The Neural Correlates of Repeated Memory Encoding and Content Reinstatement

Carolin Sievers

A thesis submitted in partial fulfilment of the requirements of the University of East Anglia for the degree of Doctor of Philosophy.

Research undertaken in the School of Psychology, University of East Anglia.
January 2018

The Neural Correlates of Repeated Memory Encoding and Content Reinstatement

Abstract

The present thesis reports findings from experiments investigating the neural correlates of subsequent source memory performance, repetition and reinstatement of item and source information. Electrophysiological and haemodynamic response data were obtained in two experimental paradigms further investigating effects of encoding modality and encoding context. The primary aim was to identify how neural pattern similarity was influenced by changes to perceptual stimulus features or changes to encoding task instructions, with a particular focus on the role of pattern reactivation. The first set of experiments (Chapters 3 & 4) examined the effects of encoding modality on source memory processes and repetition during study and test phases. Representational similarity analysis of the fMRI data revealed modality-independent and modality-dependent source memory effects, suggesting that reactivation of different stimulus features predicted source memory performance when stimuli are repeatedly presented. Overall, the results provide evidence for pattern reactivation to benefit source memory formation and retrieval. The second set of experiments (Chapters 5 & 6) investigated the effects of encoding items repeatedly in the same context or across multiple contexts. Pattern reactivation in the same task condition was shown to enhance source memory for the encoding context. However, lower levels of reactivation were associated with successful source memory performance when stimuli were associated with multiple contexts. Together with the EEG data, the results provide evidence for distinct mechanisms to underlie successful context encoding when items were either repeatedly encoded in the same context or in different contexts. Moreover, results from the EEG analyses suggested that repetition effects predict subsequent source memory performance when they occur in a similar time window as the late parietal component, which is commonly related to recollection. Taken together, the present research advances our understanding of repeated encoding of item and source memory information and leads to novel directions for future research.

Contents

List of Tables

List of Figures

Acknowledgements

I would like to thank my examiners for taking the time to read and assess this thesis. A huge thank you to my supervisory team for always providing excellent guidance and support. Thank you to my primary supervisor, Louis Renoult, for the great opportunities that came with this PhD, including all the conferences I really enjoyed, being introduced to a large number of exciting people in the field and, of course, running the first fMRI experiments at the Norfolk & Norwich University Hospital. I believe your relentless optimism and patience have made me always want to do that little bit better. Thank you to Andrew Bayliss for continuously giving the best advice and making me realise that it was all going to be ok. Thank you Heidi Bonnici for joining the supervisory team and providing not only technical fMRI support but also a safe space to express worries and concerns. Thank you to Michael Hornberger for agreeing to becoming my secondary supervisory when we needed you and for providing valuable insights.

I have to also thank Delia, Diana, Carmen and Vicky for being the best people to share this journey with. I could not have done this without you and I am truly grateful for all the unconditional emotional and professional support.

Thank you to my parents for their ongoing support and encouragement, despite having no idea what I really do “for a living”.

Thank you to Christina for being an amazing friend and not only always lifting my spirits but also giving me shelter during my final months in Norwich. Thanks to Tom and Jack for entertaining me to the maximum and looking after me.

Thank you to Fraser Smith, the radiographers at the NNUH and the Cabeza Lab for being highly instrumental in the process of obtaining and analysing all the brain data.

Finally, I would also like to extend a thank you to everyone in the School of Psychology. Thanks to the admin team for always finding solutions and making sure everything works smoothly. Thanks to students and staff for all the support that was provided at different stages and in different forms. I learned a lot, but more importantly, made many friends and thoroughly enjoyed my time at UEA.

Author’s declaration

I declare that the work contained in this thesis has not been submitted for any other award and that it is all my own work. I also confirm that this work fully acknowledges opinions, ideas and contributions from the work of others.

Parts of this work has been presented at conferences:

Poster Presentations

Sievers, C., Smith, F. W., & Renoult, L. (2017). *Neural similarity patterns across repeated memory encoding are further influenced by the modality stimuli are presented in: An fMRI study.* Presented at the Cognitive Neuroscience Society Meeting, San Francisco, March 2017.

Renoult, L., Sievers, C., Spriggs, M., & Bayliss, A. P. (2017). *The neural correlates of successful source encoding and recognition.* Presented at the Cognitive Neuroscience Society Meeting, San Francisco, March 2017.

Any ethical clearance for the research presented in this thesis has been approved. Approval has been sought and granted by the School of Psychology Ethics Committee at the University of East Anglia.

Name: Carolin Sievers

Signature:

Date:

SECTION 1

–

Neuroimaging Studies of Memory Encoding and Retrieval

Chapter 1 – General introduction: Neuroimaging studies of memory encoding and retrieval

Over the course of our lifetime, we will constantly acquire new information, integrate such novel information into existing knowledge and retrieve it when necessary. However, not everything we learn will be remembered. Moreover, sometimes, we may remember that an event took place but cannot recollect specific details about the context it took place in, such as who told us a piece of information, where we heard about it or how we felt about it. The impact of our ability to correctly remember events and associated details is far-reaching. For instance, there may be no dramatic consequences when we go swimming in the sea in Norfolk, however, if we went on holidays to California and forgot about the time David Attenborough told us about frequent shark attacks at a nearby beach, we may put ourselves in a very dangerous situation. Being able to form, store and retrieve episodic memories is regarded as important for human survival (Tulving, 2002). Moreover, understanding how the healthy brain creates new memories to later retrieve them successfully may help to further understand the numerous clinical conditions associated with memory loss or impairment.

1.1 Memory systems and processes

The complexity of human memories is reflected in the multitude of different memory systems that have been proposed. A prominent taxonomy of memory systems broadly categorises long-term memory into declarative and procedural memories (e.g., Squire, 2004). The declarative memory system allows us to explicitly store and retrieve representations with conscious awareness, while the non-declarative memory system is more concerned with implicit changes in behaviour encompassing procedural skills, conditioning and priming (see Milner, Squire, & Kandel, 1998). It has been suggested that clear-cut memory taxonomies, as proposed by the declarative/non-declarative distinction for example, are not capturing the vast complexity of memory systems and associated processing modes. The component process framework (Moscovitch, 1992), on the other hand, appears to be more consistent with evidence from functional neuroimaging. It proposes that multiple memory systems and processing modes lead to numerous different components that are involved in processing memories. Rather than attributing just one function to one brain region, it focuses on the multiple functions and connections between brain regions that have been shown to be involved in different processes (Cabeza & Moscovitch, 2013).

The present research is concerned with the formation and retrieval of declarative memories. Broadly speaking, declarative memories are sub-served by the medial temporal lobe (MTL) and stored in the neocortex (Milner et al., 1998). Declarative memories can be further divided into semantic and episodic memories (Tulving, 1972). Semantic memories include context-independent facts and general knowledge one holds about the world (Tulving, 2002). Episodic memories, on the other hand, represent personal past experiences and events that can be re-experienced (Schacter, Wagner, & Buckner, 2000; Tulving, 2002). Thus, an episodic memory includes additional information about an event, e.g., where or when it took place (Nyberg et al., 1996). These contextual details accompanying a particular event are the essence of episodic memory and the ability to re-experience events along with the retrieval of additional qualitative information is referred to as *recollection* (Tulving, 2002). However, sometimes a previously encountered item may also be recognised without the ability to recall any further details of the encoding episode, which is referred to as a *familiarity* judgement.

1.2 How declarative memory is tested

In addition to multiple memory systems, memory research may be concerned with different memory processes. Memories are the product of encoding, consolidation and retrieval of information. The present research is concerned with the encoding and retrieval of episodic memories. Neuroimaging research commonly employs subsequent memory paradigms to address questions relating to the encoding of episodic memories. In a subsequent memory paradigm, neural activity is recorded during a study phase, when relevant material is encoded while participants perform an encoding task, e.g., semantic categorization of the presented stimuli. In a subsequent test phase, retrieval of previously encoded material is probed. The behavioural results from the test phase allow us to sort the encoding trials into subsequently correct and incorrect item and source memory judgements (subsequent memory paradigm reviewed in Paller & Wagner, 2002). Resulting differences in neural activity between subsequently remembered and forgotten stimuli are termed

Dm effects or *subsequent memory effects* (Paller, Kutas, & Mayes, 1987). When neural activity is additionally recorded during the test phase, researchers can investigate both, encoding and retrieval of information.

During the test phase, several properties of episodic memories can be probed. Most commonly, participants are asked to decide whether a stimulus has been presented before (old/new judgment) to measure item memory recognition, which can be achieved by recollection or familiarity. Therefore, in addition to assessing whether particpants are able to correctly recognise an item as old, there are various ways to assess episodic memory properties, whether it is by probing contextual details (recognition-source memory paradigm), associated awareness (remember-know procedure) or degree of confidence associated with retrieval (reviewed in Diana, Yonelinas, & Ranganath, 2007). In a recognition-source memory paradigm, stimuli presented during the encoding phase are associated with different sources, i.e., contextual details that will later be probed in the test phase. In the subsequent test phase, participants are asked to make and old/new judgment followed by a source memory judgement, though the two questions assessing item and source memory have also been combined previously (e.g., Estrada-Manilla & Cansino, 2012). Source memory tasks require the retrieval of specific, criterial information from the study phase (Johnson, Hashtroudi, & Lindsay, 1993). Such criterial information may concern perceptual (e.g., background colour), emotional (e.g., emotional thoughts during encoding), semantic (e.g., semantic category of an item) or spatial details from the study phase (e.g., spatial location on screen; Mitchell & Johnson, 2009). Research has shown that source memory is functionally distinct from item memory, which was suggested to be the result of additional reconstruction and decision-making processes taking place during source monitoring (Bröder & Meiser, 2007). Source memory, therefore, provides objective insights into qualitative characteristics or richness of a memory. The recognition-source memory paradigm is considered to be an objective measure of recollection, because it directly assesses source memory for contextual features that were acquired during the study phase. In signal detection theory, correct old judgements are referred to as *hits*, correct new judgements are termed *correct rejections*, old stimuli incorrectly judged as new are termed *misses*, and new stimuli incorrectly judged as old are *false alarms* (Banks, 1970; Lockhart & Murdock, 1970). These terms will be used throughout this manuscript with a further division of *hits* into *hits+*, referring to correct item and correct source memory, and *hits*-, referring to correct item but incorrect source memory judgements.

An alternative, more subjective measure of recollection is the remember-know (R-K) procedure (Tulving, 1985), where participants judge items presented at test as ‘remember’ (recollection), ‘know’ (familiarity) or new. It has been noted that the R-K procedure may assess memory strength, i.e., low and high familiarity/recollection rather than differentiating familiarity and recollection (Eldridge, Sarfatti, & Knowlton, 2002; Wixted, 2009). Furthermore, this procedure relies upon participants’ ability to accurately identify a memory as recollected or familiar (Voss & Paller, 2008b). This is in contrast with the recognition-source paradigm, where source memory is assessed objectively and controlled, criterial reinstatement can be measured. However, although correct source memory judgements reflect recollection, incorrect source judgements may not always reflect familiarity, as an untested aspect of the encoding episode may still be remembered (see Voss & Paller, 2017). Though there may be notable differences between the recognition-source memory paradigm and the R-K procedure, some have suggested that correct source memory judgements reflect recollection, while incorrect source judgements may rely more on familiarity processes (Squire, Wixted, & Clark, 2007). Therefore, although the present research employed a recognition-source paradigm, results from research using the R-K procedure will be taken into account in the following review of the literature.

1.3 Repetition and memory

The majority of research investigating subsequent memory effects has been carried out in the context of learning during a single study episode. A large amount of information we remember, however, has been experienced multiple times, whether we consciously rehearsed it or implicitly encountered the information repeatedly. The idea that rehearsal is associated with improved retention of information has been of interest to researchers and philosophers for over a century (Ebbinghaus, 1885/1964). Subsequent memory performance has frequently been shown to be improved by repeated encoding of information (e.g., Baddeley, 1978; Cepeda, Pashler, Vul, Wixted, & Rohrer, 2006; Crowder, 1976; Davachi, Maril, & Wagner, 2001; Glenberg, Smith, & Green, 1977; Greene, 1987; Mechanic, 1964;

Opitz, 2010; Ranganath, Cohen, & Brozinsky, 2005; Reagh & Yassa, 2014; Van Strien, Hagenbeek, Stam, Rombouts, & Barkhof, 2005).

The cognitive and neural mechanisms underlying repetition-related memory improvements have been proposed in a number of theoretical accounts. Two somewhat opposing theoretical accounts, initially based on behavioural results, are the reactivation view and the encoding variability view. The reactivation view proposes that repetition leads to reactivation of the memory, making the (cognitive and/or neural) representation more stable (Benjamin & Tullis, 2010; Thios & D'Agostino, 1976). Reactivation may occur during repeated encoding or the retrieval of information with the aim to generalise across previous, related experiences in order to react to an event appropriately (see Howard Eichenbaum, 2000). Along the same lines, some psychological theories aim to explain the role of reactivation during successful retrieval. Two such theories are the encoding specificity principle (Tulving, 1983; Tulving & Thomson, 1973) and the transfer-appropriate proessing account (Morris, Bransford, & Franks, 1977). Both theories imply that some form of reactivation has to take place between encoding and retrieval, as they suggest successful retrieval to be based on similar operations taking place during study and test (see also Kolers, 1973). The encoding variability view, on the other hand, posits that each stimulus presentation is uniquely encoded, leading to an increase in number and variety of retrieval cues and traces (Bower, 1972; Hintzman, 1986; Martin, 1968; Nadel & Moscovitch, 1997). Encoding variability is based on studies demonstrating the beneficial effects of spaced learning when compared to massed learning, with the proposal that the longer the repetition lag, the more independent two events will be encoded as (e.g., Bray, Robbins, & Witcher, 1976). However, other behavioural experiments failed to report beneficial effects of encoding variability on memory retrieval (Postman & Knecht, 1983).

As the proposed concepts of multiple traces and reactivation are difficult to observe in behavioural measures and may occur outside of the participant's awareness (Levy & Wagner, 2013), theories that consider brain measures to explain psychological effects may provide further insights. One such theory is the complimentary learning systems (CLS) framework, which may also partly reconcile the discrepant proposals made by the reactivation view and the encoding variability view. The CLS account proposes that the hippocampus and neocortex play computationally and functionally distinct roles in memory processes (McClelland, McNaughton, & O’Reilly, 1995; Norman & O’Reilly, 2003; O’Reilly & Norman, 2002). It is proposed that the neocortex encodes semantic similarities between stimuli by creating general and overlapping representations. On the contrary, the hippocampus is suggested to extract unique episodic and contextual features by assigning distinct representations to each specific event despite any commonalities (Nadel & Moscovitch, 1997; Norman, 2010; O’Reilly, Bhattacharyya, Howard, & Ketz, 2014). While repetition has been shown to improve subsequent recognition memory, it was recently also demonstrated that repetition reduced participants’ ability to correctly reject similar lures (Reagh & Yassa, 2014). These results supported the competition trace theory (Yassa & Reagh, 2013), which suggests that repetition enhances item memory or familiarity at the cost of contextual details (source memory, recollection). Thus, repeated exposure to a stimulus may have differential effects on subsequent item and source memory performance. Early psychological accounts, such as the reactivation and encoding variability view, are too general to account for repetition to affect different forms of memory differently.

Concurrently with improved subsequent memory performance, reaction times (RTs) to repeated stimuli tend to decrease (e.g., Ballesteros, Bischof, Goh, & Park, 2013; Friedman, Ritter, & Snodgrass, 1996; Li, Guo, & Jiang, 2008; Ward, Chun, & Kuhl, 2013). Reductions in RTs are commonly referred to as repetition priming effects and have been attributed to decreases in cognitive demands and superior processing efficiency (Monsell, 1985; Scarborough, Cortese, & Scarborough, 1977). Repetition priming is typically achieved by repeated presentations of identical stimuli (perceptual repetition), but has also been reported when different exemplars were used (i.e., several different pictures of the same semantic concept, e.g., *a tree*), though priming effects were smaller in such conceptual repetitions (Biederman & Cooper, 1991; Cave, Bost, & Cobb, 1996; reviewed in Tulving & Schacter, 1990). Behavioural and neural repetition priming effects can be observed when stimuli are repeated immediately, within minutes, but also within hours, days or even weeks (Kolers, 1976; Mitchell, 2006; Van Turennout, Bielamowicz, & Martin, 2003; reviewed in Wiggs & Martin, 1998). While subsequent recognition memory is typically associated with explicit memory, repetition priming is usually thought to reflect implicit, automatic processes (see Henson, 2003; Tulving & Schacter, 1990). A large body of behavioural and lesion studies in healthy participants and amnesic patients suggests that repetition priming is dissociable from explicit memory

(Ballesteros & Reales, 2004; Fleischman, 2007; Gabrielili, Fleischman, Margaret Keane, Reminger, & Morrell, 1995; Graf, Squire, & Mandler, 1984; Rugg, Mark, et al., 1998; Squire, 2004; Warrington & Weiskrantz, 1974). Contrary to episodic memory performance, behavioural priming appears to be preserved in ageing (Ballesteros, González, Mayas, García-Rodríguez, & Reales, 2009; Caggiano, Jiang, & Parasuraman, 2006; Mitchell & Bruss, 2003; Wiggs, Weisberg, & Martin, 2006).

Repetition priming, as a measure of implicit memory, and recognition-source memory, as a measure of explicit memory, can be tested in the same paradigm. Many neuroimaging studies have shown that the brain is sensitive to repetition (reviewed in Friedman et al., 1996; Henson, 2005), opening up the potential to investigate the neural underpinnings of repetition-related decreases in RTs as well as associated differences in item and source memory performance. Moreover, investigations of repetition and memory formation will provide further insights into the cognitive and neural mechanisms underlying memory formation under different encoding conditions and the relative benefits of repetition on different measures of memory, i.e., item and source memory. These insights can be directly linked to real world learning, for example, by comparing the benefits of learning in different contexts to mere repetition learning.

1.4 Neuroimaging in memory research

Before the advent of neuroimaging, understanding the roles of specific brain regions was largely based on patients with brain lesions and associated deficits in behaviour. For example, the case of K.C., who suffered from selective episodic memory impairment following extensive brain damage including bilateral hippocampal lesions (see Rosenbaum et al., 2005 for more details). While such case studies have provided considerable insights into human brain functions, the results are not necessarily generalisable. Findings from neuroimaging research have informed and furthered long-standing debates, advanced our knowledge of memory processes and enabled researchers to draw comparisons between human and non-human research (see Brown, Staresina, & Wagner, 2015). For example, neuroimaging studies have provided support for dual-process models by indicating differences in the neural correlates of familiarity-based and recollection-based recognition memory (e.g., Curran, Tepe, & Piatt, 2006; Diana et al., 2007; H.

Eichenbaum, Yonelinas, & Ranganath, 2007). Although dual-process models are still highly contested in the literature, these results shed light on on-going debates sparked by behavioural data by furthering our understanding of the underlying neural processes.

1.4.1 Electroencephalography

Electroencephalography (EEG) is a non-invasive neuroimaging technique that measures changes in electrical potentials associated with discontinuities in extracellular ion concentrations. These typically reflect trans-membrane current flow, in particular, excitatory and inhibitory post-synaptic potentials. Scalp EEG does not measure activities from single neurons, instead, if a large sum of neurons receive excitatory or inhibitory post-synaptic potentials, the resulting currents can be measured in voltage changes by non-invasive scalp recordings (Luck, 2005). This makes EEG a direct measure of brain activity that can be used to investigate neurocognitive processes. The raw data from EEG recordings, however, are not suitable for those kinds of analyses as the neural signals relating to cognitive processes are practically impossible to isolate from the aggregation of neural activity making up the EEG signal (see Luck, 2014; Nieuwenhuis & De Rover, 2014). In the majority of experiments concerned with the electrophysiological correlates of cognitive processes, the experimenter is interested in identifying changes in brain activation relating to specific events occurring during the EEG recording (e.g., stimulus presentations). Averaging a large number of segments of the continuous EEG that are time-locked to such events will filter out noise and isolate the event-related potentials (ERPs). ERPs may be made up of several components characterised by peaks and troughs. Each of these components then reflects the intra-cortical currents picked up by the EEG in response to a specific event. Three features of ERP components potentially relevant to ERP researchers include the amplitude of the ERP waveform, the latency of the component and the scalp distribution (Johnson, 1992). These three features commonly constitute quantitative measures of neural activity, however, scalp distributions can also be indicative of qualitative aspects of the ERP at a specific time point (or averaged across a time window) and are often used to differentiate distinct neurocognitive processes (Michel et al., 2004). The latency of ERP components reflects the voltage peak and gives an estimate of the timing when the activity occurred. More detailed descriptions and explanations of the ERP technique exist elsewhere (e.g., Handy, 2005; Luck & Kappenman, 2011). Due to the inverse problem, the spatial resolution of EEG is relatively poor. Its strength lies in its very high temporal resolution. The ability to investigate the temporal dynamics underlying memory processes allows us to disentangle the various computations that may be involved in such processes (Voss & Paller, 2017; Wilding & Ranganath, 2012).

1.4.2 Functional magnetic resonance imaging

Magnetic resonance imaging (MRI) is another non-invasive neuroimaging method that is based on computerised analysis of the interaction between radio waves and magnetic fields generated by hydrogen atoms in body tissues and fluids. Detailed three-dimensional images are produced by varying the magnetic fields and radio waves. Functional MRI (fMRI) extends anatomical MRI by measuring regional cerebral blood flow as a proxy for cerebral function. More information regarding the underlying physics of MRI can be found elsewhere (e.g., Huettel, Song, & McCarthy, 2014). Research interested in cognitive processes typically employs fMRI to measure BOLD (blood oxygenation level dependent) fMRI responses. When brain regions become active, oxygenated haemoglobin and thereby magnetic susceptibility, increase, leading to a signal increase in the T2*-weighted MR image. As the BOLD measure is an indirect measure of neural activity, the temporal resolution of fMRI is much lower than for EEG. However, because we can overlay the BOLD measures with an anatomical MR image, the spatial resolution of fMRI data can be very high depending on the experimental design, the field of view and the strength of the scanner. Measuring blood flow as a proxy of neural activity, of course, also requires more caution with the interpretation of fMRI results (for details, see Logothetis, 2008; Logothetis & Wandell, 2004). In event-related designs, the BOLD response is most commonly modelled using a general linear model (GLM) to decompose the data into effects and error in order to obtain a statistic based on those parameter estimates. This method has been improved over the years and alternative ways of modelling the BOLD response have been developed (e.g., see Poldrack, Mumford, & Nichols, 2011). Functional neuroimaging, including fMRI and EEG/ERP investigations, has played a key role in developments and evaluations of cognitive theories and allows us to investigate region-specific associations and dissociations in task-related brain activation (Cabeza & Moscovitch, 2013).

