT/babynames/1999/top1000of70s.html</u>.

Vargha-Khadem, F., Gadian, D.G., Watkins, K.E., Connelly, A., Van Paesschen, W. & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science*, **277**, 376-380.

Verleger, R. (1991). The instruction to refrain from blinking affects auditory
P3 and N1 amplitudes. *Electroencephalography & Clinical Neurophysiology*, 78, 240-251.

Vilberg, K.L., Moosavi, R.F. & Rugg, M.D. (2006). The relationship between electrophysiological correlates of recollection and amount of information retrieved. *Brain Research*, **1122**, 161-170.

von Hippel, W. & Hawkins, C. (1994). Stimulus exposure time and perceptual memory. *Perception & Psychophysics*, **56**, 525-535.

Voss, J.L. & Paller, K.A. (2006). Fluent conceptual priming and explicit memory for faces are electrophysiologically distinct. *Journal of Neuroscience*, **26**, 926-933.

Wagner, A.D., Shannon, B.J., Kahn, I. & Buckner, R.L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Science*, **9**, 445-453.

Wheeler, M.E., Petersen, S.E. & Buckner, R.L. (2000). Memory's echo: Vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 11125-11129.

Wilding, E.L. (2000). In what way does the parietal ERP old/new effect index recollection? *International Journal of Psychophysiology*, **35**, 81-87.

Wilding, E.L. (2006). On the practice of rescaling scalp-recorded electrophysiological data. *Biological Psychology*, **72**, 325-332.

Wilding, E.L., Doyle, M.C. & Rugg, M.D. (1995). Recognition memory with and without retrieval of context: an event-related potential study. *Neuropsychologia*, **33**, 743-767.

Wilding, E.L. & Rugg, M.D. (1996). An event-related potential study of recognition memory with and without retrieval of source. *Brain*, **119**, 889-905.

Wilding, E.L. & Rugg, M.D. (1997). An event-related potential study of memory for words spoken aloud or heard. *Neuropsychologia*, **9**, 1185-1195.

Windmann, S., Urbach, T.P. & Kutas, M. (2002). Cognitive and neural mechanisms of decision biases in recognition memory. *Cerebral Cortex*, **12**, 808-817.

Wood, C.C. (1987). Generators of event-related potentials. In Halliday, A.M., Bulter, S.R. & Paul, R. (eds.) *A Textbook of Clinical Neurophysiology*. John Wiley & Sons Ltd, pp535-567.

Wood, C.C. & Allison, T. (1981). Interpretation of evoked-potentials: a neurophysiological perspective. *Canadian Journal of Psychology*, **35**, 113-135.

Woodruff, C.C., Hayama, H. & Rugg, M.D. (2006). Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Cognitive Brain Research*, **1100**, 125-135.

Yonelinas, A.P. (1994). Receiver-operating characteristics in recognition memory: Evidence for a dual-process model. *Journal of Experimental Psychology: Learning, Memory and Cognition*, **20**, 1341-1354.

Yonelinas, A.P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, **46**, 441-517.

Yonelinas, A.P., Kroll, N.E.A., Dobbins, I., Lazzara, M. & Knight, R.T. (1998). Recollection and familiarity deficits in amnesia: Convergence of rememberknow, process dissociation, and receiver operating characteristic data. *Neuropsychology*, **12**, 323-339. Yonelinas, A.P., Otten, L.J., Shaw, K.N. & Rugg, M.D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *The Journal of Neuroscience*, **25**, 3002-3008.

Yovel, G. & Paller, K.A. (2004). The neural basis of the butcher-on-the-bus phenomenon: When a face seems familiar but is not remembered. *NeuroImage*, **21**, 789-800.

Appendix I

This table lists names of famous people whose photographs were used to make stimuli for Experiments 4 and 5. All photographs were taken from the internet.

Britney Spears	Celine Dion	Shannon Doherty	Robbie Williams	
Zoe Ball Christina	Janet Jackson Catherine Zeta	Harriet Harman	Paul Daniels	
Aguilera Charlie	Jones Phillipa Forrester Sara Michelle	Beyonce Knowles	Rolf Harris Michael	
Dimmock		Al Pacino	Howard	
Kate Hudson	Geller Tasmin	Anthony Hopkins Arnold	Michael Portillo	
Sharon Stone Whitney	Outhwaite	Schwarzenegger	Michael Owen	
Houston	Dido	Bill Clinton	Prince Charles	
Kylie Minogue	Anne Charlston	John Prescott	Bruce Willis	
Mina Sovari Pamela	Tina Turner	Robert Di Niro	Pete Sampras George	
Anderson Andie	Meg Ryan	George Michael	Clooney	
McDowell	Kim Bassinger	David Blunkett	John Peel	
Julie Andrews	Liz Hurley	Kevin Costner	Tony Blair	
Anthea Turner	Julia Roberts	Lennox Lewis	Joe Pesci	
Jennifer Aniston	Cybil Shephard	Mike Tyson	Diarmuid Gavin	
Kate Winslet	Edith Bowman	Sylvester Stallone	Tommy Walsh James	
Natalie Portman	Carrie Fisher	John Malkovitch	Cromwell	
Marilyn Monroe	Nigella Lawson	Antonio Banderas	Tom Cruise	
Nicole Kidman Natalie	Mylene Klaas	Jude Law	Sean Astin	
Umbruglia	Lorraine Kelly	Denzell Washington	Scott Baio	
Cameron Diaz	Joely Richardson	Ewan McGregor	John Ritter	