1.5 Event-related potentials: Studies of episodic memory

A large body of ERP experiments has investigated the ERP correlates of remembering and forgetting. The majority of those studies examined memory effects occurring during the test phase, including old/new effects. Relatively fewer investigations focused on subsequent memory effects occurring during the study phase. The two most prominently reported ERP components in declarative memory research are the late positive parietal component (LPC) and the FN400. The LPC occurs between 500 and 700 ms post stimulus onset and is characterised by a positive deflection in the EEG with maximum amplitudes over centro-parietal electrode sites. At test, it is sometimes also referred to as the parietal old/new effect (Rugg & Curran, 2007; Wilding & Ranganath, 2012). The FN400 component is typically characterised by a negative deflection over frontal electrode sites that is observed between 300 to 500 ms after stimulus onset (Curran et al., 2006; Rugg & Curran, 2007). These two components are not only distinct in their scalp topographies and onset latencies, but also have functional differences supporting dual-process theories of recognition memory (Curran, 2000; Friedman & Johnson, 2000; Rugg & Curran, 2007; reviewed in Yonelinas, 2002). The LPC has been repeatedly linked to episodic memory and recollection (Chen, Lithgow, Hemmerich, & Caplan, 2014; Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Friedman & Johnson, 2000; Rugg & Curran, 2007; Wilding & Ranganath, 2012; Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010). The functional interpretation of the FN400, on the other hand, has been highly debated in the past. One line of research supports a role in familiarity-based recognition (e.g., Curran, 2000; Groh-Bordin, Zimmer, & Ecker, 2006). Another line of research associates the FN400 with semantic priming (e.g., Voss & Paller, 2009; Yovel & Paller, 2004), similar to another component, the centro-parietal N400 (Voss & Federmeier, 2011). The present investigations will focus on the LPC and FN400 components. Further ERPs that may be introduced as part of the literature review are the N400, generally associated with semantic processing and priming (reviewed in Kutas & Federmeier, 2011) and the late posterior negativity (LPN), previously linked to action monitoring processes during recognition-source decisions and to the retrieval of encoding-related source information (see Johansson & Mecklinger, 2003; Mecklinger, Rosburg, & Johansson, 2016).

Due to the spatial constraints of information derived from scalp EEG investigations, it is difficult to identify the brain regions that generate LPC and FN400 effects and directly compare those findings to fMRI research. Previous lesion studies showed that bilateral hippocampal lesions were associated with an absence of LPC along with amnesic symptoms (Addante, Ranganath, Olichney, & Yonelinas, 2012; Düzel, Vargha-Khadem, Heinze, & Mishkin, 2001; Olichney et al., 2000). Intracranial recordings have also suggested a number of regions generating LPC effects, including various regions within the medial temporal lobe, e.g., parahippocampal gyrus, temporal pole, perirhinal and posterior cingulate cortices, as well as the ventro-lateral prefrontal cortex (Guillem, Rougier, & Claverie, 1999; Halgren et al., 1994). The FN400 is thought to be generated across several prefrontal regions and the right intraparietal sulcus; a suggestion largely based on functional parallels between commonly reported fMRI and ERP effects (Hoppstädter, Baeuchl, Diener, Flor, & Meyer, 2015; Yonelinas, Otten, Shaw, & Rugg, 2005). However, neuronal recordings in primates suggested that familiarity signals, thought to be reflected in FN400 amplitudes, may originate in ventro-medial prefrontal cortex, orbito-frontal and anterior cingulate cortex (Xiang & Brown, 2004), adding to proposals that FN400 effects may be generated across prefrontal brain regions. These reports illustrate that the neural generators of ERP components are likely diverse, much like the brain regions typically associated with robust memory-related effects, such as the old/new effect. Moreover, the EEG and fMRI literatures are not very well connected at this point. Therefore, all parallels drawn between the two imaging techniques within this thesis will remain speculative.

1.5.1 Subsequent memory effects during a single encoding episode

Early research investigating Dm effects consistently reported long-lasting positivity enhancements for hits when compared to misses (e.g., Fernández et al., 1998; Friedman et al., 1996; Friedman & Trott, 2000; Mangels, Picton, & Craik, 2001; Neville, Kutas, Chesney, & Schmidt, 1986; Paller et al., 1987; Paller, McCarthy, & Wood, 1988; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980).

These Dm effects occur from around 300 ms post stimulus onset over parietal electrode sites, but have also been reported over frontal and central sites and are less often mapped to specific ERP components, such as the LPC and FN400 at test (reviewed in Friedman & Johnson, 2000; Paller & Wagner, 2002; Voss & Paller, 2008b, 2017; Wagner, Koutstaal, & Schacter, 1999). Therefore, the terms early frontal or late parietal ERP may be used in this review to qualify encoding effects whenever the authors did not explicit refer to LPC or FN400 effects. Late parietal, or LPC, Dm effects have been consistently observed with subsequent hits eliciting more positive ERP waveforms than misses (Angel, Isingrini, Bouazzaoui, & Fay, 2013; Griffin, DeWolf, Keinath, Liu, & Reder, 2013; Mangels, Manzi, & Summerfield, 2010; Wagner et al., 1999). Similarly, LPC amplitudes were more positive for subsequently recollected items compared to items that were given subsequent familiarity judgements (Voss & Paller, 2009; Yovel & Paller, 2004) and more positive for items subsequently recognised with high as opposed to low confidence (Mangels et al., 2010). In a study employing the recognition-source paradigm, more positive late parietal ERP waveforms were observed for faces, for which participants later also remembered the occupation (recollection), compared to faces that were judged as familiar or forgotten (Yovel & Paller, 2004). Parietal Dm effects have been suggested to reflect more elaborate encoding mechanisms (Yovel & Paller, 2004), as deeper, semantically richer processing during encoding has been linked to superior memory performance (Craik & Lockhart, 1972). As previously noted, the functional role of the FN400 component has been highly debated and support for its specific role in encoding is mixed (Curran, 2000; Voss & Paller, 2009). For example, one study found an early (340 ms) frontal negative deflection to be more negative for subsequent recollection and familiarity judgements than misses (Mangels et al., 2001). In contrast, another study reported that an early (400 ms) frontal positive deflection had greater amplitudes for subsequent recollection and familiarity judgements than for subsequent misses (Duarte et al., 2004). Similar discrepancies have been found in research employing the source-recognition paradigm. Greater negative amplitudes over frontal sites were reported for subsequent hits+ judgements compared to hits- judgements (Cansino, Trejo-Morales, & Hernandez-Ramos, 2010), while larger positive amplitudes for hits+ than hits- judgements were reported in other studies (Angel et al., 2013; Cansino & Trejo-Morales, 2008). Finally, a number of ERP experiments failed to detect any Dm effects relating to subsequent familiarity/recollection judgements or source memory performance (Guo, Duan, Li, & Paller, 2006; Senkfor & Van Petten, 1998; Smith, 1993). Overall, parietal Dm effects appear much more robust than frontal Dm effects. It is noteworthy that the above-cited research is highly heterogeneous in terms of study designs, specifically in terms of types of stimuli and encoding tasks that were employed. Several reviews of ERP research have highlighted the need for further research elucidating the influences of stimulus type and encoding context on Dm effects (e.g., Voss & Paller, 2008b; Wilding & Ranganath, 2012). While parietal Dm effects appear to be relatively robust, it may be that frontal ERP waveforms are highly affected by other factors, such as task difficulty or stimulus modality. Heterogeneity in experimental designs then makes it difficult to establish a clearer role for FN400-like Dm effects during encoding until possibly confounding effects have been identified.

1.5.2 Memory and repetition

ERP repetition effects have been reported as a wide-spread, positive-going deflection observed from 200 ms onwards with strongest effects around 400 – 600 ms post-stimulus onset (Henson, Rylands, Ross, Vuilleumeir, & Rugg, 2004; Rugg & Doyle, 1994; Schendan & Kutas, 2003; Swick & Knight, 1997). Moreover, multiple stimulus presentations were shown to affect the LPC and N400 differentially in that the LPC amplitude increases linearly with repetitions (Renoult, Wang, Calcagno, Prévost, & Debruille, 2012; Segalowitz, Van Roon, & Dywan, 1997; Van Strien et al., 2005) while the N400 amplitude only increased from the first to second presentation but plateaued thereafter (Renoult et al., 2012). Early work on repetition priming suggested priming effects to be greater when stimuli are repeated in the same modality as opposed to presenting them in different modalities across repetitions (Clarke & Morton, 1983; Jacoby & Dallas, 1981; Kirsnert & Smith, 1974; Roediger & McDermott, 1993; Scarborough, Gerard, & Cortese, 1979). It was therefore concluded that repetition priming relied on consistency in presentation modality (Henderson, 1982), which is in line with proposals from the reactivation view (Thios & D'Agostino, 1976). More recently, it was shown that conceptual and perceptual priming were dissociable as perceptual priming effects were shown in frontal P170 amplitudes, while conceptual priming was indexed by amplitude changes in the FN400, but only when stimuli (geometrical shapes) were rated as meaningful (Voss, Schendan, & Paller, 2010). Similar qualitative and quantitative ERP differences between perceptual (visual-visual) and conceptual (visual-auditory) priming were found between 200 and 400 ms post stimulus onset (unpublished, cited in Rugg & Allan, 1999). An experiment comparing ERPs to a measure of implicit memory, i.e., reductions in reaction times, and ERPs to a measure of explicit memory, i.e., recognition memory, reported that implicit memory processes were indexed by a positive deflection over occipito-parietal electrode sites beginning around 300 ms post stimulus onset. In contrast, explicit memory was reflected in a slightly later but more widely spread ERP effect (Paller & Gross, 1998), most likely reflecting the long-lasting positivity enhancement associated with Dm effects.

The repetition-related increase in positivity over parietal electrode sites was further shown to correlate with subsequent memory performance (Griffin et al., 2013; Groh-Bordin, Busch, Herrmann, & Zimmer, 2007; Olichney et al., 2000). Such increases in LPC amplitudes were interpreted as reflecting a graded increase in memory strength (Groh-Bordin et al., 2006; Van Strien et al., 2005) or the extraction of unique events (Renoult et al., 2012). Both interpretations are compatible with the association of the LPC with episodic memory and recollection. Furthermore, the observed repetition-related patterns during encoding were suggested to be reminiscent of old/new effects typically reported during the test phase (Griffin et al., 2013). Evidence for an earlier, frontally distributed repetition effect relating to subsequent memory is, again, less convincing. A frontal Dm effect (300 – 500 ms) was found at the third stimulus presentation with more positive waveforms for subsequent hits than misses (Mangels et al., 2010). In another study, the FN400 was observed to be sensitive to repetition but this effect was not related to subsequent memory outcome (Griffin et al., 2013). Overall, the links between perceptual and conceptual repetitions and implicit and explicit memory processes remain somewhat unknown. As some research also reported main effects of repetition that did not interact with memory (Friedman et al., 1996), it may be that repetition occurs independently of subsequent memory performance or simply that some experimental designs as well as traditional averaging methods are not sensitive enough to detect the complex interactions between memory systems and repetitions.

1.5.3 Memory effects at test

A large body of ERP research on memory processes has investigated the old/new effect during the test phase. This effect is characterised by more positive-going ERP waveforms to old stimuli, i.e., stimuli previously presented during the study phase, than new stimuli, i.e., lures included in the old/new recognition memory test (reviewed in Johnson, 1995). In old/new paradigms, which also assess source memory, the LPC is consistently found to elicit more positive-going ERPs to hits+ judgements compared to correct rejections (Rugg, Schloerscheidt, & Mark, 1998; Wilding, 2000; Wilding & Rugg, 1996; Woroch & Gonsalves, 2010). Some studies further observed more positive waveforms for hits+ than hits- judgements (Addante, Ranganath, & Yonelinas, 2012; Cansino & Trejo-Morales, 2008; Mollison & Curran, 2012, experiment 1). These results have been further supported by patient studies that showed amnesic patients whose recollection is impaired also had reduced or even absent LPC amplitudes (Addante, Ranganath, Olichney, et al., 2012; Olichney et al., 2000, 2006). Similar to the LPC, FN400 waveforms are typically found to elicit more positive-going ERPs to hits+ judgements than correct rejections (Addante, Ranganath, & Yonelinas, 2012; Cansino & Trejo-Morales, 2008; Wilding, 2000). In addition, fewer studies found the FN400 to be more positive for hits- judgements than correct rejections (Addante, Ranganath, & Yonelinas, 2012) as well as more positive-going FN400 waveforms for hits+ compared to hits- judgements (Addante, Ranganath, & Yonelinas, 2012; Cansino & Trejo-Morales, 2008). Such frontal source memory effects contradict the general notion that the FN400 is related to familiarity recognition judgements but not to recollection (see Curran et al., 2006 for review). It is noteworthy that, similar to the study phase, FN400 effects appear less robust than LPC effects at test. The FN400 has sometimes been reported to be modulated by item memory but not by source memory (Mollison & Curran, 2012, experiment 2; Woroch & Gonsalves, 2010). Finally, some studies reported no FN400 old/new effect (Cycowicz & Friedman, 2003; Cycowicz, Friedman, & Snodgrass, 2001). This heterogeneity in frontal old/new effects has been suggested to be attributable to the degree to which item and source information can be unitised; in such cases, familiarity processes may be sufficient to lead to hits+ judgements (Diana, Van Den Boom, Yonelinas, & Ranganath, 2011; Mollison & Curran, 2012). Notably, very little attempt has been made so far, to link repetition-related changes in ERP amplitudes to psychological theories of memory formation.

ERPs measured at test have also been shown to be sensitive to the type of content that is being retrieved from the study phase. For example, in one ERP experiment, participants studied line drawings paired with either words, spatial locations or colours (Rösler, Heil, & Hennighausen, 1995). In a subsequent retrieval task, participants were only presented with the line drawings and asked to recall the associated information. Event-related slow waves, measured up to 6 seconds post-stimulus onset, were found to differ qualitatively depending on the content the stimulus was previously paired with. Similar patterns emerged with other stimulus pairs, .e.g., words were paired with faces and spatial locations at study but cued only as words at test (Khader, Heil, & Rösler, 2005). The authors suggested those qualitative differences in scalp topographies to reflect differences in groups of cells that were activated by the reactivation of additional contextual content from an earlier study phase. However, research investigating traditional ERP components, such as the LPC and FN400, in paradigms manipulating encoding modality (visual vs. auditory) or encoding task (deep vs shallow) did not report such qualitative differences at test. Instead, ERPs were found to differ quantitatively in accordance with encoding task (Allan, Robb, & Rugg, 2000). Similarly, in a recognition-source memory paradigm, LPN amplitudes differed quantitatively relative to the content of the source that was retrieved (Mecklinger, Johansson, Parra, & Hanslmayr, 2007). Analogous content-specific retrieval effects were yielded for ERPs occurring from around 300 ms post stimulus onset in a R-K paradigm (Johnson, Minton, & Rugg, 2008). Moreover, a recent EEG investigation used a classifier-based approach to investigate the time course of reinstatement-related processes (Johnson, Price, & Leiker, 2015). It was demonstrated that encoding-related reactivation processes during retrieval occurred in the LPC time window and that such reactivation was related to memory performance. Overall, since the LPC has repeatedly been linked to recollection, it could therefore be inferred that this recollection process holds further information about the encoding episode and may index reinstatement of source information.

1.6 Haemodynamic responses: fMRI studies of episodic memory

Functional MRI studies of episodic memory commonly focus on a number of core regions that make up the episodic recollection network (Cabeza, Ciaramelli, &

Moscovitch, 2012; Johnson & Rugg, 2007; King, de Chastelaine, Elward, Wang, & Rugg, 2015; Rugg & King, 2017; Rugg & Vilberg, 2013). This network includes MTL regions, the prefrontal cortex (PFC) and lateral parietal cortices. Much of the current interest in MTL regions was initially spurred by the case of Henry Molaison (HM), who was unable to remember new events after a resection of MTL structures, primarily including the hippocampi but also adjacent structures such as parahippocampal, perirhinal and entorhinal cortex (Corkin, 2013; Scoville & Milner, 1957). In one of the first event-related fMRI Dm experiments, participants studied words in a scanned encoding phase and performed a recognition task shortly after the scan. Subsequent hits were found to be associated with more activation in left prefrontal and left temporal brain regions compared to subsequent misses (Wagner et al., 1998). In the same year, another study reported similar Dm effects but this time participants studied photographs of scenes and Dm effects were observed in right prefrontal and bilateral parahippocampal cortices (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998). Dm effects in MTL and PFC have been replicated numerous times (Blumenfeld & Ranganath, 2007; Fletcher, Stephenson, Carpenter, Donovan, & Bullmore, 2003; H. Kim, 2011; Persson & Söderlund, 2015; Spaniol et al., 2009). Well-established memory and learning theories, such as the CLS account, propose that the allocortical hippocampus plays a computationally and functionally distinct role from neocortical areas in memory encoding and recognition (McClelland et al., 1995; Norman & O’Reilly, 2003; O’Reilly & Norman, 2002). More specifically, the neocortex is suggested to encode commonalities between stimuli and their semantic features by assigning overlapping, general representations. The hippocampus on the other hand, is suggested to extract specific contextual, episodic features and to create distinct representations even for seemingly similar events (Nadel & Moscovitch, 1997; Norman, 2010; O’Reilly et al., 2014). The contributions of different brain regions in memory encoding and retrieval as well as differences between memory systems and processes involved during study and test can be further investigated with event-related fMRI research.

1.6.1 Subsequent memory effects during a single encoding episode

Numerous fMRI experiments have been carried out to identify brain regions in which Dm effects occur. While, MTL and PFC regions may be critically involved in memory encoding, Dm effects are not exclusive to those two areas of the brain. For example, results from large meta-analyses have reported wide-spread positive Dm effects, i.e., activation is higher for subsequent hits than misses, in left inferior frontal cortex, medial temporal regions including the hippocampal formation, fusiform, premotor and posterior parietal cortices (Kim, 2011; Spaniol et al., 2009). Studies have also identified reversed Dm effects with misses being associated with higher mean activation than hits (Daselaar, Prince, & Cabeza, 2004; Kim, 2011; Otten & Rugg, 2001c). However, this does not necessarily imply that an increase in activation in regions showing reversed Dm effects contributes to forgetting but rather that certain regions deactivate to aid successful encoding by reallocating neural resources to other regions (Daselaar et al., 2004). Brain areas showing such deactivations are often associated with the default-mode network, namely anterior and posterior midline cortex, superior frontal cortex, posterior cingulate cortex and temporo-parietal junction (Kim, 2011).

Further divisions of hits into source memory performance or recollection and familiarity have often focused on MTL sub-regions separately. Those MTL sub-regions include perirhinal and parahippocampal cortices and the hippocampal formation, which can be further sub-divided into dentate gyrus, hippocampus proper with its cornu ammonis (CA) fields, subicular complex and entorhinal cortex. Activation in the perirhinal cortex has been suggested to predict subsequent item memory, while activation of hippocampus is associated with subsequent recollection (see e.g., Davachi, 2006; Diana et al., 2007; Kensinger & Schacter, 2006; Mayes, Montaldi, & Migo, 2007; Ranganath et al., 2004). The hippocampus has been shown to exhibit greater mean activity for subsequent hits than misses (as outlined above), for subsequent remember than know responses (Diana et al., 2007; Otten, 2007; Ranganath et al., 2004; Uncapher & Rugg, 2005) and for subsequent hits+ than hits- judgements (Davachi, Mitchell, & Wagner, 2003; Kensinger & Schacter, 2006). The hippocampus has long been highlighted in the context of binding features of memories together into a coherent representation (Dudai, 2012; Josselyn, Köhler, & Frankland, 2015; Moscovitch, 1992; Moscovitch & Winocur, 1992; Tonegawa, Pignatelli, Roy, & Ryan, 2015), which appears particularly valuable in the context of recollection. These binding processes are suggested to be reliant on converging inputs from perirhinal and parahippocampal cortices to the hippocampus (see Brown et al., 2015). However, differences in mean activation relating to subsequent recollection are not exclusive to MTL-regions either. In a recognition-source memory paradigm, positive subsequent source memory effects were also reported in left inferior frontal cortex (Duarte, Henson, & Graham, 2011). The authors further found reversed, i.e., negative, subsequent source effects in precuneus, posterior cingulate, intraparietal sulcus and bilateral posterior hippocampus though the hippocampal effects only reached statistical significance in region of interest (ROI) analyses. These areas are partially overlapping with those showing reversed item memory effects, except the hippocampus has typically been shown to be more activated for subsequent source hits compared to misses. The authors suggested that this reversed hippocampal source memory effect may reflect recollection of non-criterial details among the subsequent hits- trials (Duarte et al., 2011) and pointed out that similar results have been yielded in other source and relational memory paradigms (Astur & Constable, 2004; Rekkas et al., 2005). Overall, the research examples highlight the longstanding roles of MTL and PFC in memory encoding, but recent research has placed additional emphasis on posterior parietal regions, such as the angular gyrus and precuneus, whose specific roles require further investigations.

1.6.2 Memory and repetition

When stimuli are repeatedly presented in event-related fMRI experiments, a regional decrease in mean activation has been observed across those repetitions (Epstein, Parker, & Feiler, 2008; Grill-Spector, Henson, & Martin, 2006; Henson, Shallice, & Dolan, 2000; Naccache & Dehaene, 2001; Stern et al., 1996). This is referred to as repetition suppression and thought to be the neural correlate of behavioural repetition priming (Epstein et al., 2008; Henson & Rugg, 2003; Schacter & Buckner, 1998; Wiggs & Martin, 1998). The degree of repetition suppression was found to correlate with implicit memory as measured in RTs (Ballesteros et al., 2013; Ward et al., 2013). The effect typically occurs in brain regions implicated in perceptual or semantic processing (see Grill-Spector et al., 2006; Schacter, Wig, & Stevens, 2007). Similar to behavioural priming effects, repetition suppression has been attributed to decreases in cognitive demands and superior processing efficiency (Buckner et al., 1998; Grill-Spector et al., 2006; Henson & Rugg, 2003; Schacter et al., 2007; Wig, Grafton, Demos, & Kelley, 2005). Reductions in neural activity, particularly in the hippocampus, have sometimes been reported as a linear decrease in activation across repetitions (Grill-Spector & Malach, 2001; Henson et al., 2000; Sayres & Grill-Spector, 2006; Suzuki, Johnson, & Rugg, 2011; Vannini, Hedden, Sullivan, & Sperling, 2013), however, this decrease plateaus after around six repetitions (Sayres & Grill-Spector, 2006). Furthermore, perceptual and conceptual priming were found to be dissociable in an experiment which showed that applying transcranial magnetic stimulation to the left frontal cortex was associated with decreases in behavioural and neural priming effects indexing conceptual priming, while neural priming effects in sensory areas remained unaffected (Wig et al., 2005). Although the interpretation of repetition suppression effects is still debated (Davis & Poldrack, 2013), it was suggested to reflect highly similar stimulus-processing or highly similar stimulus representations in the region where repetition suppression occurs (Bakker, Kirwan, Miller, & Stark, 2009; Lacy, Yassa, Stark, Muftuler, & Stark, 2011). Overall, it appears that repetition suppression is primarily related to implicit memory processes and reallocation of resources within the default-mode network as reflected in regional deactivations (see Vannini et al., 2013).

In addition to repetition suppression, research has further reported repetition enhancement, which refers to an increase in activation across stimulus repetitions (reviewed in Segaert, Weber, de Lange, Petersson, & Hagoort, 2013). It has been suggested that repetition enhancement may reflect a number of neurophysiological mechanisms, including predictive coding (Friston, 2005) and the formation of novelty networks (Henson et al., 2000). Repetition enhancement has also been reported in the context of overlapping but distinct repetitions in associative memory tasks, potentially signalling stimulus novelty paired with higher integration demands (Zeithamova, Manthuruthil, & Preston, 2016). While it is less often reported than repetition suppression, repetition enhancement has also been associated with recognition processes, suggesting that voluntary or involuntary explicit retrieval may take place in implicit encoding tasks (Henson, 2003). This notion was strengthened by similar regions being implicated in repetition enhancement at study and memory retrieval at test (Kim, 2017; Korsnes & Magnussen, 2014; Schott et al., 2005). Repetition enhancement in the perirhinal cortex was found to predict subsequent memory (Heusser, Awipi, & Davachi, 2013). More evidence that repetition enhancement rather than suppression is related to explicit memory comes from reports of a relationship between parietal repetition-related increases in mean activation and subsequent memory performance (Kremers et al., 2014; Vannini et al., 2013). Together, these results suggest that repetition suppression is more likely to be associated with behavioural priming and implicit memory, while repetition enhancement effects have often been related to explicit memory performance. Repetition-related increases, however, are less well understood and not as commonly reported in the literature (Segaert et al., 2013). Few studies have made distinctions between perceptual and conceptual repetition enhancement effects (but see Heusser et al., 2013) and related those results to implicit and explicit measures of memory.

1.6.3 Memory effects at test

Research, including neuroimaging and lesion studies, has identified a network of brain regions central to recollection processes. This network is comprised of prefrontal, medial temporal and parietal areas, with the anterior PFC particularly involved in the monitoring and decision-making processes underlying successful retrieval of source information (reviewed in Mitchell & Johnson, 2009; Rugg & Vilberg, 2013; Simons, Garrison, & Johnson, 2017; Simons & Spiers, 2003). More specifically, hits+ judgements have been associated with higher activation than hits- judgements in left medial and ventromedial prefrontal and bilateral orbitofrontal cortices, angular gyrus, posterior cingulate/retrosplenial cortex, insula, superior and middle temporal gyri and bilateral hippocampus (Duarte et al., 2011; Thakral, Wang, & Rugg, 2015). However, previous reviews and meta-analyses have pointed to inconsistencies across the literature regarding memory effects at test, especially in MTL areas (Henson, 2005; Spaniol et al., 2009). Similar inconsistencies were also observed in the prefrontal cortex for source memory effects (Simons et al., 2017), with several studies not reporting any significant effects for old > new or hits+ > hits- contrasts (e.g., Henson, Cansino, Herron, Robb, & Rugg, 2003; Herron, Henson, & Rugg, 2004). Discordant prefrontal cortex results in source memory tasks have been suggested to be partly explained by the diversity of source information, especially internally and externally generated information, that is to be retrieved across different experiments (Simons et al., 2017; Simons, Owen, Fletcher, & Burgess, 2005). The absence of old/new effects in the MTL and, in particular the hippocampus, was proposed to reflect the encoding of new items during the test phase (Stark & Okado, 2003). Moreover, old/new effects were found to be weaker than recollection/familiarity or source memory effects in regions that are part of the default network (Kim, 2016) as well as in the left prefrontal cortex (reviewed in Mitchell & Johnson, 2009). Weak old/new effects at test may therefore reflect potentially different hippocampal activation patterns that are either related to encoding of new items or to retrieval of old items. Analyses based on mean activation may not be sensitive enough to distinguish these two activation patterns. As outlined above, at encoding, the hippocampus' role in binding contextual information together has been highlighted as vital for later successful retrieval. At test, it has been suggested that hippocampal activity varies with the amount of contextual detail that is retrieved (Rugg et al., 2012). This notion is in line with results showing greater activity in the hippocampus for recollection than familiarity judgements and for hits+ than hits- judgements (Duarte et al., 2011). However, it may also account for failures to observe such differences. A meta-analysis reported only subjective and not objective hippocampal recollection effects (Kim, 2016). Such findings may be attributed to one of the pitfalls of source memory paradigms: recollection of non-criterial details may take place during incorrect source judgements (Parks, 2007; Vilberg & Rugg, 2008; Yonelinas & Jacoby, 1996), which would be associated with higher hippocampal activation and in turn explain the absence of objective recollection/source memory effects in some cases.

Similar to EEG research, fMRI investigations of mean activation during the test phase have examined the correlates of encoding-related reinstatement. The cortical reinstatement hypothesis proposes that cortical representations created during the study phase will be reactivated during retrieval, making reinstatement a critical process for successful memory performance (see Rugg, Johnson, Park, & Uncapher, 2008). Indeed, a number of fMRI experiments have shown encoding-retrieval overlap, particularly in sensory regions (Danker & Anderson, 2010; Diana, Yonelinas, & Ranganath, 2013; Khader, Burke, Bien, Ranganath, & Rösler, 2005; Nyberg, Habib, Mcintosh, & Tulving, 2000; Wheeler, Petersen, & Buckner, 2000). While such investigations of content-specific reactivation, indexed by differences in mean activation, can inform us about general processes underlying recollection and retrieval of contextual information to some extent, they cannot elucidate the nature of item-specific pattern reinstatement. More recent examinations of reinstatement used multivariate analysis approaches (see Rugg & Vilberg, 2013), which have been shown to be more sensitive to effects that cannot be examined with univariate analyses. These reinstatement effects will be discussed later in this chapter (1.7.2).

1.7 Univariate and multivariate analyses

The results introduced above are yielded with univariate statistical approaches. While univariate analyses can inform our understanding about changes in mean activation (of either ERP amplitudes or fMRI BOLD), multivariate statistical approaches (also referred to as multivoxel pattern analysis; MVPA) allow us to investigate distributed activation patterns across voxels or ROIs in relation to specific events or stimuli. It has been suggested that results from univariate whole-brain analyses are sensitive to global task-engagement, while searchlight MVPA results can provide additional insights into distributed coding of information. Therewith, multivariate analyses led to the development of new research questions that could be addressed with those techniques (Haxby, 2001; Jimura & Poldrack, 2012; Kriegeskorte & Bandettini, 2007; Norman, Polyn, Detre, & Haxby, 2006; Ward et al., 2013). MVPA is typically used in one of two forms, either as a classifier-based approach or as a pattern similarity approach. Classifier-based MVPA is based on machine learning algorithms for pattern classification. These algorithms aim to decode and differentiate between stimulus- or event-specific multivoxel patterns (Norman et al., 2006; Pereira, Mitchell, & Botvinick, 2009; Rissman & Wagner, 2012). Research included in the present manuscript employed the pattern similarity MVPA approach to primarily test hypotheses regarding processes of reactivation and multiple trace formation during memory encoding and retrieval. The pattern similarity approach is widely known as representational similarity analysis (RSA; Kriegeskorte, Mur, & Bandettini, 2008). RSA has been argued to allow us to test hypotheses regarding the neural mechanisms underlying successful memory formation and retrieval (e.g., Brown et al., 2015). In traditional RSA approaches a correlation coefficient, e.g., Pearson's *r*, is computed across voxels and between events or stimuli of interest. This correlation coefficient is then used as an index of pattern similarity. RSA can help to distinguish brain regions based on their feature-sensitivity. For example, regions displaying higher pattern similarity between a chocolate-coated pancake and a brown ball (likely reflecting overlapping features in 2-dimensional shape and colour) than between the same pancake and a tub of Ben &

Jerry's ice cream may be sensitive to visuo-perceptual stimulus features. On the other hand, regions that show more pattern similarity between the pancake and the ice cream tub than between the pancake and the brown ball may be more sensitive to conceptual features, i.e., both are deserts. Analogously, pattern similarity between two events may be interpreted as highly overlapping representations if the similarity index is high and distinguishing between two events when the similarity index is low. The same logic can then be applied to memory processes, as described in the following. So far, memory research has typically investigated how pattern similarity relates to memory performance.

1.7.1 Repeated encoding, representational similarity and memory

Psychological theories have proposed different explanations for why repetition aids memory encoding (see Chapter 1.3). The reactivation view suggests that repetitions make memory representations more stable by reactivating the same memory (Benjamin & Tullis, 2010; Thios & D'Agostino, 1976). The encoding variability view proposes that a larger number of retrieval cues and traces is available when items are encoded uniquely (Bower, 1972; Hintzman, 1986; Martin, 1968; Nadel & Moscovitch, 1997). Although these theories initially made predictions regarding underlying cognitive processes, they have since been extended to incorporate neural results and refine their predictions (e.g., Benjamin & Tullis, 2010; Nadel & Moscovitch, 1997). Additionally, the CLS account proposes distinct roles for different brain regions in memory encoding, more specifically, the hippocampus extracts unique episodic features, while the neocortex generalises information to integrate overlapping features into a coherent representation (McClelland et al., 1995; Norman & O'Reilly, 2003; O'Reilly & Norman, 2002). One experiment employing RSA reported evidence in support of the CLS account (LaRocque et al., 2013). The authors computed similarity between items with respect to subsequent memory outcome. They found higher pattern similarity between items that were subsequently remembered compared to those subsequently forgotten in extra-hippocampal regions, namely perirhinal and parahippocampal cortices. However, in the hippocampus, more neural pattern dissimilarity between items was associated with better subsequent memory outcome. These results largely support prevalent notions that the hippocampus encodes items by creating distinct representations while the MTL cortex encodes overlapping features between items.

An alternative approach, using RSA to assess reactivation vs. multiple traces, is to investigate how similarity patterns change across repeated stimulus encoding. One study computed the similarity between repeated stimulus presentations and found that, overall, cortical similarity patterns were higher for subsequent hits compared to misses (Xue et al., 2010). Related results were yielded in a study that compared results from two distinct statistical approaches to investigating repetition-related changes in BOLD signal, repetition suppression and RSA, in the light of implicit and explicit measures of memory (Ward et al., 2013). At study, participants made indoor/outdoor judgements to repeatedly presented scenes. Implicit memory, as measured by repetition priming, was associated with repetition suppression across prefrontal, parietal and occipito-temporal regions. Importantly, RSA results were not predictive of the level of repetition priming. The opposite results were shown for explicit memory. Explicit subsequent memory was related to similarity patterns across repetitions and although some of those effects were found in regions overlapping with those displaying repetition priming effects, repetition suppression did not predict explicit subsequent memory. Pattern similarity predicted subsequent memory most consistently across occipito-temporal regions. In a follow-up analysis of an already published dataset (Experiment 3, Xue et al., 2010), it was revealed that the distributed similarity patterns, which were previously reported to predict subsequent memory performance, correlated with fronto-parietal activation (Xue et al., 2013). The authors suggested that this activity enhances cortical pattern similarity by strengthening cortical representations, which eventually leads to richer input to MTL regions. RSA has also been used in conjunction with a source memory task (van den Honert, McCarthy, & Johnson, 2016) though the authors referred to it as *mnemonic discrimination* (participants had to discriminate whether two presentations at encoding were similar or identical). Occipito-temporal, hippocampal and parahippocampal pattern similarity between the first and second presentation was related to subsequent mnemonic discrimination of scenes. A similar effect was found for objects but only in the fusiform gyrus. These results were interpreted as evidence for reactivation mediated by the hippocampus to aid subsequent source memory (van den Honert et al., 2016). Reverse effects were found when participants encoded stimuli across different tasks. Pattern similarity in lateral occipital cortex between the first and second presentation during the encoding phase was associated with poorer subsequent source memory performance (Kim, Norman, & Turk-Browne, 2017). Generally, it appears effects of pattern similarity predicting subsequent memory are more widely distributed, i.e., reported across more ROIs, for stimuli that are perceptually richer, such as scenes. Furthermore, effects are most consistently reported in visuo-perceptual areas, which bears a question as to how much conceptual encoding of the stimulus is necessary to evoke such similarity patterns. Additionally, one limitation of most of the above studies examining neural similarity patterns across repeated encoding is that both, encoding modality and encoding task were held constant across repetitions, making it difficult to infer the contributions of perceptual and conceptual features to pattern similarity.

1.7.2 Encoding-retrieval representational similarity and memory

Another line of research has examined encoding-retrieval similarity (ERS) patterns. On one hand, investigating ERS patterns may be seen as a natural extension to looking at repeated encoding similarity, as the stimulus presentation at test could be considered a repetition in itself. However, it is important to consider that, unlike repeated encoding conditions, the test phase requires explicit retrieval of information. The motivation to investigate similarities between encoding- and retrieval-related processes is highlighted in numerous theoretical accounts. For example, the aforementioned *encoding specificity principle* (Tulving, 1983; Tulving & Thomson, 1973) and the *transfer-appropriate processing* account (Morris et al., 1977), which imply that similar operations have to take place at study and test in order to successfully retrieve an item. Finally, the *cortical reinstatement hypothesis* proposes that the successful retrieval of episodic memories relies on reinstatement, implying that brain regions that were active during encoding are reactivated during retrieval (Nyberg et al., 2000; Rugg et al., 2008; Wheeler et al., 2000). While regional overlaps in mean activation between study and test phase have been reported (Johnson & Rugg, 2007; Persson & Nyberg, 2000), results from mass-univariate analyses do not reflect pattern reinstatement of item-specific information.

An investigation of ERS demonstrated higher pattern similarity, especially in occipito-temporal cortices, was associated with better memory performance (Ritchey, Wing, LaBar, & Cabeza, 2013). Furthermore, ERS predicted memory performance in many regions of frontal, parietal and occipital cortices that did not show memory effects when using a univariate approach. The authors suggested that, compared to similarity across multiple encoding episodes (e.g., Xue et al., 2010), ERS is based on different tasks during the study and test phase. Therefore, similarities are likely to reflect item-specific perceptual or otherwise important mnemonic features occurring at successful encoding and retrieval. Furthermore, this study found that the relationship between cortical ERS and memory performance was mediated by the hippocampus (Ritchey et al., 2013). These results were interpreted as evidence that hippocampal-cortical interactions are important for successful retrieval. Another study investigated different levels of ERS (Wing, Ritchey, & Cabeza, 2015). The authors first computed item-level ERS by correlating patterns separately for each item and suggested that item-level ERS reflected reactivation of stimulus properties. Additionally, they also computed set-level ERS by correlating the pattern of each specific item with all the other items of the same memory category. Set-level ERS was suggested to index reactivation of more general information and processes that were shared between all stimuli of one category, e.g., all remembered stimuli. Finally, they also calculated the difference between item-level and set-level similarity, hereafter referred to as item-specific similarity, reflecting item-specific pattern reinstatement that was distinct from all other stimuli within the same category. Item-level similarity in occipito-temporal cortex increased with memory success. Additionally, ERS in posterior cingulate cortex was higher at the item- than the set-level, suggesting stimulus-specific representations to be stored in this region. Finally, ERS in ventrolateral PFC increased with memory success at both, the item- and the set-level. Computing item-level and item-specific ERS appears to be indispensable as those indices provide additional stimulus-specific information rather than reflecting more general process as reflected in set-level similarity. However, it has also been pointed out that perceptual feature overlap between encoding and retrieval may partly drive such similarity patterns (Xiao et al., 2017). Xiao and colleagues (2017) demonstrated item-specific reinstatement in the parietal lobe in a design that controlled for such perceptual similarities, showing that conceptual reinstatement can be observed in the absence of overlapping perceptual features between encoding and retrieval. Though not the focus of the present research, it is important to mention that classifier-based approaches have repeatedly provided evidence for content-specific reinstatement mediated by the hippocampus (Bosch, Jehee, Fernández, & Doeller, 2014; Gordon, Rissman, Kiani, & Wagner, 2014; Liang & Preston, 2017; Staresina, Henson, Kriegeskorte, & Alink, 2012). Moreover, the observed reinstatement patterns in MTL areas were predictive of source memory outcome (Liang & Preston, 2017). Notably, reinstatement was also reported when familiarity-based judgements were made, suggesting that processes of neural pattern reinstatement are not exclusive to recollection (Johnson, McDuff, Rugg, & Norman, 2009). Taken together, these results highlight again the complexity of memory processes reflected in the number of brain regions involved and the diversity of results, which, in turn, encourage further whole-brain searchlight analysis approaches in order to tie in those various accounts. Moreover, because the studies introduced here typically used the same stimuli at study and test, it is unclear whether ERS patterns reflect reinstatement of perceptual or conceptual information (Xiao et al., 2017). Finally, compared to item memory reinstatement, little is known about the relationship between pattern similarity indexing reinstatement of episodic contextual features and source memory performance. Employing a source memory measure in addition to an item memory measure will provide novel insights into the role of reactivation in recollection judgements.

1.8 Aims and objectives of the present research

The present research investigates the effects of repetition on subsequent memory performance as well as reinstatement of information from the encoding phase during the test phase. Electrophysiological and haemodynamic response data were obtained. Univariate and multivariate data analyses were conducted and, where appropriate, results are qualitatively related and discussed between the two experimental designs and the two neuroimaging approaches. The primary aim of the present investigations was to gain a richer understanding of the neural predictors of successful encoding and retrieval of episodic memories. To achieve that, this thesis investigates the relationship between memory performance and fMRI pattern reactivation between repeated encoding episodes and between encoding and retrieval. Previous research typically repeatedly presented the same perceptual stimuli and participants repeatedly performed the same encoding tasks. It is therefore not clear, how similarity patterns may be affected by changes to encoding modality or task instructions. In two experimental designs, effects of encoding modality and encoding task on memory processes at study and test will be further examined. The here presented experiments will offer insights into cognitive and neural mechanisms underlying increases in memory performance during repeated encoding. In particular, this thesis is concerned with the effects of different encoding strategies on memory performance and underlying neural patterns predicting memory performance.

In the first set of experiments, participants repeatedly encoded stimuli in one of three different encoding modality conditions: as pictures only, as words only and as pictures and words alternately. At test, participants performed item and source recognition tasks while stimuli were cued as words only. This design allowed investigations of modality-related subsequent memory effects as well as perceptual and conceptual repetition effects at study and reinstatement of encoding modality and modality-related memory effects at test. The results from this set of experiments (EEG data presented in Chapter 3, fMRI data presented in Chapter 4) will provide insights into the complex interactions between memory processes, repetition and encoding modality. Some heterogeneity in univariate results in the literature may be explained by systematically testing for modality-related memory effects in ERP and fMRI data. The multivariate analyses will further extend our knowledge with respect to the reactivation hypothesis and the multiple trace theory in that we will be able to evaluate the relative contributions of perceptual and conceptual similarity to reactivation patterns in a recognition-source paradigm.

In the second set of experiments, participants repeatedly encoded stimuli under two different encoding task conditions: repeatedly performing the same task and performing a different task at each of the four encoding presentations. At test, participants performed item and source recognition tasks. This design allowed investigations of subsequent source memory and priming effects under two different task conditions at study as well as differences in encoding-retrieval similarity relating to encoding of stimuli in the same and in different contexts. Univariate analyses will test for repetition effects in the two different encoding task conditions. Multivariate analyses will provide insights into the role of reactivation in the formation of memory traces when different encoding operations are required at study. The results form this set of experiments will inform theoretical approaches to repeated encoding and subsequent item and source memory, such as the reactivation view and encoding variability hypothesis.

SECTION 2

-

Experimental Chapters

Chapter 2 – General methods

2.1 Participants

Healthy adult participants, aged 18 – 35 years, were recruited through opportunity sampling including the School of Psychology's paid participant panel mailing list and posters displayed on campus. Participants were right-handed, native English speakers with normal or corrected-to-normal vision. Exclusion criteria included a history of head injury with loss of consciousness longer than five minutes and other neurological or medical conditions known to compromise brain function. Participants could only take part in one of the four experiments to avoid familiarity with the experimental design, in particular, with the surprise memory test. Informed consent was obtained from all participants and this research was approved by the Research Ethics Board of the University of East Anglia. Participants were reimbursed for their time in accordance with the School of Psychology's standard payment rates.

2.2 Materials

Experimental tasks were programmed and delivered through the stimulus presentation software Presentation 18.1.

2.2.1 EEG

The EEG recordings were obtained using a Brain Vision UK actiCAP system with 63 active electrodes embedded in an elastic nylon cap (10/10 system extended). An additional electrode was placed under the left eye in order to monitor vertical eye movements (lower electrooculogram; lEOG). Participants' button presses throughout the task were made on a Black Box ToolKit response pad. For the experimental procedure, participants were seated in front of a computer screen, placed 1m from their eyes, on which instructions and experimental tasks were presented.

2.2.2 fMRI

Functional and anatomical MRI data were obtained with a 3 Tesla wide bore GE 750w MRI scanner. Stimuli and task instructions were presented on a screen via an AVOTEC silent vision projector. The screen was placed within the scanner, approximately 90cm from participants' eyes. Behavioural responses were recorded with a Fiber Optic Response Device and logged with Presentation 18.1. Participants wore earplugs to minimise scanner noise and head motion was reduced using foam pads.

2.3 General task and procedure

Participants were briefed and informed consent was obtained before the beginning of the experiment. For fMRI experiments, MRI safety was assessed prior to the scan.

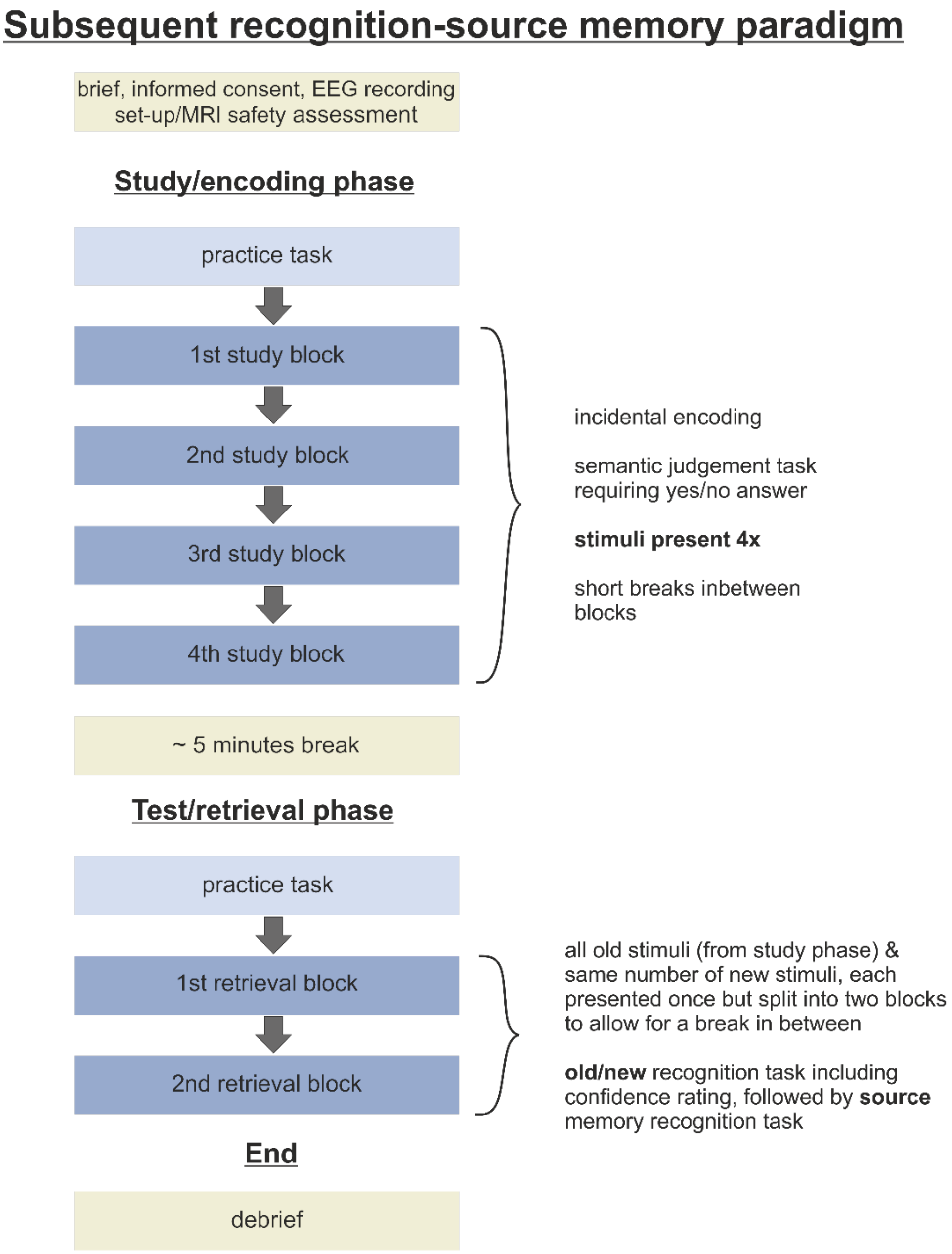


Figure 2.1. The subsequent recognition-source memory paradigm.