Carole	Charlotta Churah	Laonarda DiCanria	Poh Hosking	
Voluennan			DUU HUSKIIIS	
Drew Barrymore	Jamie Lee Curtis	Nicholas Cage	Didier Agathe Prince Naseem	
Jodie Foster	Katie Melua	David Bowie	Hamed	
Cindy Crawford	Kelly Brook	Sean Connery	Ian Rankin	
Princess Diana	Christina Ricci Scarlet	Pierce Brosnan	Ron Atkinson	
Courtney Cox	Johansson Rebecca De	Matt Damon	Rodger Waters	
Cher Gwyneth	Mornay	Alec Baldwin	Frankie Detori Stephen	
Paltrow	Helen Hunt Alyson	David Beckham	Hawking	
Goldie Hawn	Hannigan	David Duchovny	David Gower Duncan	
Geri Halliwell	Julia Stiles Tara Palmer	John Cleese	Goodhew	
Kim Bassinger	Tomkinson	Mel Gibson	Kurt Cobain	
Judy Finnigan	Patsy Kensit	Martin Kemp	Giovanni Ribisi	
Uma Thurman	Jennifer Grey Andrew Lloyd	John Major	Eric Sykes Benicio Del	
Alan Shearer	Webber	Jeffrey Archer	Torro	
Tara Reid	Eric Clapton	Damon Albarn	Christopher Lee	
Joanna Lumley	Emelio Estevez	Guy Pierce	Steve Buscemi	
Winona Ryder	Iggy Pop	Jimmy Carr	David Gray Michael	
Davina McCall Barbara	Richard Madley Christopher	Kris Kristofferson	Madson	
Streisand	Eccleston	Mark Wahlberg	Rob Lowe	
Jennifer Lopez	Chris Rock			

Appendix II

This table lists the names used as study phase stimuli in Experiments 1,2,3 and 5. Names were taken from US social security records

(<u>http://www.ssa.gov/OACT/babynames/1999/top1000of70s.html</u>), and represent the most common names chosen for children born in the 1970s. To enhance ecological validity, some Scottish names have been added to the American names in the list.

Aaron	Chad	Flo	Joseph	Misty	Sebastian
Adam	Charles	Frances	Joshua	Monica	Seumas
Alana	Charlotte	Frank	Juan	Monty	Shane
Alasdair	Cheryl	Fraser	Julie	Nancy	Shannon
Alexander	Christina	Gary	Justin	Nathan	Sharon
Alison	Christine	Gemma	Karen	Nicholas	Simon
Amanda	Christopher	George	Kathleen	Nicole	Sophie
Amber	Christy	Geraldine	Keith	Nina	Stacy
Amy	Corey	Glenn	Kelly	Oliver	Stanley
Andrea	Craig	Gordon	Kendra	Olivia	Stephanie
Andrew	Crystal	Graham	Kenneth	Pamela	Steven
Angela	Cynthia	Gregory	Kevin	Patricia	Susan
Ann	Dana	Harry	Kimberly	Patrick	Tammy
Annette	Daniel	Heather	Kristin	Patsy	Tanya
Anthony	Danielle	Heidi	Larry	Paul	Tara
April	David	Hilda	Laura	Percy	Teresa
Archie	Dawn	Holly	Lauren	Peter	Terry
Arnold	Dean	Hugh	Leonard	Phillip	Thomas
Audrey	Deborah	Ian	Leslie	Rachel	Tiffany
Barbara	Denise	Imogen	Lianne	Randy	Timothy
Benjamin	Dennis	James	Linda	Raymond	Tina
Betsy	Derek	Jamie	Lisa	Rebecca	Todd
Bill	Diane	Jane	Lori	Reginald	Tonya
Bob	Dionne	Jason	Luis	Richard	Tracy
Bradley	Donald	Jeffrey	Marcus	Robert	Travis
Brandon	Donna	Jemima	Maria	Robin	Troy
Brandy	Douglas	Jennifer	Mark	Rodney	Veronica
Brenda	Edward	Jeremy	Martha	Ronald	Victor
Brian	Edwin	Jerry	Mary	Ruairidh	Vivien
Bridget	Elizabeth	Jesse	Matilda	Russell	Wanda
Bruce	Emelda	Jessica	Matthew	Ryan	Wendel
Calum	Emily	Jill	Maurice	Samuel	Wendy
Camila	Eric	Joel	Melanie	Sandra	Wilbur
Carlos	Erica	John	Melissa	Sarah	William
Carrie	Erin	Jonathan	Michael	Scott	Xavier
Catherine	Fiona	Jose	Michelle	Sean	Yann