A subsequent memory paradigm assessing item and source memory was employed in all present experiments. Participants performed an incidental encoding task during a study phase, which was divided into four blocks/runs to allow for breaks in between. During the study phase, each stimulus was repeated four times. Stimuli were presented on screen for 1000 ms. In an ensuing test phase (divided into two blocks/runs), participants performed an old/new recognition task including confidence ratings and a source memory measure. Each phase was preceded by a short practice task. The subsequent recognition-source memory paradigm is displayed in Figure 2.1.

2.4 Data acquisition and preprocessing

2.4.1 EEG

Continuous EEG data were recorded at a sampling rate of 500 Hz with FCz as reference and AFz as ground electrode. A connection impedance below 20 kΩ was assured for all electrodes before the beginning of the recording.

The continuous EEG data were pre-processed offline using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014). All continuous EEG data were downsampled to 250 Hz. A high-pass filter with a cut-off at 1Hz was applied in preparation for independent component analysis (ICA). Research has shown that ICA yields best results when EEG data are high-pass filtered with a cut-off at 1Hz (Winkler, Debener, Muller, & Tangermann, 2015). Data were segmented into epochs of 2200 ms (from -200 ms to 2000 ms relative to stimulus onset). Data were manually screened and bad channels were removed along with noisy epochs in order to yield better ICA results. EEGLAB's ICA decomposition algorithm runica (extended) was used to perform ICA on the downsampled, high-pass filtered and epoched data. The same raw data were then preprocessed again, this time a band-pass filter was applied with a half-amplitude cut-off at 0.1 and 40Hz, downsampling and epoching of the data remained the same. The previously calculated ICA weight matrix was then transferred from the first high-pass filtered dataset to this second dataset. Ocular artefacts (blinks and vertical eye movements) were identified based on scalp topographies and removed from the data. Previously excluded noisy channels were interpolated with a function implemented in EEGLAB to perform spherical interpolation. Trials containing excessive artefacts were rejected using a step function (Luck, 2014) with the voltage threshold set to ± 100 µV in moving windows of 200 ms, with a window step of 50 ms. EEG data were then re-referenced to an average reference and finally epochs were averaged to ERPs.

2.4.2 fMRI

Structural scanning started with a fast spin echo 3-plane localiser scan. To obtain a structural MRI, a 3D T1-weighted image was acquired using a gradient echo pulse sequence (BRAVO; brain volume imaging, a fast IR-prepared gradient echo sequence with high isotropic resolution). Slices were angled parallel to the falx cerebri, the centre of the field of view (FOV) was angled to AC-PC (TR = 7.25, TE = 2.55, flip angle = 9°, FOV = 230 mm^2, matrix size = 256 x 256, slice thickness = 0.9 mm, number of slices = 196). Functional scans acquired 2T*-weighted images using a gradient-echo, EPI sequence (TR = 2000 ms, TE = 28 ms, flip angle = 90°, FOV = 213 mm^2, matrix size = 64 x 64, slice thickness = 3 mm, number of slices per volume = 35, number of volumes = 260 for encoding blocks, 318 for recognition blocks). In most cases, full brain coverage was not possible, so that the FOV was angled to primarily include the temporal and parietal lobes and prefrontal cortex (see Figure 2.2).

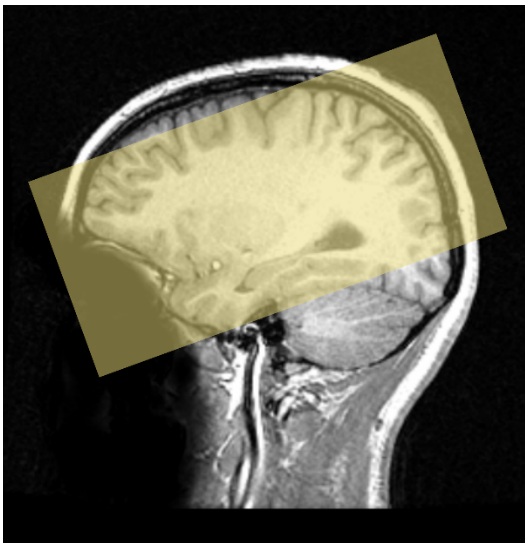


Figure 2.2. Example of the field of view applied during functional MRI scans.

DICOM files were converted to nifti files using MRIcron software. Preprocessing and statistical analyses were carried out using SPM12 (Wellcome Trust Center, London, UK, www.fil.ion.ucl.ac.uk), a toolbox implemented in Matlab (The Mathworks, Inc., Natick, MA, USA). The first six volumes acquired during each run were discarded from preprocessing and analyses. Functional images were slice-timing corrected before spatial realignment as suggested for interleaved sequences (Ashburner et al., 2016). The reference slice for slice-timing correction was chosen based on neuroanatomy (spatial middle slice rather than temporal middle slice) to avoid the reference slice being in an "extreme" region. The parameters for spatial realignment were kept at default, i.e., relatively high quality (0.9), 4 mm sampling distance between points in the reference image, spatial smoothing with a 5 mm full-width-half-maximum (FWHM) Gaussian kernel, images were registered to their mean, 6th degree B-Spline interpolation method, no wrapping, no differential weighting of voxels. Before coregistration, the origin of the anatomical image was set to the anterior commissure. Then the structural image was coregistered to the mean functional image. The coregistered structural data were segmented into grey and white matter, bias corrected and spatially normalised to Montreal Neurological Instutite (MNI) space by selecting forward deformation. Those deformation parameters were then used to spatially normalise all functional data and the bias corrected structural image, with images being sampled by a 6th degree B-Spline interpolation. Functional images were resampled to a voxel size of 3 mm^3 (isotropic), the structural image was resampled to a voxel size of 1 mm^3. These voxel sizes were closely matched with the original ones. Finally, the normalised images were smoothed using a 6 mm FWHM Gaussian kernel.

For any ROI analyses that were conducted, ROIs were chosen from the Anatomic Automatic Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002), masks were generated using the WFU Pickatlas (Maldjian, Laurienti, Kraft, & Burdette, 2003) and resliced in SPM12.

2.5 Analysis

2.5.1 EEG

2.5.1.1 ERP analysis

Planned ERP analyses were be conducted to investigate two ERP components, an early frontal FN400-like and a late parietal LPC-like ERP. The early frontal ERP was measured between 300 – 500 ms post stimulus onset at electrode sites F1/F2, F3/F4, FC1/FC2 and FC3/FC4. The late parietal ERP was measured between 500 - 700 ms post stimulus onset at electrode sites P1/P2, P3/P4, P5/P6 and PO3/PO4. These two components of interest are illustrated in Figure 2.3.

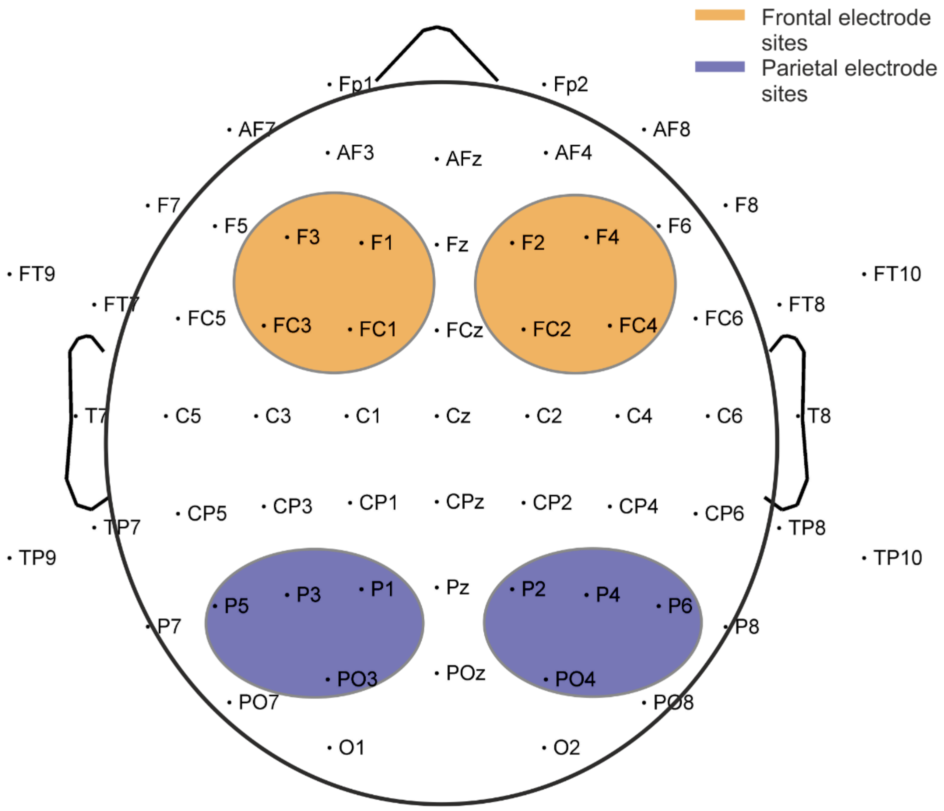


Figure 2.3. Two ERP components of interest to the present investigations: A frontal FN400-like component made up of electrodes sites within the orange circle and a parietal LPC-like component made up of electrode sites within the purple circle.

2.5.2 fMRI

2.5.2.1Univariate analysis

Statistical mass-univariate analyses were performed on the preprocessed and smoothed functional images in two stages. In a 1st-level analysis, neural activity was modelled as a delta function at the onset of each trial/stimulus. To model the BOLD response, these delta functions were convolved with the canonical haemodynamic response function (HRF). Customised masks were created for each participant based on the normalised mean functional image and normalised-segmented grey matter, white matter and cerebrospinal fluid, which were used as explicit within-brain masks during model estimation. Mean activation was modelled to the onset of the stimulus. This was the case during both, the study and test phase, although the test phase trials were longer, as participants first responded to an item recognition task and then to a source recognition task. Each condition of interest was modelled as a regressor in the GLM. Any trials that were not of interest were modelled in a nuisance regressor. Further regressors included the six movement parameters that were estimated during realignment to account for any remaining linear artefacts that were not corrected during realignment. Parameters for each regressor were estimated for each voxel by using a maximum-likelihood estimation with a temporal high-pass filter cut-off at 128s (removing low-frequency drifts) and temporal autocorrelations across scans were modelled using the AR(1) process, an SPM built-in. Contrasts of parameters estimates for each regressor of interest and for each participant were included in 2nd-level analyses. Finally, to remove between-subject variance, covariates that modelled the mean activation for each participant were included in the 2nd-level models. For any effect of interest, statistical parametric maps (SPMs) were created based on the T-statistics. Unless otherwise specified within the chapters, whole-brain analyses were conducted using the statistical methods implemented in SPM12. Contrasts of interest were thresholded at $p < .001$ and clusters significant at $p < .001$ (uncorrected) or $p < .05$ (*FWE-corrected*) are reported. Experiment-specific GLM information and details on 2nd-level analyses will be outlined in the experimental chapters.

2.5.2.2 Multivariate analysis

Similarity scores for RSA were calculated from the preprocessed, unsmoothed images. Customised masks were used as explicit within-brain masks during model estimation. Single-trial betas were estimated using the *Least Squares – Separate* (LSS) approach, where separate GLMs are estimated for each trial with a regressor for the trial of interest and a second regressor modelling all other trials (for more information see Mumford, Turner, Ashby, & Poldrack, 2012). The single-trial beta estimates were then submitted to ROI and searchlight RSAs. These RSAs computed the representational similarities between stimulus presentation pairs (see results sections for information on which presentation pairs were used). Beta values were extracted for every voxel, for each stimulus (i) at each of the four presentations (r) during the study phase S_{ir} and the test phase T_i. The single trial beta series were windsorised (SD = 3) and correlations were computed between the presentation pairs for each stimulus $S_{ir}S_{ir}$ (encoding similarity) and between the study and test phase $S_{ir}T_i$ (ERS). Based on an identity matrix, item match and item mismatch similarities were calculated corresponding to item-level similarity and set-level similarity, respectively (see Wing et al., 2015). Item-level similarity was calculated by correlating the beta estimates corresponding to a stimulus at one presentation of the stimulus and another presentation of the stimulus. This measure of similarity reflects the degree to which stimulus properties are reactivated. Set-level similarity was calculated based on the correlations between a specific stimulus and all other stimuli in the same category (e.g., subsequent source hits). The resulting values were averaged at the voxel level to make up set-level similarity. Set-level similarity provides an index of more general information or processes that are shared between stimuli of the same category, e.g., all remembered stimuli. Additionally, the z-score difference between item match and item mismatch was calculated to obtained a measure of item-specific similarity reflecting item-specific pattern reactivation distinct from all other items within the same category. Similarity scores were represented by Fisher transformed Pearson correlation coefficients. For searchlight approaches, the resulting images containing the 3x3x3 voxel-wise similarity scores were smoothed using a 6 mm^3 FWHM Gaussian kernel for whole-brain analyses. For 2nd-level analyses of whole-brain RSA, statistical methods implemented in SPM12 were used with the same thresholds as for univariate analyses.

Chapter 3 – Encoding modality, repetition and memory (EEG)

3.1 Introduction

Behavioural evidence suggests modality-dependent differences in memory performance with pictures being remembered better than words, termed the *picture superiority effect* (e.g. Shepard, 1967; Standing, Conezio, & Haber, 1970). Previous research on picture and word learning suggested that concepts in general activate a shared semantic store independent of the modality they are presented in (Caramazza, 1996) but that words access more universal semantic information than pictures do (Durso & Johnson, 1979). In addition to behavioural evidence, a large body of research supports the notion of a largely shared semantic system, while physical features of pictures and words are processed differently by the brain (e.g., Grady, Mcintosh, Rajah, & Craik, 1998; Khateb, Pegna, Michel, Landis, & Annoni, 2002; Menard, Kosslyn, Thompson, Alpert, & Rauch, 1996; Starrfelt & Gerlach, 2007; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Watson, Azizian, Berry, & Squires, 2005). If different operations are carried out by the brain simply in response to stimulus modality, it is conceivable that memory and repetition effects may differ depending on the modality stimuli are initially presented in, even if they represent the same concept, i.e., a picture of a tree and the written word '*tree*'. In the following part of this chapter introduction, research relating to effects of encoding modality, repetition and subsequent memory as well as reinstatement effects of encoding modality at test will be reviewed.

Previous research has shown that ERPs measured during a continuous recognition task differed quantitatively and qualitatively depending on the modality stimuli were presented in, i.e., pictures and words (Berman, Friedman, & Cramer, 1991). Pictures generally elicited larger mean amplitudes than words. Moreover, material-dependent effects of repetition lag were reported with lag effects only occurring in ERPs to word stimuli, suggesting at least partly distinct processes to underlie picture and word processing. However, the authors did not test for interactions between repetition (old vs. new) and encoding modality (Berman et al., 1991). Another experiment compared ERPs to picture and word stimuli, measured during a recognition task (Khateb et al., 2002). ERPs were found to be similar for earlier components from 100 – 150 ms but differentiated the two modalities from about 200 ms onwards. Picture stimuli were associated with more posterior activation, while words activated more left anterior and posterior areas. These results suggest modality-specific stimulus processing can be observed in ERPs and provide further evidence for processing differences between picture and word stimuli.

As outlined in the general introduction, perceptual and conceptual repetition priming have been associated with dissociable ERP components (Rugg & Allan, 1999; Voss et al., 2010). In a study investigating the effects of same and mixed modality encoding of picture and word stimuli, ERP amplitudes to pictures were generally found to be more positive than to words (Kazmerski & Friedman, 1997). At the second presentation, one group of participants performed an explicit recognition task while another group performed the same implicit semantic judgement task as at the first presentation. Stimuli were either repeated as pictures or words or their modality was changed resulting in four conditions: picture-picture, picture-word, word-word and word-picture. Decreases in RTs for implicit and explicit tests were significant when stimuli were repeated in the same modality but showed only weak trends of RT reductions in the changed modality conditions, indicating decreased priming effects. Items repeated in the same modality produced reliable old/new ERP effects irrespective of task. However, when the modality changed between the first and the second presentation, an old/new ERP effect was only observed when participants performed an explicit recognition task and when the modality changed from word to picture. Furthermore, the authors reported differences in scalp topographies during the explicit recognition task: items that were presented in the same modality again elicited ERPs with a more posterior distribution than those for which the modality was switched. It was concluded that quantitative and qualitative differences in perceptual and conceptual priming and modality-specific as well as modality-non-specific processes underlie the encoding and retrieval of pictures and words. Furthermore, the authors noted that transfer-appropriate processing (Morris et al., 1977) and reactivation (Thios & D'Agostino, 1976) accounts were insufficient to explain these results. (Kazmerski & Friedman, 1997). A large number of reported ERP repetition effects were based on amplitude differences between old and new items at test or amplitude differences between the same items at study and test. However, these effects are likely contaminated by retrieval operations and differences in repetition effects occurring during implicit and explicit tasks have been shown (Kazmerski & Friedman, 1997). Using a repeated incidental encoding paradigm followed by an explicit recognition task may be more effective to investigate repetition-related ERP differences. Additionally, the relationship between RT reductions and repetition-related ERP effects is not yet clear. In a study investigating the relationship between the P300 component and RTs, the authors highlighted the value of single-trial analyses in order to preserve some of the dynamic characteristics of ERP components that can be lost when using traditional averaging methods (Holm, Ranta-aho, Sallinen, Karjalainen, & Muller, 2006). P300 amplitudes and latencies were shown to be related to RTs in that faster RTs were associated with larger P300 amplitudes but shorter latencies. However, this study was not concerned with testing these relationships within the context of repetition or subsequent explicit memory. Relating item-specific RT reductions to changes in amplitudes will likely give novel insights into the EEG correlates of repetition and elucidate on whether the relationship between repetition-related changes in EEG measures and RTs may also predict explicit memory.

With respect to reinstatement during the test phase, multivariate frequency-analyses of intracranial EEG recordings have successfully demonstrated reinstatement effects (Yaffe et al., 2014; Zhang et al., 2015). In ERP research, studies investigating the involvement of traditional ERP components, such as the LPC, have found quantitative differences (e.g., Allan et al., 2000). The effects of two encoding manipulations on ERP effects during a cued recall task were tested in two experiments: 1) effects of shallow and deep encoding tasks, 2) effects of visual and auditory stimulus encoding. Although quantitative differences in ERPs at test were displayed, the main focus of the paper was to test encoding-related differences in old/new effects rather than reinstatement of the encoding manipulation during test. Quantitative but not qualitative effects of both encoding manipulations on the old/new ERPs were reported (Allan et al., 2000). On the other hand, experiments examining long-lasting slow waves that were recorded for up to 6 seconds after stimulus onset have reported qualitative differences at test relating to encoding-specific manipulations with no differences between study and test ERPs within the same modality (e.g. Khader, Heil, et al., 2005; Rösler et al., 1995). Those results suggest that encoding and retrieval operations overlap to a certain extent but those operations are modality-specific. Although content-dependent retrieval has been the focus of many previous investigations (e.g., Johnson et al., 2008), the extent to which ERPs at test differ depending on study phase information and the interpretation of such reinstatement-like effects is not entirely clear at this point.

The present experiment employed a subsequent memory paradigm with four spaced repetitions of each stimulus, followed by a surprise source-recognition task. Participants repeatedly studied stimuli presented in one of three encoding modality conditions: repeatedly presented as pictures (referred to in-text as *Picture*), repeatedly presented as words (referred to in-text as *Word*) or alternately presented as pictures and words (referred to in-text as *Picture&word*). At test, all stimuli were cued with words and participants made item memory judgements (old/new) and source memory judgements (previously learned as Picture, Word or Picture&word). This paradigm allowed investigations of the effects of perceptual and conceptual repetition, interactions between subsequent memory and encoding modality. Based on the literature, no strong predictions could be made regarding the directions of the interactions between subsequent source memory, repetition and encoding modality. Instead, the aim was to further investigate subsequent source memory and repetition effects during the study phase in the context of different encoding modalities. Furthermore, this paradigm allowed test phase investigations of reinstatement of picture stimuli at test in the absence of the original picture, i.e., when cued with the word. Based on the LPC's role in episodic recollection at test (reviewed in Friedman & Johnson, 2000; Rugg & Curran, 2007; Wilding & Ranganath, 2012), LPC amplitudes are hypothesised to be sensitive to information relating to the encoding phase, i.e., LPC amplitudes may discriminate stimuli encoded in different modalities.

3.2 Method

3.2.1 Participants

Thirty participants (16 women) were recruited. They were aged 18 to 34 years (M_{age} = 21±4) and had completed an average of 15±2 years of education. Data from two participants were excluded from all behavioural and neurophysiological analyses due to technical faults during testing. Data from another three participants were excluded from EEG analyses only because of poor data quality.

3.2.2 Materials

Stimuli presented throughout the study phase were pictures and written words of common objects and animals (e.g., doors, boat, monkey). A total of 288 stimuli were selected from the Bank of Standardized Stimuli (BOSS) Phase II (Brodeur, Guérard, & Bouras, 2014). Stimuli were matched across all tasks and conditions in terms of frequency, familiarity, name agreement and letter length (see Table 1). Words were presented in white Courier New 36 font. Picture dimensions were 400x400 pixels. All stimuli were presented in the centre of a black background. In between the study and the test phase, participants performed a distractor task in the form of a trail-making task (see Appendix B).

Table 3.1. *Experiment 1 (EEG): Means (in bold) and standard deviations (italicised, in parentheses) of frequency, familiarity, name agreement and letter length of stimuli presented in study and test phase.*

	Study Phase				Test Phase		
	All	Picture	Word	PW*	All	Old	New
Frequency	**29.81**	**30.02**	**29.67**	**29.73**	**29.43**	**29.81**	**29.43**
	(7.77)	*(7.61)*	*(7.85)*	*(8.02)*	*(8.08)*	*(7.77)*	*(8.08)*
Familiarity	**4.31**	**4.28**	**4.34**	**4.31**	**4.32**	**4.31**	**4.32**
	(0.40)	*(0.34)*	*(0.36)*	*(0.50)*	*(0.38)*	*(0.40)*	*(0.38)*
Name Agreement	**0.75**	**0.76**	**0.74**	**0.74**	**0.74**	**0.75**	**0.74**
	(0.17)	*(0.17)*	*(0.18)*	*(0.16)*	*(0.18)*	*(0.17)*	*(0.18)*
Letter Length	**5.99**	**6.10**	**5.79**	**5.79**	**5.94**	**5.99**	**5.94**
	(2.03)	*(2.16)*	*(2.11)*	*(1.83)*	*(1.87)*	*(2.03)*	*(1.87)*

* PW = picture-word multi-modal condition.

3.2.3 Task & procedure

During the study phase, a subset of 144 of the total of 288 selected stimuli were presented one-by-one. Participants were instructed to press one of two buttons on the four-button response device corresponding to whether they thought the presented object was typically found indoors or outdoors. Each stimulus was presented four times, once during each of the four encoding blocks, resulting in a total of 576 EEG encoding trials. Stimuli were presented in one of three modality conditions (with the same number of stimuli in each condition, i.e., 48): repeatedly as a picture (picture uni-modal), repeatedly as a word (word uni-modal) or alternately as a picture or a word (picture-word multi-modal). The average inter-trial interval (ITI) was 4100 ms. The experimental procedure is illustrated in Figure 3.4.

At the end of the encoding phase participants performed a trail-making distractor task.

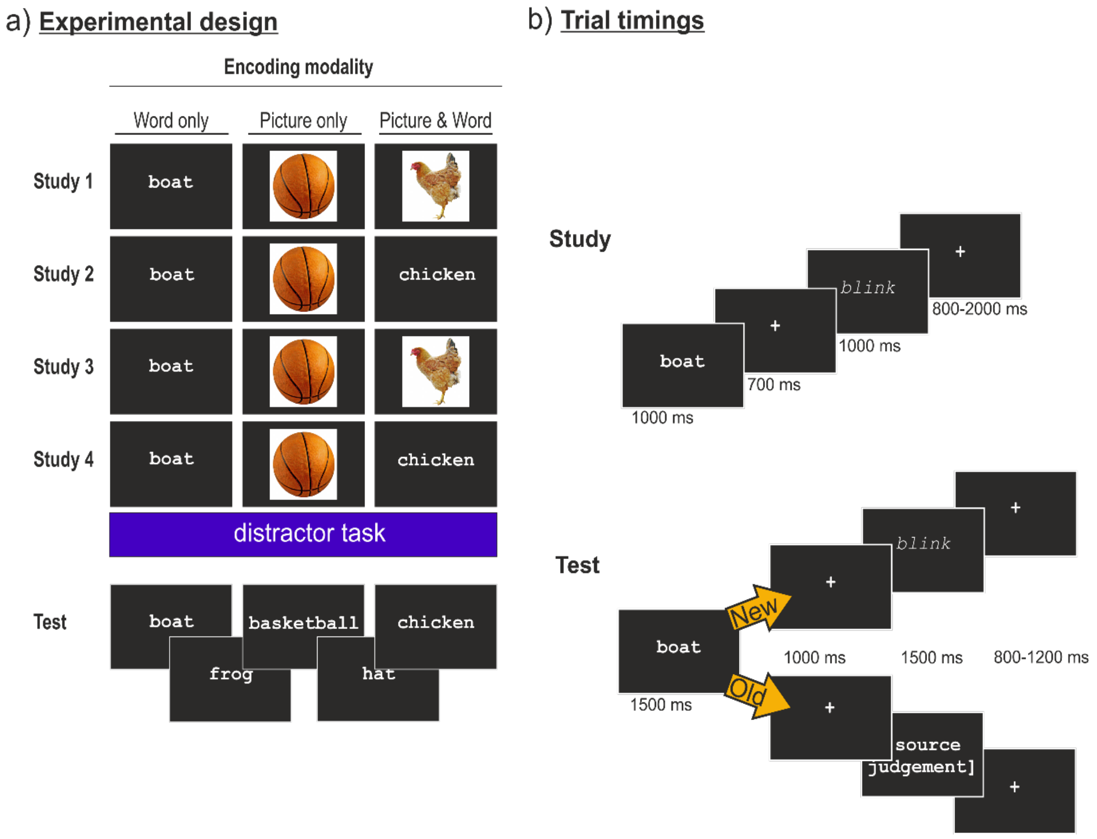


Figure 3.4. Experiment 1 (EEG): a) the experimental paradigm with four encoding presentations during the study phase, followed by the test phase, with b) trial timings displayed.

In an incidental recognition-source memory test, all 144 old stimuli from the indoor/outdoor categorisation task were presented along with 144 new stimuli (the remaining half of the stimuli that had not been presented at study) from the same two semantic categories. All stimuli were presented as white written words in Courier New 36 font on black background. Participants were instructed to make an old/new item memory judgement by indicating whether they thought an object had been presented in the preceding study phase or not. Participants pressed one of four buttons on the response pad corresponding to the following responses: definitely old, perhaps old, perhaps new, and definitely new. Whenever responses indicated that an object had been shown during encoding, i.e., was old, a new screen appeared with a follow-up question assessing source memory by asking participants how the object had been presented. The response options were *picture*, *word*, *picture & word* and *I don't know*. Stimuli were presented for 1500 ms, followed by a fixation cross for 1000 ms. Depending on participants' old/new response, either a fixation cross or the source memory question appeared for 1500 ms. Another fixation cross of random duration (800 – 1200ms) then indicated the beginning of the next trial (average ITI = 5000 ms).

3.3 Results

The repeated-measures design included three factors of interest at study and two at test: subsequent memory (hits+, hits-; behavioural analyses further include misses), repetition (presentation 1,2,3,4; only at study) and encoding modality (uni-modal picture, uni-modal word, multi-modal picture&word). Hits+ trials were characterised as high confidence item hits followed by correct source memory. Hits- trials included hits in the old/new task, irrespective of confidence judgement, followed by an incorrect source memory response or no response, indicating the source could not be retrieved. High memory performance, as indicated by discriminability scores (see 3.3.1.2), meant that misses are only included in behavioural analyses and were excluded from neuroimaging analyses due to low trial counts. Because of a lack of low confidence responses, confidence was not included in further analyses. In the present experiment, participants' responses to the item memory question indicated that they were more often highly confident of their response ($M\%_{HC}$ = 89.93 ±16) than responding with low confidence ($M\%_{LC}$ = 10.17 ±16), $t_{27} = 12.748$, $p < .001$.

3.3.1 Behavioural results

3.3.1.1 Reaction times at study

RTs to the indoor/outdoor judgement task during the study phase are illustrated in Figure 3.5. RT data were analysed in a 3 x 3 x 4 repeated-measures ANOVA with the factors subsequent memory (hits+, hits-, misses), encoding modality (picture, word, picture&word) and presentation (1,2,3,4). Main effects of presentation, $F_{3,66} = 68.976$, $p < .001$ and modality, $F_{2,44} = 9.188$ p = .001 were found. RTs overall decreased with repetition, all $p < .008$. RTs to stimuli repeatedly presented as pictures were significantly faster than to stimuli presented in either of the other two encoding modalities, all $p < .016$.

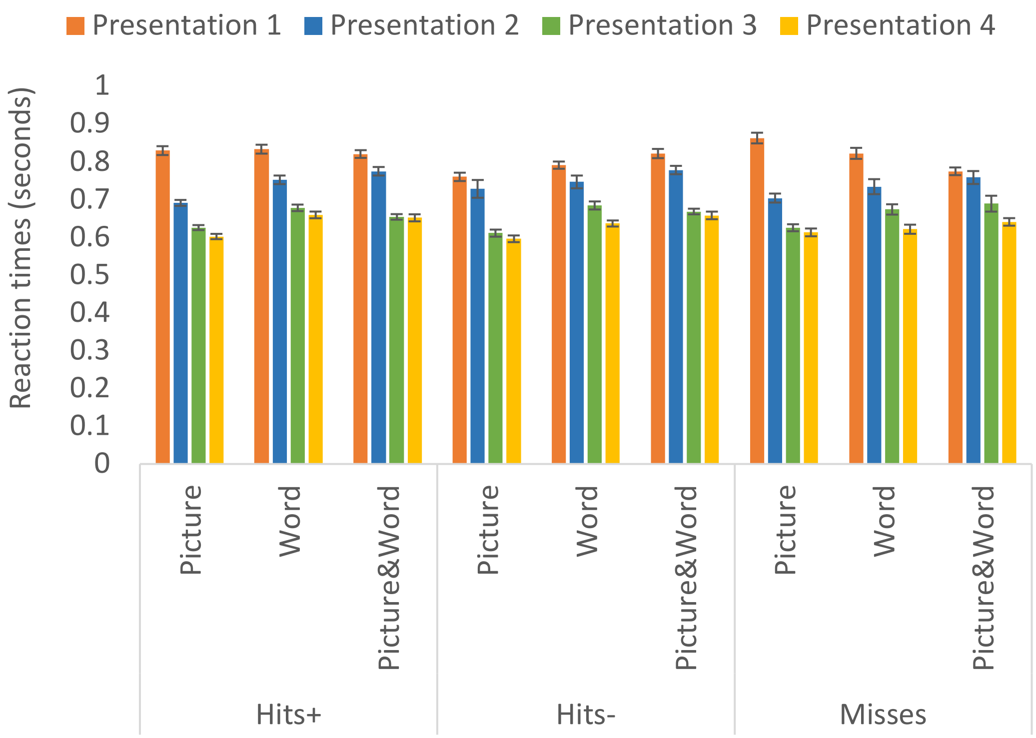
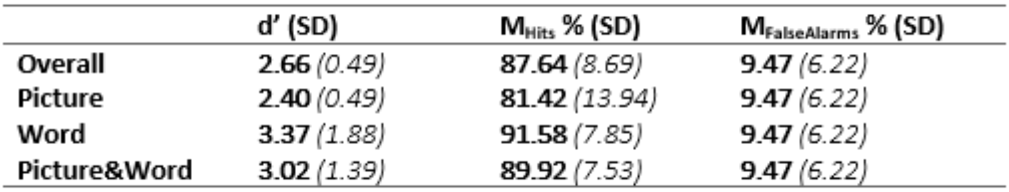


Figure 3.5. Reaction times (in seconds) in experiment 1 (EEG) for all four presentations during the study phase, separately for subsequent memory performance and encoding modalities. Error bars denote standard error.

3.3.1.2 Discriminability analysis

Discriminability scores (d') were calculated based on the frequencies of hits and false alarms. The normalised probabilities of overall hits and false alarms were compared in a paired-samples t-test. The t-test showed that participants' performance in the recognition memory task was statistically significantly above chance, $t_{24} = 43.924$, $p < .001$. Mean and standard deviations of *d'* scores and percentages of hits and false alarms are illustrated in Table 3.2. Those individual *d'* scores indicate that recognition memory performance was highest in the word uni-modal condition (verging on a ceiling effect) and lowest in the picture uni-modal condition.

Table 3.2. *Experiment 1 (EEG): The mean d' scores and mean % of Hits and False Alarms with standard deviations (in brackets) for overall memory performance and across the three modality conditions, picture only, word only and picture&word.*



	d' (SD)	M_{Hits} % (SD)	$M_{FalseAlarms}$ % (SD)
Overall	**2.66** *(0.49)*	**87.64** *(8.69)*	**9.47** *(6.22)*
Picture	**2.40** *(0.49)*	**81.42** *(13.94)*	**9.47** *(6.22)*
Word	**3.37** *(1.88)*	**91.58** *(7.85)*	**9.47** *(6.22)*
Picture&Word	**3.02** *(1.39)*	**89.92** *(7.53)*	**9.47** *(6.22)*

3.3.1.3 Behavioural performance at test

Frequencies of hits+, hits- and misses (memory performance) were analysed across modalities (picture uni-modal, word uni-modal, picture-word multi-modal) in a 3 x 3 repeated-measures analysis. Descriptive statistics of the data included in the analysis are displayed in Figure 3.6. The ANOVA revealed a main effect of memory performance, $F_{2,48} = 116.500$, $p < .001$ and an interaction between memory performance and encoding modality, $F_{4,96} = 26.545$, $p < .001$. Post-hoc tests revealed that all three levels of memory performance differed from each other in terms of frequencies, all $p < .001$. The majority of responses were hits+ judgements (correct item memory, correct source memory), followed by hits- judgements (correct item memory, incorrect source memory) and the least responses resulted in misses; all memory conditions differed from each other at $p < .001$. As illustrated in Figure 3.6, the picture-word alternated encoding condition was associated with the fewest hits+ responses compared to the two uni-modal encoding conditions, all $p < .001$. Hits- frequencies differed between all three encoding conditions, all $p < .001$. The alternated picture&word condition was associated with the most hits- judgements, followed by the word only encoding condition and the picture only condition resulted in the fewest hits- judgements. Picture only encoding was associated with significantly more misses than the other two encoding modalities, all $p < .001$.

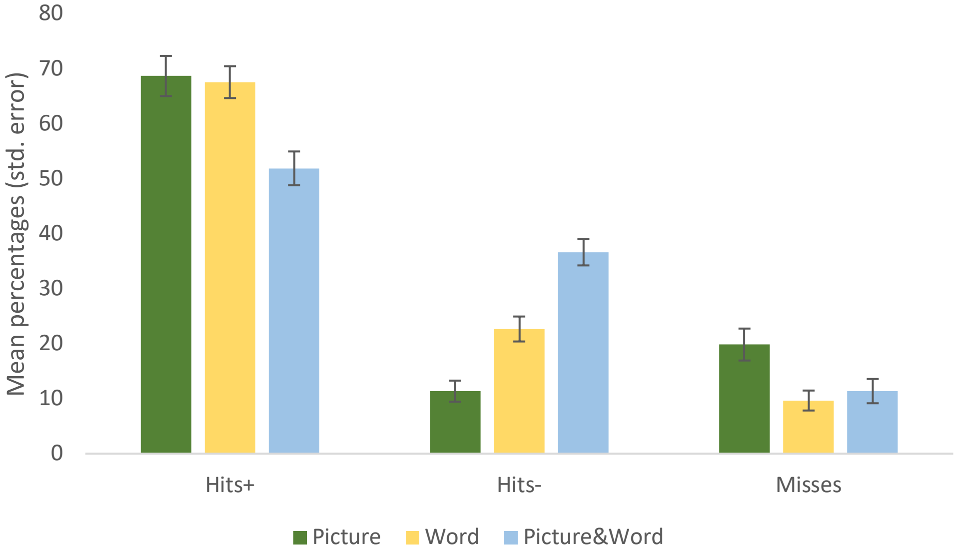


Figure 3.6. Behavioural performance in experiment 1 (EEG). Mean percentages of the three levels of memory performance and encoding modality. Error bars denote standard errors.

3.3.1.4 Reaction times at test

RTs obtained during the test phase were analysed in two repeated-measures ANOVAs. First, RTs to the item memory (old/new) task were examined in a 3 x 3 ANOVA with the factors memory performance and encoding modality. In a second analysis, RTs to the source memory task were analysed. In this 2 x 3 repeated-measures ANOVA, the factors were memory performance (note, only two levels as misses were not followed up with a source memory question) and encoding modality.

The analysis of item memory RTs revealed main effects of memory performance, $F_{2,44} = 8.991$, $p = .003$ and modality, $F_{2,44} = 5.362$, $p = .008$. Follow-up analyses revealed that RTs to misses were significantly slower than to hits+ judgements, $p = .013$, and to hits- judgements, $p = .016$. Furthermore, responses to stimuli previously presented in the picture&word multi-modal condition were significantly faster than to stimuli presented in the picture uni-modal condition during encoding, $p = .014$.

The ANOVA on source memory RTs revealed a main effect of memory performance (hits+, hits-), $F_{1,23} = 9.795$, $p = .005$ with RTs to hits+ being faster than to hits- judgements.

3.3.2 ERP analysis

Based on previous research, two ERP components were selected. The early frontal FN400-like ERP was measured between 300 – 500 ms post stimulus onset at electrode sites F1/F2, F3/F4, FC1/FC2 and FC3/FC4. The late parietal LPC-like ERP was measured between 500 - 700 ms post stimulus onset at electrode sites P1/P2, P3/P4, P5/P6 and PO3/PO4.

ERP analyses at study focused on interactions between the factors subsequent source memory, repetition and encoding modality. Due to insufficient trial numbers across subsequent hits- judgements, it was not possible to analyse all three factors in one ANOVA. Therefore, a first analysis investigated effects of subsequent memory and repetition when collapsed across encoding modality. A second analysis was conducted to examine effects of subsequent memory and encoding modality when averaged across the presentation factor. A third analysis examined interactions between encoding modality and repetition only including subsequent hits+ trials. Further data-driven exploratory analyses were carried out in order to follow-up on repetition effects using mass-univariate and single-trial analyses (presented in 3.3.2.2) and to further investigate quantitative and qualitative differences employing extensive univariate (presented in 3.3.2.4).

Two ERP analyses were performed on ERPs measured during test. A first analysis combined the old/new effect with source memory, i.e., the factor memory had three levels (correct rejections, hits+, hits-). A second analysis looked at ERP differences at test due to encoding modality within hits+ judgements. Subsequently, data-driven exploratory analyses were carried out testing for the same effects as in the planned ERP analyses but across a wider range of time windows (presented in 3.3.2.4).

3.3.2.1 Study phase

Subsequent memory and repetition

Two separate 2 x 4 x 2 x 4 repeated-measures ANOVAs were conducted to investigate interactions between subsequent memory and multiple stimulus presentations. The factors included subsequent source memory (hits+, hits-), presentation (1,2,3,4), hemisphere (left, right) and electrode pair (see 3.3.1.2 for details on electrode pairs). For the frontal component, a main effect of presentation was found to be significant, $F_{3,72} = 9.491$, $p < .001$ with mean amplitudes increasing in negativity across presentations. However, the interaction between subsequent source memory and presentation was non-significant, $F_{3,72} = 0.484$, $p = .694$ (iluustrated in Figure 3.7a).

Similar results were observed over parietal sites with a statistically significant main effect of presentation, $F_{3,72} = 11.900$, $p < .001$, reflecting a general increase in positivity across repetitions with mean amplitudes at presentation 1 being significantly less positive than all subsequent presentations, all $p < .002$. However, the interaction between subsequent source memory and presentation was non-significant, $F_{3,72} = 0.620$, $p = .113$ (illustrated in Figure 3.7b).

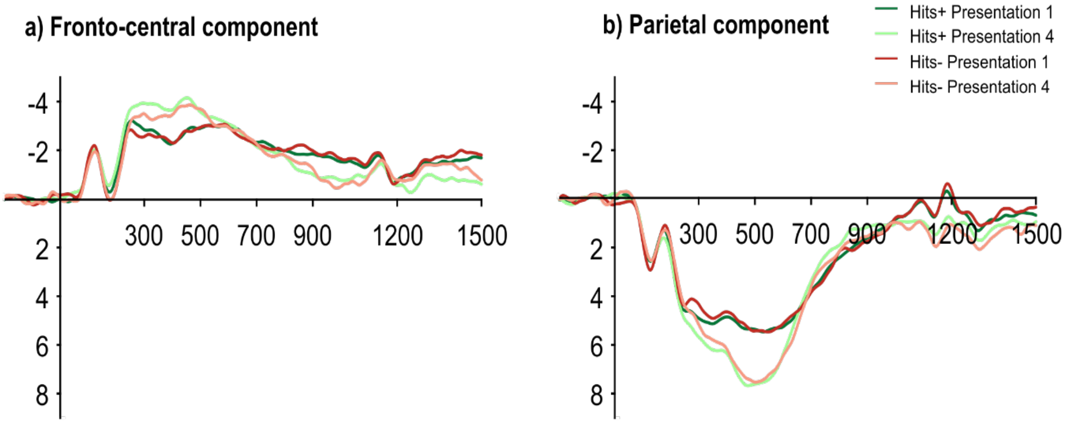


Figure 3.7. Experiment 1 (EEG): Grand average ERPs (N = 25) to presentations 1 and 4 for subsequent hits+ and hits- judgements, illustrating the non-significant interactions between subsequent source memory and multiple stimulus presentations in a) the fronto-central component, measured between 300 – 500 ms, averaged across electrode sites F1/F2, F3/F4, FC1/FC2 and FC3/FC4 and b) the parietal component, measured between 500 – 700 ms, averaged across electrode sites P1/P2, P3/P4, P5/P6 and PO3/PO4.

Subsequent memory and encoding modality

Two separate 2 x 3 x 2 x 4 repeated-measures ANOVAs were conducted, one for each ERP component (FN400, LPC), with the factors subsequent memory (hits+, hits-), encoding modality (picture only, word only, picture&word), hemisphere (left, right) and electrode pair (see 3.3.1.2 for details on electrode pairs). For the early frontal component, the main effects of source memory and modality were both significant, $F_{1,24} = 6.689$, $p = .016$ and $F_{2,48} = 56.995$, $p < .001$, respectively. However, the interaction between subsequent source memory and modality was non-significant, $F_{2,48} = 0.682$, $p = .510$ (illustrated in Figure 3.8a). Subsequent hits+ judgements were found to elicit more positive waveforms than subsequent hits- judgements. ERPs to all three encoding modalities differed significantly from each other, all $p < .001$, with pictures eliciting the most negative ERPs and words eliciting the least negative ERPs.

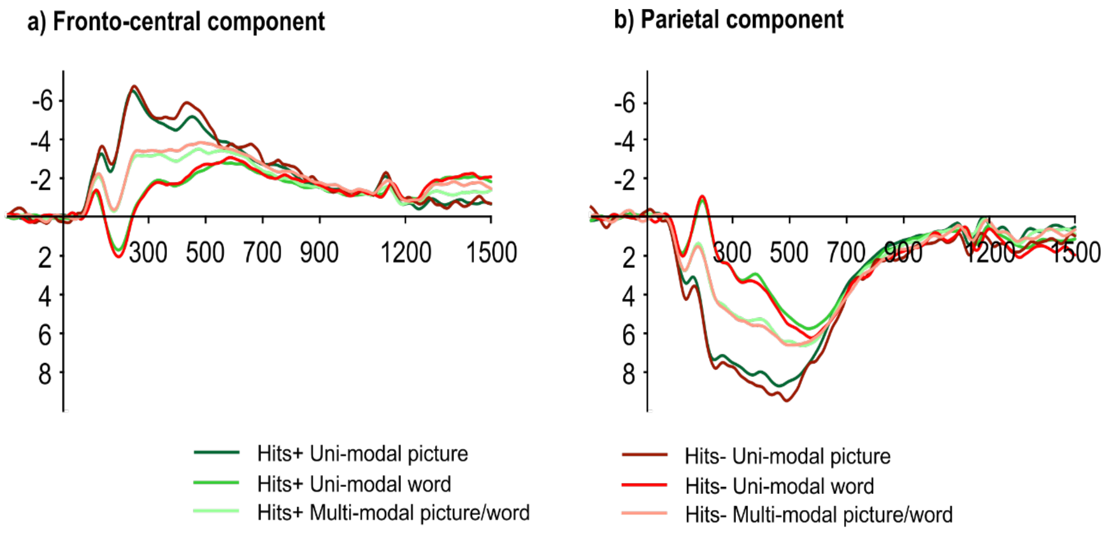


Figure 3.8. Experiment 1 (EEG): Grand average ERPs (N = 25) to subsequent hits+ and hits- judgements separately for the three encoding modality conditions, illustrating the non-significant interactions between subsequent source memory and encoding modality in a) the fronto-central component, measured between 300 – 500 ms, averaged across electrode sites F1/F2, F3/F4, FC1/FC2 and FC3/FC4 and b) the parietal component, measured between 500 – 700 ms, averaged across electrode sites P1/P2, P3/P4, P5/P6 and PO3/PO4.

For the LPC-like parietal component, the repeated-measures ANOVA revealed a main effect of modality, $F_{2,48} = 14.229$, $p < .001$. Additionally, the main effect of subsequent source memory was nearing statistical significance, $F_{1,24} = 3.371$, $p = .079$ with hits- judgements associated with more positive mean amplitudes than hits+ judgements. However, again, the interaction between subsequent source memory and encoding modality was non-significant, $F_{2,48} = 1.259$, $p = .293$ (see Figure 3.8b). Following up on the main effect of modality, it was revealed that ERPs to the uni-modal picture condition were more positive than both, stimuli presented as words only and stimuli alternately presented as pictures and words, $p = .001$, while the latter two conditions did not differ from each other in terms of LPC mean amplitudes, *p* = .233.

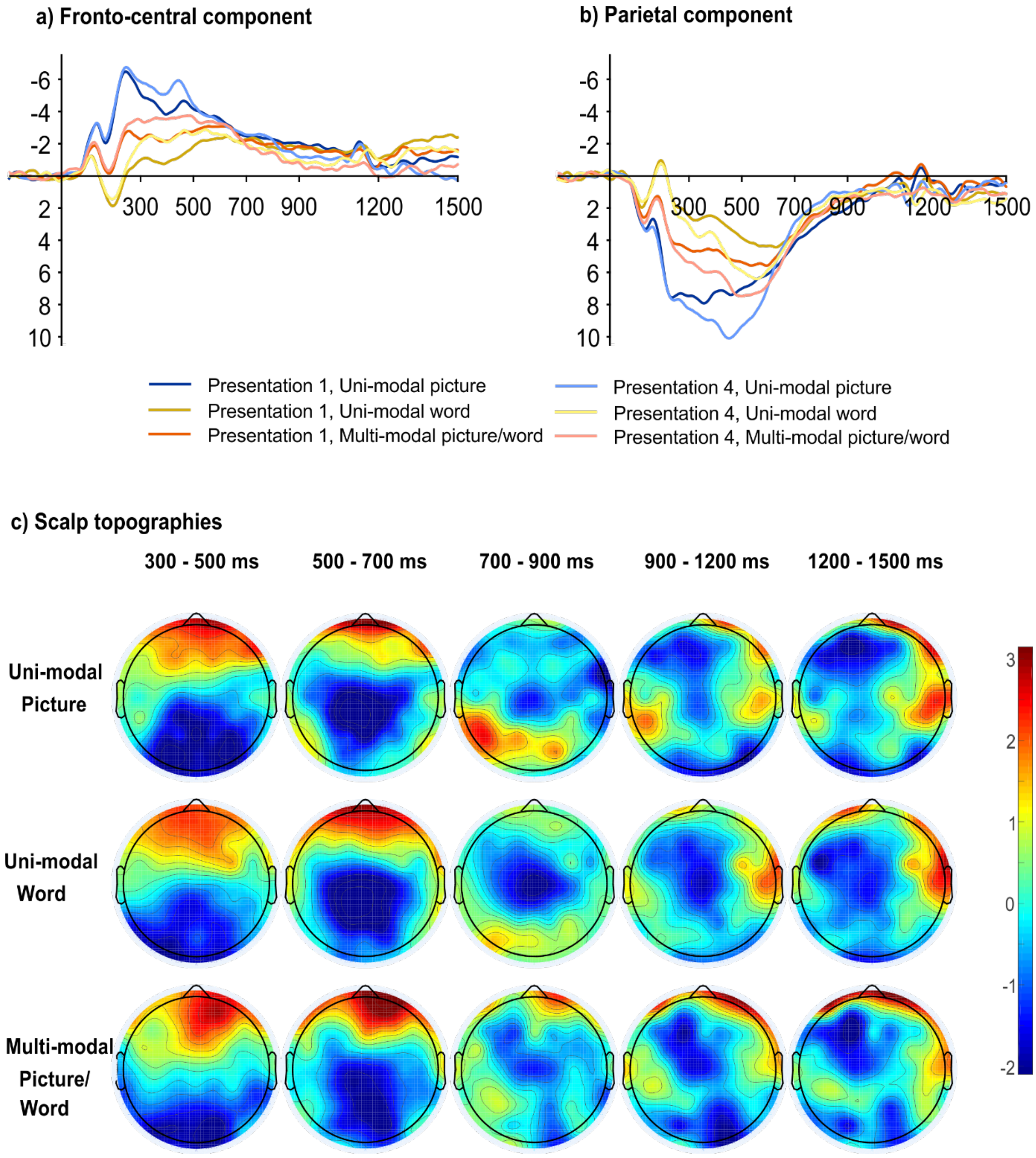


Figure 3.9. Experiment 1 (EEG): Grand average ERPs (N = 25) to presentations 1 and 4, separately for the three encoding modality conditions, illustrating the non-significant interactions between multiple stimulus presentations and encoding modality in a) the fronto-central component, measured between 300 – 500 ms, averaged across electrode sites F1/F2, F3/F4, FC1/FC2 and FC3/FC4 and b) the parietal component, measured between 500 – 700 ms, averaged across electrode sites P1/P2, P3/P4, P5/P6 and PO3/PO4. C) Topographic maps displaying the scalp distributions of the repetition effect (presentation 4 – presentation 1) separately for the three encoding modalities across 5 different time windows.

Encoding modality and repetition in successful item and source encoding

Another two separate 3 x 4 x 2 x 4 repeated-measures ANOVAs were conducted to investigate interactions between encoding modality and multiple stimulus presentations only including trials associated with subsequent hits+ judgements. The factors included modality, presentation, hemisphere and electrode pair. For both, the frontal and parietal, components the interaction between presentation and encoding modality was non-significant, $F_{6,144} = 1.249$, $p = .285$ and $F_{6,144} = 1.325$, $p = .250$, respectively (see Figure 3.9a,b). The scalp topographies of the repetition effect, separately displayed for picture, word and picture&word encoding (see Figure 3.9c), suggest that a repetition effect occurs largely independent of encoding modality in the FN400 and LPC time windows.

3.3.2.2 Exploratory single-trial analyses (follow-up repetition effect)

ERP analyses indicated a widespread repetition effect occurring roughly between 300 – 600 ms. This effect appeared to be largely independent of subsequent source memory and encoding modality. However, previous research employing single-trial analyses have indicated that traditional averaging approaches may not be sensitive enough in order to detect any further interactions (Holm et al., 2006). In an attempt to further explore the quantitative and qualitative differences relating to repetition, a data-driven mass-univariate ERP approach (Groppe, Urbach, & Kutas, 2011a) was employed to “isolate” the repetition effect. To detect reliable repetition effects ERPs to presentation 1 and presentation 4 were submitted to a repeated-measures, two-tailed cluster-based permutation test. This approach is based on the cluster mass statistic (Bullmore et al., 1999; Maris & Oostenveld, 2007) with a 0.05 family-wise alpha level. It was previously demonstrated that the cluster mass statistic provides good power for wide-spread ERP effects (Groppe, Urbach, & Kutas, 2011b; Maris & Oostenveld, 2007). A total of 201 data points measured between 200 and 1000 ms from a frontal subset of 21 electrodes and a parietal subset of 21 electrodes was included in the analysis resulting in 8442 comparisons with 24 t-score degrees of freedom. 2,500 random permutations were performed. During each permutation, clusters were formed on the basis of significant t-scores (0.05 uncorrected). Adjacent time points were considered as temporal neighbours. The “mass” of a cluster is based on the sum of the t-scores with the most extreme cluster mass in each of the 8442 comparisons being used to estimate the distribution of the null hypothesis. The *p*-value was acquired from the permutation cluster mass percentile ranking of each of the clusters assigned to each member in the cluster. A total of 11 negative clusters (Fp1, AF3, F1, F3, Fz, Fp2, AF4, AF8, F2, F4, F8), reflecting a decrease in mean amplitudes, and 9 positive clusters (CP1, P1, P3, PO3, CPz, Pz, CP2, P2, PO4), reflecting an increase in mean amplitudes, were found to be significant. A negative frontal and a positive parietal cluster were formed based on overlapping time points showing a repetition effect; the frontal effect was measured from 308 – 568 ms post stimulus onset and the parietal repetition effect was measured from 404 – 608 ms post stimulus onset.

Positivity/negativity enhancement across repetitions

Mean amplitudes were extracted for each single trial and separately for the positive and negative cluster. The aim of the first analysis was to investigate whether the repetition effects as reflected in positivity enhancement for the parietal cluster and negativity enhancement for the frontal cluster (reported in section 3.3.1.2.1) were related to repetitions of individual items. For each stimulus and each consecutive presentation pair (Presentation 1 and 2, Presentation 2 and 3, Presentation 3 and 4), positivity enhancement was calculated by subtracting the earlier from the later presentation. Analogously, negativity enhancement was calculated by subtracting the later from the earlier presentation. As a control value for enhancement, the same differences were calculated except that the amplitude values from the trial occurring right before the actual stimulus repetition were used. Paired-samples t-tests were used to test whether stimulus-related repetition effects differed from the control. The only enhancement effect that differed from the control enhancement value was in the positive cluster between presentation 1 and 2, t_{24} = 0.125, *p* = .044. This result suggests that, apart from a novelty effect measured between the first and second presentation of a stimulus and only in the parietal cluster, the repetition effects reported in section 3.3.2.1 may not be directly related to repetition at the item-level. This parietal novelty effect did not discriminate subsequent hits+ and hits- judgements (positive cluster: t_{24} = -0.838, *p* = .410; negative cluster: t_{24}= -1.392, *p* = .177). This is in line with the ERP results and indicates that these enhancement effects are largely independent of explicit subsequent source memory and item-specific repetition with the exception of a novelty effect over parietal sites. Testing for modality-related differences in the observed parietal novelty effect revealed a trend, $F_{2,48} = 3.125$, $p = .053$, for the increase between presentation 1 and 2 to be highest in the picture&word encoding condition and lowest in the picture only encoding condition.

Amplitude enhancement effects and implicit memory (RTs)

To test whether amplitude enhancement effects were related to implicit memory, i.e., behavioural repetition priming effects as reflected in repetition-related decreases in RTs, the previously calculated differences in amplitude measures were correlated across trials with RT differences between the same consecutive presentation pairs. The resulting correlation coefficients for the frontal and the parietal cluster from each participant were submitted to one-sample t-tests. The results indicated that the extent of repetition priming was related to positivity enhancements across the parietal cluster, $t_{24} = 12.856$, $p < .001$, and to negativity enhancements across the frontal cluster, $t_{24} = 4.186$, $p < .001$. In both cases, higher amplitude enhancement was associated with a higher decrease in RT. These results are supportive of a relationship between repetition-related changes and implicit memory.

3.3.2.3 Test phase

Source memory

Two separate 3 x 2 x 4 repeated-measures ANOVAs were conducted, one for each ERP component (FN400, LPC), with the factors memory (correct rejections, hits+, hits-), hemisphere and electrode pair. For the FN400, the ANOVA did not reveal a main effect of memory, $F_{2,48} = 0.594$, $p = .516$ (see Figure 3.10a). For the LPC, a main effect of memory was found $F_{2,48} = 21.927$, $p < .001$. Follow-up analyses, however, revealed that although hits+ and hits- judgements differed from correct rejections, $p < .001$, by eliciting more positive mean amplitudes, hits+ and hits- did not differ from each other, $p = .850$ (see Figure 3.10b).

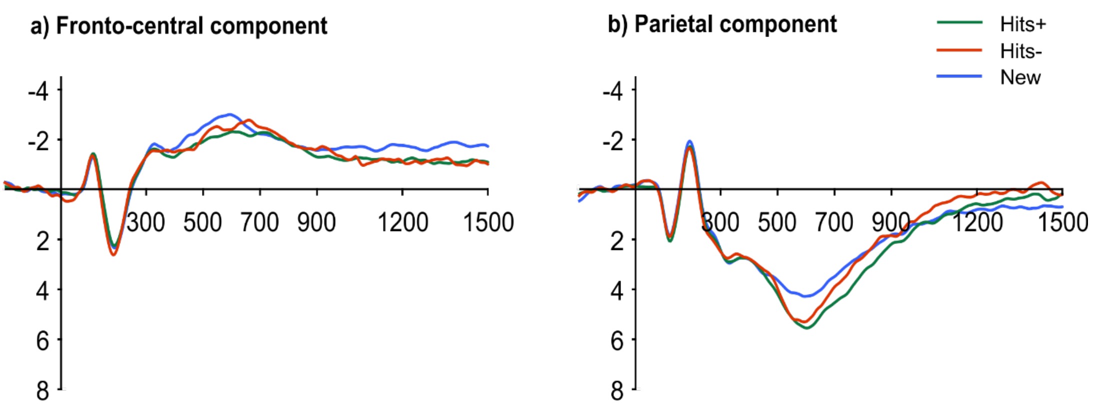


Figure 3.10. Experiment 1 (EEG): Grand average ERPs (*N* = 25) to hits+, hits- and high confidence new judgements during the study phase in a) the fronto-central components, measured between 300 – 500 ms, averaged across electrode sites F1/F2, F3/F4, FC1/FC2 and FC3/FC4 and b) the parietal component, measured between 500 – 700 ms, averaged across electrode sites P1/P2, P3/P4, P5/P6 and PO3/PO4.

Encoding modality at test

Two separate 3 x 2 x 4 repeated-measures ANOVAs were conducted, one for each ERP component (FN400, LPC), with the factors encoding modality (uni-modal picture, uni-modal word, multi-modal picture&word), hemisphere and electrode pair. For the FN400, the ANOVA revealed a significant interaction between encoding modality and hemisphere, $F_{2,48} = 3.475$, $p = .039$ (illustrated in Figure 3.11a). Follow-up analyses showed that stimuli that were encoded repeatedly as pictures elicited more negative mean amplitudes in left compared to right hemisphere, $p = .038$. LPC mean amplitudes were found to differ between the encoding modalities, $F_{2,48} = 5.666$, $p = .006$. Stimuli previously presented repeatedly as pictures elicited significantly less positive ERPs than words, $p = .041$, and those presented in the multi-modal condition, $p = .012$ (see Figure 3.11b).

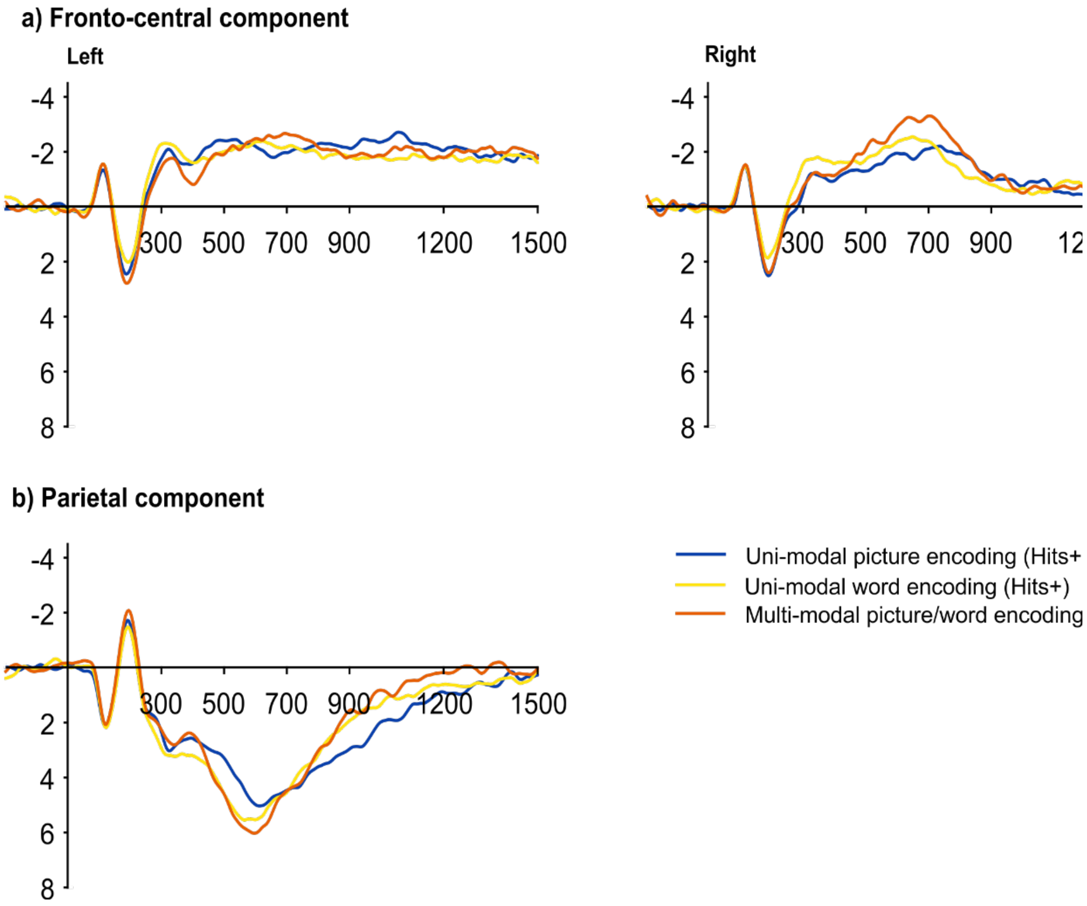


Figure 3.11. Experiment 1 (EEG): Grand average ERPs (N = 25) to the three encoding modalities, only including hits+ judgements, in a) the fronto-central component, measured between 300 – 500 ms, averaged across electrode sites F1/F2, F3/F4, FC1/FC2 and FC3/FC4 and b) the parietal component, measured between 500 – 700 ms, averaged across electrode sites P1/P2, P3/P4, P5/P6 and PO3/PO4.

3.3.2.4 Exploratory ERP analyses

Visual inspection of scalp maps and ERP waveforms indicated that some effects might have occurred outside of the hypothesised time windows. Therefore, the ANOVAs reported in section 3.3.1.2 were carried out for the same two electrode sets (frontal and parietal) across five time windows (300 – 500 ms, 500 – 700 ms, 700 – 900 ms, 900 – 1200 ms, 1200 – 1500 ms). The results are presented in Table 3.3.

During the study phase, additional main effects of subsequent source memory were found in the time window 700 – 900 ms post stimulus onset. Generally, differences between subsequent hits+ and hits- judgements over frontal electrode sites showed that hits+ were associated with more positive waveforms than hits-judgements. Over parietal electrode sites, the inverse effect was reported with ERPs to subsequent hits- judgements being more positive than hits+ judgements. The interactions between subsequent source memory and modality, occurring over parietal sites from 900 ms onwards, indicated that source effects may be easier detected when only pictures are presented at encoding compared to only words or multi-modal encoding. Analogously, the interaction between modality and repetition suggested that repetition effects were strongest in the picture only encoding condition.

During the test phase, an additional old/new effect was found over left frontal electrode sites between 500 – 700 ms and between 900 – 1200 ms. Visual inspection of those ERPs suggests that the peak latency of the frontal component was later than in the predicted 300 – 500 ms time window. The LPC amplitudes did not discriminate between hits+ and hits- judgements as predicted, using the original 500 – 700 ms time window (3.3.1.2.2). However, LPC mean amplitudes between 700 and 900 ms post stimulus onset did discriminate between hits+, hits- and correct rejections, with hits+ eliciting the most positive ERP waveforms and correct rejections the least positive. This effect had a standard left-parietal distribution (e.g., Rugg & Yonelinas, 2003). Additional effects relating to encoding modality were found as well, however, the strongest effect was reported in the hypothesised LPC time window.

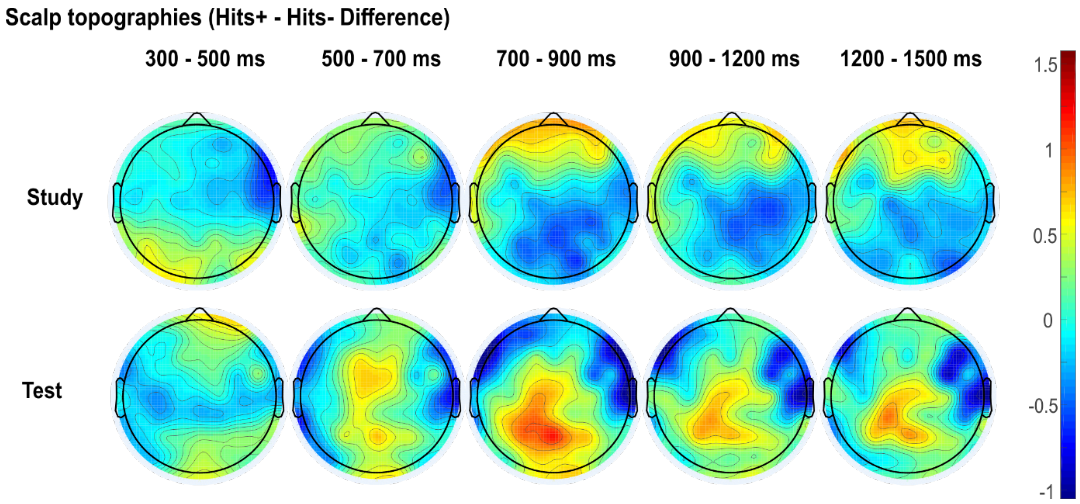


Figure 3.12. Topographic maps for data from experiment 1 (EEG) displaying the scalp distributions of the contrast between hits+ and hits- judgements (hits+ - hits-) at study and test.

Table 3.3 *Results (F statistics and significance level) from comprehensive exploratory repeated-measures ANOVAs at study and test phase.*

	300 – 500 ms		500 – 700 ms		700 – 900 ms		900 – 1200 ms		1200 – 1500 ms	
	Frontal	Parietal	Frontal	Parietal	Frontal	Parietal	Frontal	Parietal	Frontal	Parietal
<u>Study phase</u>										
Dm & Repetition										
S	*ns*	*ns*	*ns*	*ns*	5.819** S x E	5.030*	*ns*	*ns*	7.250*	
P	9.491***	16.771***	5.461**	11.900***	4.208*	*ns*	3.783*	*ns*	3.444*	
S x P	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	
Dm & Modality										
S	6.689*	*ns*	*ns*	*ns*	4.518* S x E	3.927^	4.288* S x E	*ns*	*ns*	*ns*
M	56.995***	77.536***	8.162*	14.229***	*ns*	*ns*	*ns*	*ns*	5.537*	*ns*
S x M	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	5.440* S x M x H	*ns*	7.243** S x M x H
Repetition x Modality										
P x M	*ns*	*ns*	*ns*	*ns*	*ns*	2.832*^[8]	*ns*	2.501*	*ns*	*ns*
<u>Test phase</u>										
Source memory										
S	*ns*	*ns*	9.038** S x H	21.927***	*ns*	8.457**	5.498* S x H	*ns*	*ns*	*ns*
Encoding modality										
M	3.475* M x H	3.435* M x H	*ns*	13.944**	*ns*	*ns*	*ns*	6.012**	*ns*	*ns*

1

S = Subsequent Source Memory; P = Presentation; M = Modality; H = Hemisphere, E = Electrode Pair.
*** = $p < .001$; ** = $p < .01$; * = $p < .05$; ^ = $p = .059$ with hits- more positive than hits+; *ns* = non-significant.

3.4 Discussion

In this experiment, EEG data were recorded during a study phase, with multiple presentations of stimuli in different modalities, and during a test phase, including a recognition-source memory test. During the study phase, interactions between subsequent source memory, repetition and encoding modality were examined. A repetition effect was found to be largely independent of subsequent source memory performance and encoding modality. At test, LPC amplitudes were predicted to be sensitive to source memory as well as to encoding modality. ERPs to correct item and source memory judgements were found to discriminate stimuli based on how they were previously encoded.

Behavioural results

Both item and source memory performance were nearing a ceiling effect. The absence of superior memory performance for stimuli presented as pictures as compared to words is most likely due to the use of words to cue memory at test in the present experiment. Previous research has highlighted the importance of encoding-retrieval interactions implicated in the picture superiority effect (McBride & Dosher, 2002). The "cue congruency effect" (Rugg et al., 2008) for words may indeed have cancelled the usual mnemonic advantage for pictures, consistent with the principle of transfer appropriate processing (Morris et al., 1977; Tulving & Thomson, 1973; Weldon & Roediger, 1987). However, RTs to pictures were found to be fastest at encoding. This suggests faster processing of picture stimuli and may therefore support the notion that word stimuli activate more concept-generic information than pictures do, thus processing time for words would be longer than for pictures (Durso & Johnson, 1979).

ERP results

Based on previous literature, mean amplitudes for a frontal component were measured between 300 – 500 ms post stimulus onset and mean amplitudes for a parietal component were measured between 500 – 700 ms. These components resembled the FN400 and LPC, which are frequently reported during recognition tasks (Curran, 2000; Friedman & Johnson, 2000), enabling investigations of commonly studied test ERPs during the study phase. Due to low frequencies of hits-trials, the three factors of interest, source memory performance, encoding modality and presentation (only at study), could not all be analysed in one ANOVA. Thus, three separate analyses were performed including two of the factors and averaging across the third. Planned analyses did not reveal any meaningful interactions between the factors subsequent source memory, presentation and encoding modality. Exploratory single-trial analyses following up on the repetition-related ERP effects revealed that only a parietal novelty effect between presentations 1 and 2 was related to stimulus-specific repetition. Moreover, repetition-related changes at the single-trial level were associated with implicit memory/repetition priming for a frontal and a parietal cluster. At test, a parietal old/new effect was observed, however, only a slightly later occurring parietal effect also discriminated hits+ and hits- judgements. Finally, during the test phase, evidence was found that ERPs to hits+ judgements differed based on encoding manipulations, potentially reflecting some form of reinstatement at test.

Study phase – planned analyses

At study, the planned analyses did not reveal any significant interactions between the factors. Moreover, only one main effect of subsequent source memory reached statistical significance, FN400 amplitudes to subsequent hits+ judgements elicited more positive waveforms than to subsequent hits- judgements. For the LPC-like component, no main effect of source memory was significant in the predicted time window. However, a trend indicated that, especially for the picture only encoding condition, mean amplitudes were more positive for subsequent hits- than hits+ judgements. These results relating to main effects of subsequent source memory do not support a role for the frontal component in familiarity judgements and the parietal component in recollection (Curran, 2000; Groh-Bordin et al., 2006). The FN400 being more positive for hits+ than hits- judgements suggests that it is modulated by subsequent source memory performance. This is in line with previous research (Angel et al., 2013; Cansino & Trejo-Morales, 2008) indicating that FN400 amplitudes may be modulated by subsequent source memory accuracy and not solely be associated with familiarity judgements. The absence of a statistically significant LPC effect discriminating subsequent hits+ and hits- judgements as well as the polarity of the observed trend are contrary to previous research (see Yovel & Paller, 2004). Weak or absent effects relating to source memory may be due to participants recollecting non-criterial contextual information, i.e., hits- judgements are potentially contaminated by recollection trials (Mulligan & Hirshman, 1997; Yonelinas & Jacoby, 1996). One important factor may be how source information itself is processed at encoding. In the present study, the encoding task did not require participants to pay attention to the source of the stimulus (encoding modality) which was later assessed in the source memory task at test. Results of studies using the recognition-source paradigm, in which participants were either aware of or focused their attention on source information, suggest that explicit attention to source during encoding can sometimes lead to more robust subsequent memory effects (Angel et al., 2013; Cansino & Trejo-Morales, 2008; Cansino et al., 2010). The interactions between the factors are potentially confounded by averaging across the third factor. For example, a main effect of subsequent source memory in FN400 amplitudes was only found when averaging across the presentation factor, but not in the analysis that averaged across the modality factor. This suggests that averaging across one factor, due to low trial counts, may have prevented a bigger picture from emerging. Moreover, it has been suggested that pictures of objects are verbalised to some extent (Persson & Söderlund, 2015), which may explain the absence of interactions between source memory and encoding modality.

Exploratory single-trial analyses (repetition effects)

Exploratory analyses of study phase data focused on the observed effect of presentation. Cluster-based mass-univariate analyses were performed to isolate the repetition effect, as measured by contrasting ERPs to the first and fourth presentation. Results indicated repetition-related ERP changes over frontal and parietal electrode sites. The frontal component was found to be sensitive to repetition between around 300 – 550 ms post stimulus onset, which largely overlaps with the hypothesised time window for the FN400. The parietal component was sensitive to repetition around 400 – 600 ms, which is slightly earlier than the here predicted LPC time window though not uncommon (see Curran et al., 2006). Mean amplitudes across those time points were extracted for each trial and averaged across electrode sites within the two clusters (negative frontal and positive parietal). Repetition-related amplitude enhancements were calculated for each consecutive presentation pair of each stimulus. Additionally, a control value was computed by calculating the same amplitude enhancement but for the trial occurring prior to the actual stimulus repetition. When comparing item-specific and control enhancement values, it was found that only the difference between first and second presentation over parietal electrode sites was directly related to the repetition of a stimulus. This raises the question what the observed increase in parietal positivity and frontal negativity in mean amplitudes is related to if not item repetition. Previous research has reported ERPs to be sensitive to repetition (Renoult et al., 2012; Rugg & Doyle, 1994; Segalowitz et al., 1997), a finding which was replicated in the present ERP analyses. However, these single-trial measures shed new insights into these repetition effects, suggesting that only a parietal novelty effect is related to stimulus-specific repetition. It may be that the general amplitude changes are associated with repeated task performance rather than item repetition. Moreover, the observed enhancement effects did not discriminate between subsequent hits+ and hits- judgements, suggesting the repetition effect to be independent of recollection. Future investigations should probe whether these effects are also independent of subsequent item memory. The frontal negativity and the parietal positivity enhancement were both related to implicit memory as measured by RTs. Existing fMRI research has already established a relationship between repetition suppression and implicit (RTs) and explicit (memory performance) memory processes at the individual stimulus level (van den Honert et al., 2016; Ward et al., 2013). However, this approach is not yet common to EEG research. The present finding will have to be replicated in future studies to establish its reliability and further investigate what underlies the repetition-related ERP changes previously reported. While results from exploratory analyses have to be interpreted with caution, it was recently highlighted that data-driven approaches can help us to avoid tunnel-vision during data analysis (Paré & Quirk, 2017), which is certainly reflected in the present results.

Test phase – planned analyses

At test, no FN400 source memory effects were observed in the hypothesised time window. As outlined in the general introduction (section 1.5.3), results relating to the FN400 are generally mixed with some research reporting ERP differences between hits and correct rejections (Addante, Ranganath, & Yonelinas, 2012;

Cansino & Trejo-Morales, 2008; Wilding, 2000) and others reporting source memory effects with amplitudes discriminating hits+ and hits- judgements (Addante, Ranganath, & Yonelinas, 2012; Cansino & Trejo-Morales, 2008). However, the absence of an old/new effect in the FN400 has also been reported (Cycowicz & Friedman, 2003; Cycowicz et al., 2001). Cycowicz and Friedman (2003) noted that the majority of previous studies reporting frontal recognition effects had employed word rather than picture stimuli. Additionally, and more relevant to the present paradigm, where concepts encoded as pictures were cued as words during the test phase, Kazmerski and Friedman (1997) reported modality-specific differences in scalp distributions of the old/new effect that were not observed when pictures were presented at study but cued with words at test. Therefore, the role of the FN400 is still unclear. Systematic testing of modality effects, as already carried out by Kazmerski and Friedman (1997), will have to be replicated in sufficiently powered designs to establish whether word stimuli elicit larger old/new FN400 effects than picture stimuli. LPC amplitudes to hits+ and hits- judgements differed from correct rejections, which is in line with a large body of research (Rugg, Schloerscheidt, et al., 1998; Wilding, 2000; Wilding & Rugg, 1996; Woroch & Gonsalves, 2010), adding to the robustness of the parietal old/new effect. However, LPC amplitudes in the 500 – 700 ms time window did not discriminate hits+ and hits- judgements as predicted based on the literature (Addante, Ranganath, & Yonelinas, 2012; Cansino & Trejo-Morales, 2008; Mollison & Curran, 2012, experiment 1). Discrepancies in paradigms may partly contribute to the absence of the source memory effect, because previous studies typically presented the same stimulus at study and test, whereas in the present research, perceptual features of the studied concept did not always overlap between the two phases, i.e., stimuli encoded as pictures only, were cued with words at test. In fact, the observed ERP differences at test relating to encoding modality suggest that ERPs to successful source recognition differed depending on encoding modality; stimuli encoded as pictures elicited less positive ERPs compared to stimuli encoded in the other two modalities This is in line with previous research (e.g., Allan et al., 2000), further suggesting that information from the study phase is reinstated at test and this reinstatement can be measured with ERPs. The direction of this effect is somewhat unexpected, as previous research would lead to the prediction that memories based on word stimuli may be associated with fewer perceptual details than memories formed from viewing picture stimuli (Johnson, Kounios, & Nolde, 1997). If more perceptual details are available, these can be retrieved by activating the visual cortex, thereby enhancing positivity over posterior electrode sites. When fewer perceptual details are available, participants may be required to retrieve more semantic and self-generated information relating to a stimulus, which may be reflected in more frontally distributed activation (Johnson et al., 1997)**.** Moreover, it is conceivable that the encoding modality effect at test is reflecting a change in modality from study to test phase rather than true reinstatement. Further research is needed to test whether the reinstatement effects interact with source memory performance and to what extent they reflect encoding operations.

Study and test phase – additional exploratory ERP analyses

Exploratory ERP analyses were performed as the visualisations of the ERP waveforms indicated that some of the predicted effects might have occurred outside of the predicted time windows. Indeed, at study as well as at test, parietal amplitudes between 700 – 900 ms post stimulus onset discriminated between hits+ and hits- judgements, though these effects had opposite polarities at study and test. The LPC at study was found to be associated with more positive-going amplitudes for hits- than hits+, which is contrary to the predicted direction of this effect but in line with the trend observed in the planned LPC analyses in the 500 – 700 ms time window. However, this later, statistically significant effect was found during the up-phase of the LPC, while around the peak, a small and statistically non-significant effect indicated hits+ to be more positive than hits- trials. The later occurring interactions between source memory and modality at frontal sites and between modality and repetition at parietal sites largely reflected that effects were strongest in the picture only encoding modality. At test, an additional effect relating to source memory was also found over frontal electrode sites in the time windows 500 – 700 ms and 900 – 1200 ms. Taken together, the exploratory ERP analyses revealed ERP differences relating to explicit source memory. These effects were observed during both, the study and test phase, and appear to be slightly later occurring than hypothesised. However, there are notable differences between the effects at study and test. First, at study ERPs to subsequent hits+ judgements were associated with less positive mean amplitudes than hits-, while the opposite was observed at test. Second, qualitative differences appear in scalp topographies of these later source memory effects, with a centro-parietal topography at study and a more left-parietal at test.

Overall, during the study phase, there appears to be an earlier occurring parietal component that is related to indirect memory measures (RTs) and novelty. An early frontal effect, potentially reflecting the FN400, was only related to RTs but not to novelty or item-specific repetition. Subsequent source memory effects are reported in a slightly later time window and not significant at the peak. The finding of an early component associated with an indirect memory measure and a later component associated with an explicit memory test is partly consistent with a previous ERP investigation of implicit and explicit memory processes (Paller, Hutson, Miller, & Boehm, 2003; Voss & Paller, 2008a). The finding that the parietal component was sensitive to item-specific novelty is reminiscent of an old/new effect, which in turn may indicate that some retrieval processes are taking place during the incidental encoding phase. However, the latencies differ between previously reported old/new effects and the here observed novelty effect at study, as the old/new effect typically occurs slightly later around 500 – 800 ms (Johnson, 1995). It is therefore likely that repetition shifts the peak forward, as previously reported (Renoult et al., 2012). Subsequent memory effects may then be confounded by this, thus appearing somewhat different-looking than those reported from paradigms only involving a single presentation. This repetition effect being largely independent of encoding modality (especially in the alternated modality), is somewhat indicative of the finding that the repetition effect was also not bound to item-level repetition, but instead appeared to be more of a global effect of time course of the experiment. Previous research has reported modality-independent repetition effects (see Khader, Heil et al. 2005), however, to the author's knowledge, none of those studies have investigated repetition at the item-specific level.

Chapter 4 – Encoding modality, repetition and memory (fMRI)

4.1 Introduction

A number of investigations of haemodynamic responses have reported material-dependant memory effects (e.g., Duarte et al., 2011; Kim, 2011; Persson & Söderlund, 2015). For example, one investigation probed material-dependent source memory effects by presenting participants with words, pictures of objects and pictures of scenes during study and test phase (Duarte et al., 2011). A number of regions displayed modality-independent source memory effects at study, including left inferior frontal cortex, posterior hippocampus, medial and lateral parietal cortices and left temporal gyrus. At test, modality-independent differences in mean activation for hits+ and hits- judgements was reported in left angular gyrus, posterior cingulate, retrosplenial cortex, temporal and frontal gyri, right superior occipital gyrus, bilateral anterior and posterior hippocampi, bilateral middle cingulate and right frontal gyrus. Modality-specific subsequent source memory effects were reported in left posterior inferior frontal gyrus, where subsequent source memory effects (hits+ > hits-) were greater for words than pictures of objects or scenes. An inverse effect of subsequent source memory (hits- > hits+) was found in left perirhinal cortex for pictures of objects but not words or pictures of scenes. Moreover, even though the hippocampus is generally expected to be modality-independent and functionally more involved in binding item and context information (H. Eichenbaum et al., 2007), Dm effects in the hippocampus were also reported to be greater for pictures of objects than for words (Kim, 2011). Additionally, stronger Dm effects were found for pictorial than verbal material in right fusiform cortex and for verbal compared to pictorial material in left inferior frontal cortex. Another meta-analysis has reported modality-specific differences in the hippocampus along its long-axis (anterior-posterior) as well as hemispheric differences (Persson & Söderlund, 2015). Encoding of verbal material, was related to higher activation in the left anterior hippocampus, while encoding of pictorial material was associated with elevated activation in right posterior hippocampus. Finally, the authors also tested effects of mixed modalities in the context of associative encoding. They found that multi-modal associative encoding recruited the right hippocampus more than uni-modal encoding of either pictures only or words only, while both, uni-modal word encoding and mixed modality encoding was found to recruit the left anterior hippocampus as well. These results are suggestive of modality-dependent and –independent roles of the hippocampus (Persson & Söderlund, 2015) and, while the hippocampus takes on a domain-general role in encoding and retrieval of memories, the content of the material may be represented differentially within the hippocampi.

Memory operations at test, appear less modality-dependent than at study. Meta-analysis results indicated that modality-specific effects in the hippocampus were less clearly differentiated than during study (Persson & Söderlund, 2015). Activation was generally found to be highest in posterior hippocampus and higher for pictures than words but the modality-dependent hippocampal hemispheric long-axis dissociation reported at study was not shown at test (Persson & Söderlund, 2015). Similarly, Duarte and colleagues (2011) reported no modality-dependent source memory effects at test. Overall, these results suggest that subsequent source memory effects are modality-specific in some brain regions but that retrieval operations are largely modality-independent. The absence of modality-dependent source effects at test was suggested to be explained by the nature of the source memory question, i.e., perceptual features of stimuli were non-criterial and may therefore not have been recollected.

Similar to modality-specific subsequent source memory effects occurring in regions associated with the processing of modality-specific features (Duarte et al., 2011), repetition suppression effects have been reported in regions specific to the processing of verbal/semantic material (e.g., Rossell, Price, & Nobre, 2003) or pictorial/visual material (e.g., Horner & Henson, 2008; Koutstaal et al., 2001). These reports are in contrast to the EEG results reported in Chapter 3, which found that repetition-related changes in mean amplitudes did not differ between the encoding modalities. Considering the diversity in proposed neural generators of the ERPs of interest (see section 1.5), especially the LPC, what is measured with scalp EEG may not reflect activation of specific brain regions as they have been reported in fMRI research. A meta-analysis including 137 neuroimaging studies reporting repetition suppression and enhancement effects, reported repetition suppression to words in left inferior frontal and fusiform areas (Kim, 2017). Pictures of objects were associated with repetition suppression in bilateral inferior frontal cortex and occipito-temporal regions. Additionally, across verbal and pictorial materials, repetition-related increases were reported in frontal and parietal regions, which are typically associated with explicit memory retrieval (Blondin & Lepage, 2005; Kuperberg, 2004; Rossell et al., 2003). Previous research has shown conceptual and perceptual priming effects to be dissociable (Wig et al., 2005). One may expect conceptual priming effects to occur in regions related to semantic processing and conceptual feature integration. Generally, research on conceptual priming of visually presented stimuli that required semantic processing during encoding has reported reductions in RTs and neural activation in occipito-temporal areas, e.g., fusiform and occipital gyri, and frontal cortices, e.g., lateral inferior PFC (Buckner et al., 1998; Grill-Spector et al., 1999; Henson, 2003; Koutstaal et al., 2001; Schacter & Buckner, 1998; Vuilleumier, Henson, Driver, & Dolan, 2002; Wig et al., 2005; Zago, Fenske, Aminoff, & Bar, 2005). The occipito-temporal areas were shown to code perceptual stimulus representations, while frontal regions are implicated in retrieving semantic knowledge related to the encoding task (Bunzeck, Schütze, & Düzel, 2006; Daselaar, Veltman, Rombouts, Raaijmakers, Jeroen, & Jonker, 2005; Maccotta & Buckner, 2004; reviewed in Schacter et al., 2007). However, in an experiment where stimuli were repeated in the same modality, i.e., repeatedly presented as spoken words, written words or pictures, or across those modalities, repetition suppression in the cross-modality condition was only reported in the perirhinal cortex (Heusser et al., 2013).

As introduced here, a large body of research has already addressed questions regarding modality-specific item and source memory effects. Similarly, perceptual and conceptual priming effects have been widely covered. However, how repetition suppression and enhancement effects of stimuli presented in different encoding modalities interact with subsequent source memory remains largely unknown.

Representation Similarity Analysis

Previous research has typically contrasted similarity patterns relating to subsequent item hits and misses (Ward et al., 2013; Xue et al., 2010) or ERS effects to item hits and misses (Ritchey et al., 2013; Wing et al., 2015). These studies showed that cortical pattern similarity was higher for items that were remembered than those that were forgotten; generally supporting that reactivation is critical in forming and retrieving memories. Based on the CLS framework, it may be suggested that higher levels of reactivation reflect neocortical processes of creating more general representations of the items. However, when contrasting different levels of remembering, i.e., familiarity and recollection or source memory outcome, it may be critical for items to be encoded more uniquely and, therefore, items may be represented less similarly in order to later on retrieve additional details specific to the learning episode. Two recent investigations have contrasted source rather than item memory hits and misses and reported different roles for pattern reactivation in source memory formation (Kim et al., 2017; van den Honert et al., 2016). One study reported higher pattern similarity in lateral occipital cortex between encoding presentations to be associated with source memory misses rather than hits (Kim et al., 2017). Results from the other investigation found lateral occipital cortex similarity patterns to be higher for subsequent source hits than misses (van den Honert et al., 2016). The discrepancy in results may partly be explained by differences in experimental designs. In the first example, object stimuli were used and the source memory task prompted participants to retrieve details about the task they had performed during the first item presentation (Kim et al., 2017). The other study (van den Honert et al., 2016) included two experiments. Object stimuli were used in the first experiment, but effects were found to be much larger in the second experiment employing scenes. At test, a discrimination task assessed whether participants remembered that two stimuli were presented as identical stimuli or as different exemplars during the study phase (van den Honert et al., 2016). It may be that different task-related processes associated with a stimulus were represented less similarly, enabling subsequent retrieval of those task operations, while exemplar repetition led to some degree of reactivation, mediated by the hippocampus, as suggested by the authors (van den Honert et al., 2016). Additionally, neither of the two investigations included an item memory test, therefore, source misses may have been intermixed with item misses, making the interpretation of results more difficult. Further investigations into similarity patterns underlying subsequent source memory performance will be needed to understand how different regions represent items for which additional details can later be recollected.

In addition to differences in pattern similarity associated with source memory outcomes, the present research is concerned with the effects of encoding stimuli in different modalities. Xue and colleagues (2010) reported pattern similarity results from three different experiments. Across all experiments, they generally found cortical pattern similarity to be higher across encoding presentations for subsequent hits compared to misses. However, between experiments, the ROI results differed slightly, with face but not word stimuli showing effects in lateral occipital regions and word but not face stimuli resulting in subsequent memory effects in the left hippocampus and bilateral fusiform and middle temporal gyri. This is somewhat unsurprising, as some regions of interest will be more or less implicated in the processing of certain stimulus types in the first place. However, it also suggests that pattern similarity discriminating between subsequent hits and misses might be modality-specific in certain brain areas. It has previously been shown that activation patterns in lateral occipital cortex carry information about the visual content associated with a stimulus (e.g., Cichy, Chen, & Haynes, 2011; Eger, Ashburner, Haynes, Dolan, & Rees, 2008). Using a classifier-based MVPA approach, it was reported that structures within the temporal lobe contained information about the visual category stimuli fell into (faces or scenes) and moreover, higher classified-based estimates were associated with superior subsequent memory performance (Kuhl, Rissman, & Wagner, 2012). Additionally, previous research provided evidence that multi-voxel patterns in the lateral parietal cortex, and in particular the angular gyrus, differentially represented stimulus categories, i.e., faces and scenes, and were predictive of objective vividness of events (Kuhl & Chun, 2014). At least one previous fMRI study employing RSA is central to probing the relationship between modality-specific encoding and memory. The authors investigated representational similarity patterns for the semantic category effects in word and picture stimuli with the aim of identifying modality-specific and modality-independent semantic systems (Devereux, Clarke, Marouchos, & Tyler, 2013). Participants viewed words and pictures and performed a category-naming task. Model-based RSA revealed modality-independent effects of semantic category in left intraparietal sulcus, left angular gyrus and left posterior middle temporal gyrus. Modality-specific semantic processing effects were found in ventral temporal cortex for pictures and anterior middle temporal gyrus for words. A second model-free cluster-based approach extended those findings by showing that although semantic category effects occurred in the left middle temporal gyrus in both modalities, they differed across modalities (Devereux et al., 2013). Overall, these results strongly suggest that the physical features of a stimulus impact similarity patterns differently in different regions, however, it is unclear in what ways pattern similarity will be affected by modality-changes across repetitions. Therefore, systematic comparisons of Dm effects in pattern similarity across different modalities, i.e., modality-independent subsequent memory effects and modality-specific effects, will enhance the general understanding of how similarity patterns can predict subsequent memory performance.

Finally, the present research is concerned with pattern reinstatement effects between the study and test phases. Using the representational similarity index as a proxy for pattern reactivation, reinstatement effects can be assessed using RSA. Research has demonstrated that patterns observed during encoding are later reactivated during successful retrieval, for example in ventral occipito-temporal cortex (Gordon et al., 2014; Kuhl & Chun, 2014; Kuhl, Rissman, Chun, & Wagner, 2011), lateral parietal cortex (Kuhl & Chun, 2014) and for word-scene associations in parahippocampal cortex (Staresina et al., 2012). However, mere pattern reinstatement at retrieval does not tell us much about those patterns themselves, i.e., whether they represent perceptual, conceptual, item-specific or domain-general information. For example, word-scene associations led to parahippocampal reactivations but word-colour associations did not (Staresina et al., 2012). Kuhl and Chun (2014) reported that reinstatement patterns in the angular gyrus discriminated between individual items that were remembered. These findings indicate that the observed patterns may represent domain-specific information, item-specific information or more general retrieval operations depending on the region they are observed in. To avoid perceptual similarities between encoding and retrieval, Xiao and colleagues (2017) employed a paradigm in which participants encoded word-scene associations, where each scene was paired with two different words and cued with only one of those words during a subsequent recognition test. They reported that items that were initially represented in ventral visual areas at encoding were reinstated in the frontoparietal cortex during the retrieval phase. These results were somewhat surprising in the light of theories proposing similar operations to take place at study and test (Kolers, 1973; Morris et al., 1977; Tulving, 1983; Tulving & Thomson, 1973). Experimental factors may have played a role in obtaining these findings, as participants were over-trained on the stimuli and tasks in a prescan phase, therefore, the encoding-retrieval similarity in this study may be more appropriately interpreted as retrieval-retrieval similarity. The authors also implemented a slow event-related design, thus it cannot be precluded that item representations were not initially reactivated in the same areas at encoding. Overall, this study did raise concerns that pattern reinstatement may be confounded by the perceptual overlap of stimuli presented during the encoding and the recognition phase.

The present fMRI experiment employed the same experimental design as the EEG investigation in Chapter 3, with only minor differences in total number of trials (see 4.2.2). A subsequent memory paradigm was used with four spaced repetitions of each stimulus, followed by a surprise source-recognition task. Participants repeatedly studied stimuli presented in one of three encoding modality conditions: repeatedly presented as pictures (referred to in-text as *picture*), repeatedly presented as words (referred to in-text as *word*) or alternately presented as pictures and words (referred to in-text as *picture&word*). At test, all stimuli were cued with words and participants made item memory judgements (old/new) and source memory judgements (previously learned as picture, word or picture&word). The present experiment was primarily designed to address differences in similarity patterns relating to source memory effects and encoding modality. Therefore, the univariate analyses will only be concerned with how conceptual and perceptual repetition effects may predict subsequent source memory and further investigate repetition suppression and enhancement. Additionally, results from control analyses will be presented, i.e., picture-word and hits+-hits- contrasts to assess the reliability of the data. Based on previous research (Grady et al., 1998; Vandenberghe et al., 1996), it is hypothesised that picture stimuli be associated with higher activation in occipito-temporal regions when compared to word stimuli. Furthermore, at test, Duarte and colleagues (2011) demonstrated higher hippocampal activation for hits+ than hits- judgements, which was found to be modality-independent. Further regions where source memory effects may be expected are the medial prefrontal and retrosplenial cortices as well as superior and middle temporal gyri (Duarte et al., 2011; Thakral et al., 2015) as well as the wider recollection network (Cabeza et al., 2012; Johnson & Rugg, 2007; King et al., 2015; Rugg & King, 2017; Rugg & Vilberg, 2013). RSA is predicted to reveal modality-independent source memory effects in regions that are part of the recollection network. In addition to modality-independent source memory effects, further modality-specific source memory effects are hypothesised to occur in regions implicated in processing of modality-specific features and in posterior parietal regions reflecting feature-integration processes in the alternated picture&word modality. Finally, picture reinstatement effects are predicted to be observed in occipito-temporal regions in the absence of pictorial information at test, when items are cued with words.

4.2 Method

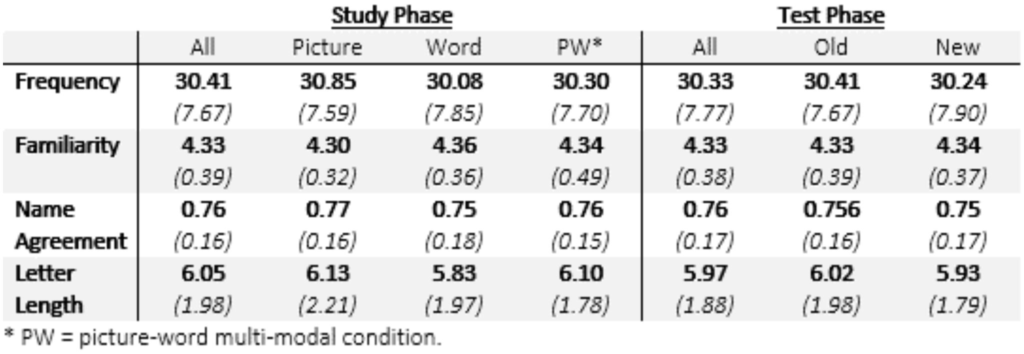
4.2.1 Participants

Twenty-five healthy adult volunteers (14 females), aged 18 to 35 years old (M_{age} = 22±3), with an average of 16±2 years of education were recruited. Data of seven participants were excluded from behavioural and fMRI analyses due to technical faults during scanning, resulting in N = 18 (9 females).

4.2.2 Materials

Stimuli presented throughout the study phase were pictures and written words of common objects and animals (e.g., doors, boat, monkey). A total of 240 stimuli were selected from the 288 stimuli used in the EEG version of this experiment (see 3.2.2). Stimuli were selected from the Bank of Standardized Stimuli (BOSS) Phase II (Brodeur et al., 2014) and were matched across all tasks and conditions in terms of frequency, familiarity, name agreement and letter length (see Table 4.4). Words were presented in white Courier New 36 font. Picture dimensions were 400x400 pixels. All stimuli were presented in the centre of a black background.

Table 4.4. *Experiment 2 (fMRI): Means (in bold) and standard deviations (italicised, in parentheses) of frequency, familiarity, name agreement and letter length of stimuli presented in study and test phase.*



	Study Phase				Test Phase		
	All	Picture	Word	PW*	All	Old	New
Frequency	**30.41** *(7.67)*	**30.85** *(7.59)*	**30.08** *(7.85)*	**30.30** *(7.70)*	**30.33** *(7.77)*	**30.41** *(7.67)*	**30.24** *(7.90)*
Familiarity	**4.33** *(0.39)*	**4.30** *(0.32)*	**4.36** *(0.36)*	**4.34** *(0.49)*	**4.33** *(0.38)*	**4.33** *(0.39)*	**4.34** *(0.37)*
Name Agreement	**0.76** *(0.16)*	**0.77** *(0.16)*	**0.75** *(0.18)*	**0.76** *(0.15)*	**0.76** *(0.17)*	**0.756** *(0.16)*	**0.75** *(0.17)*
Letter Length	**6.05** *(1.98)*	**6.13** *(2.21)*	**5.83** *(1.97)*	**6.10** *(1.78)*	**5.97** *(1.88)*	**6.02** *(1.98)*	**5.93** *(1.79)*

* PW = picture-word multi-modal condition.

4.2.3 Task & procedure

During the study phase, half of the selected stimuli were presented one-by-one. Participants were instructed to press one of two buttons on the four-button response device, corresponding to whether they thought the presented object was typically found indoors or outdoors. Each stimulus was presented four times, once during each of the four encoding runs, resulting in a total of 480 encoding trials. Stimuli were presented in one of three modality conditions (40 stimuli in each condition): repeatedly as a picture (picture uni-modal), repeatedly as a word (word uni-modal) or alternately as a picture or a word (picture&word multi-modal). The average inter-trial interval (ITI) in both experiments was 4100 ms. The experimental procedure is illustrated in Figure 4.13. At the end of the encoding phase, participants had a short break during which they could rest their eyes.

In a surprise recognition-source memory test, all old stimuli from the indoor/outdoor categorisation task were presented along with new stimuli, made up of the remaining half of the stimuli set that had not been presented at study, from the same two semantic categories. Participants were instructed to make an old/new judgement (item memory) indicating whether they thought an object had been presented in the preceding study phase or not. Participants pressed one of four buttons on the response pad corresponding to the following responses: definitely old, perhaps old, perhaps new, and definitely new. Whenever responses indicated that an object had been shown during encoding, i.e., was old, a new screen appeared with a follow-up question assessing source memory by asking participants how the object had been presented. The response options were *picture*, *word*, *picture & word* and *I don't know*. Stimuli were presented for 1500 ms, followed by a fixation cross for 1000 ms. Depending on participants' old/new response, either a fixation cross or the source memory question appeared for 1500 ms. Another fixation cross of random duration (800 – 1200ms) then indicated the beginning of the next trial (average ITI = 5000 ms).

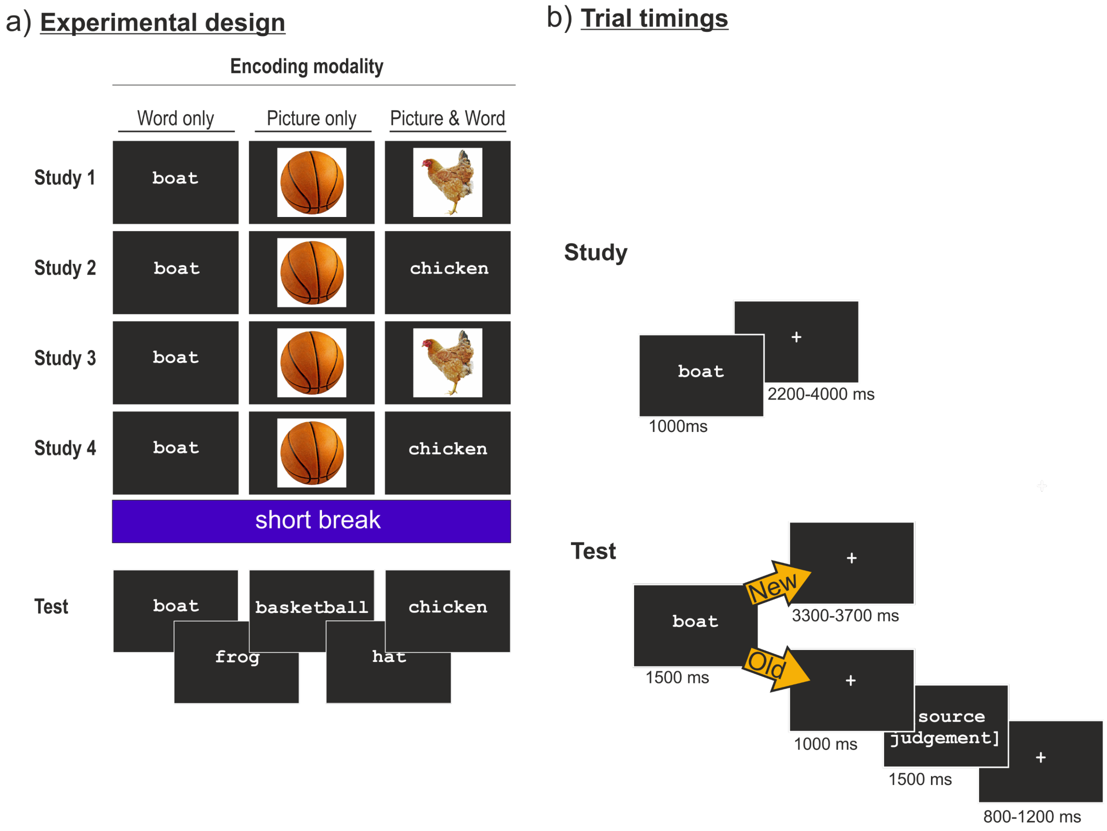


Figure 4.13. Experiment 2 (fMRI): a) the experimental paradigm with four encoding presentations during the study phase, followed by the test phase, with b) trial timings displayed.

4.3 Results

The repeated-measures design included three factors of interest at study and two at test: subsequent memory (hits+, hits-; behavioural analyses further include misses), repetition (presentation 1,2,3,4; only at study) and encoding modality (uni-modal picture, uni-modal word, multi-modal picture&word). As in the EEG version (Chapter 3), hits+ trials were characterised as high confidence item hits followed by correct source memory. Hits- trials included hits in the old/new task, irrespective of confidence judgement, followed by an incorrect source memory response or no response, indicating the source could not be retrieved. High memory performance, as indicated by discriminability scores presented in a subsequent section (4.3.1.2), meant that misses are only included in behavioural analyses and were excluded from neuroimaging analyses due to low trial counts. Because of a lack of low confidence responses, confidence was not included in further analyses. Participants' responses to the item memory question indicated that they were more often highly confident of their response ($M\%_{HC}$ = 91.81 ± 9) than responding with low confidence ($M\%_{LC}$ = 8.19 ± 9), $t_{17} = 20.307$, $p < .001$.

4.3.1 Behavioural results

4.3.1.1 Reaction times at study

RTs to the indoor/outdoor judgement task during the study phase were analysed in a 3 x 3 x 4 repeated-measures ANOVA with the factors subsequent memory (hits+, hits-, misses), encoding modality (picture, word, picture&word) and presentation (1,2,3,4). Mean RTs are illustrated in Figure 4.14. RTs were not significantly different across the three levels of memory performance, $F_{2,18} = 0.253$, $p = .780$. Although the mean RTs presented in Figure 4.14 indicate a trend for RTs to decrease across presentations, this was not statistically significant after Greenhouse-Geisser correction for violations of sphericity, $F_{1,12} = 3.858$, $p = .066$. However, a main effect of encoding modality was revealed, $F_{1,12} = 8.141$, $p = .011$. Participants responded significantly faster to stimuli presented as pictures only compared to stimuli presented as words only, $p = .018$, and to stimuli presented as pictures and words alternately, $p = .002$.

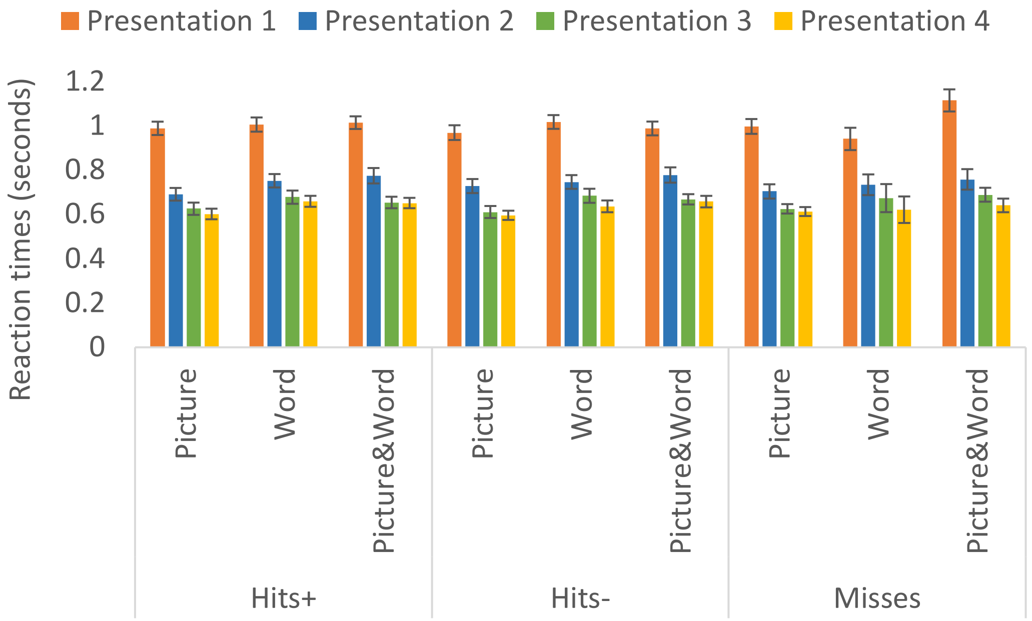


Figure 4.14. Reaction times (in seconds) in experiment 2 (fMRI) for all four presentations during the study phase, separately for subsequent memory performance and encoding modalities. Error bars denote standard error.

4.3.1.2 Discriminability analysis

Discriminability scores (*d'*) were calculated based on the frequencies of hits and false alarms. The normalised probabilities of overall hits and false alarms were compared in a paired-samples t-test. The t-test showed that participants' performance in the recognition memory task was statistically significantly above chance, $t_{17} = 13.442$, $p < .001$). Mean and standard deviations of *d'* scores and percentages of hits and false alarms are illustrated in Table 4.5. Those individual *d'* scores indicate that recognition memory performance was highest in the word uni-modal condition (verging on a ceiling effect) and lowest in the picture uni-modal condition.

Table 4.5. *Experiment 2 (fMRI): The mean d' scores and mean % of Hits and False Alarms with standard deviations (italicised, in parentheses) for overall memory performance and across the three modality conditions, picture only, word only and picture&word.*

	d' *(SD)*	M_{Hits} **%** *(SD)*	$M_{FalseAlarms}$ **%** *(SD)*
Overall	**2.82** *(0.89)*	**90.42** *(7.49)*	**11.39** *(10.79)*
Picture	**2.27** *(0.76)*	**79.17** *(11.73)*	**11.39** *(10.79)*
Word	**4.09** *(2.31)*	**93.47** *(6.60)*	**11.39** *(10.79)*
Picture&Word	**4.12** *(2.34)*	**94.03** *(6.81)*	**11.39** *(10.79)*

4.3.1.3 Behavioural performance at test

Frequencies of hits+, hits- and misses (memory performance) were analysed across modalities (picture uni-modal, word uni-modal, picture-word multi-modal) in a 3 x 3 repeated-measures analysis. Descriptive statistics of the data included in the analysis are displayed in Figure 4.15.

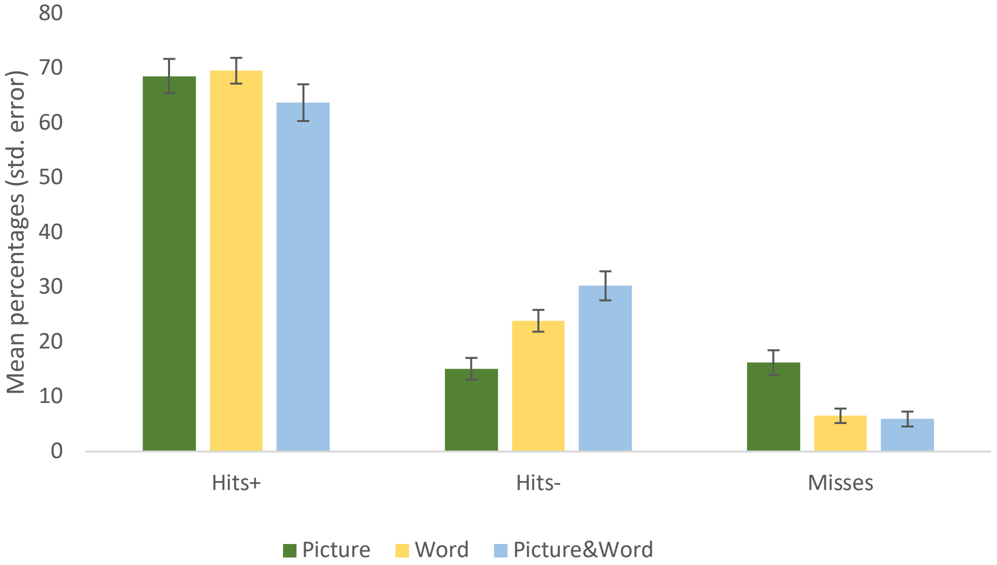


Figure 4.15. Behavioural performance in experiment 2 (fMRI). Mean percentages of the three levels of memory performance and encoding modality. Error bars denote standard errors.

The ANOVA revealed a main effect of memory, $F_{1,23} = 107.288$, $p < .001$ and an interaction between memory performance and encoding modality, $F_{2,41} = 10.775$, $p < .001$. Post-hoc tests revealed that all three levels of memory performance differed from each other in terms of frequencies, all p < .001. The majority of responses were hits+ judgements (correct item memory, correct source memory), followed by hits- judgements (correct item memory, incorrect source memory) and the least responses resulted in misses. This difference in memory was significant across all three levels of modality, $p < .001$, with the exception of the picture modality, where frequencies of hits- judgements and misses did not differ significantly, $p = .744$. As illustrated in Figure 4.15, the two uni-modal encoding conditions were associated with more hits+ judgements compared to the picture&word condition. This difference was only statistically significant for the word only encoding condition, $p = .032$. All three encoding modalities differed in terms of frequencies of hits- judgements, all $p < .016$, with the picture&word condition being associated with the most hits- judgements and the picture only condition with the fewest hits- judgements. Finally, the picture only encoding condition was associated with more misses than the other two conditions, $p < .001$.

4.3.1.4 Reaction times at test

RTs obtained during the test phase were analysed in two repeated-measures ANOVAs. First, RTs to the item memory (old/new) task were examined in a 3 x 3 ANOVA with the factors memory performance and encoding modality. In a second analysis, RTs to the source memory task were analysed. In this 2 x 3 repeated-measures ANOVA, the factors were memory performance (note, only two levels, as misses were not followed up with a source memory question) and encoding modality.

The ANOVA on item memory RTs revealed no statistically significant main effects or interactions, all $p > .150$.

The ANOVA on source memory RTs revealed a main effect of memory performance (hits+, hits-), $F_{1,17} = 14.755$, $p = .001$ and a significant interaction between memory performance and encoding modality, $F_{2,34} = 5.889$, $p = .006$. RTs to hits+ judgements were significantly faster than to hits- judgements. This difference, however, was not significant in items that were presented as pictures at encoding, $p = .674$.

4.3.2 fMRI mass-univariate results

One GLM was constructed with 24 regressors of interest modelling the effects of source memory (hits+, hits-), presentation (1,2,3,4) and encoding modality (picture, word, picture&word). A nuisance regressor modelled all trials that were not included in main analyses, e.g., subsequent misses and low confidence correct source judgements. A first set of whole-brain results is centred around repetition-related changes in BOLD signals and their relationships with subsequent source memory and encoding modality. Two additional whole-brain contrasts of previously well-established effects relating to differences between picture and word stimuli at study and between hits+ and hits- judgements at test are presented.

4.3.2.1 Study phase repetition effects

In order to investigate repetition effects, 12 whole-brain contrasts modelling modality-specific repetition suppression and enhancement were created at a second level analysis. Repetition effects were modelled as a linear change (Grill-Spector & Malach, 2001; Henson et al., 2000; Sayres & Grill-Spector, 2006; Suzuki et al., 2011; Vannini et al., 2013). Separate t-contrasts modelled linear changes, i.e., suppression and enhancement, across repetitions for the three encoding modalities, i.e., picture only priming, word only priming and picture-word priming. Additional t-contrasts assessed whether the repetition-related changes were stronger for subsequent hits+ than hits- judgements.

Results from whole-brain analyses are presented in Table 4.6. Both uni-modal encoding conditions showed repetition suppression effects that did not differ depending on subsequent source memory performance. For the picture only encoding condition a statistically significant cluster was found in the left medial temporal lobe, including the left hippocampus and fusiform gyrus. Repetition suppression effects in the word only encoding condition were found in left pre- and postcentral gyri. Finally, the picture-word encoding condition was associated with repetition enhancement in inferior parietal regions, including the precuneus, which was higher for subsequent hits+ than hits- judgements, however, the small cluster did not survive FWE-corrections.

Table 4.6. *Mass-univaraite results from experiment 2 (fMRI) illustrating the regions that show modality-specific repetition effects and interactions between repetition and subsequent source memory performance as measured during the study phase.*

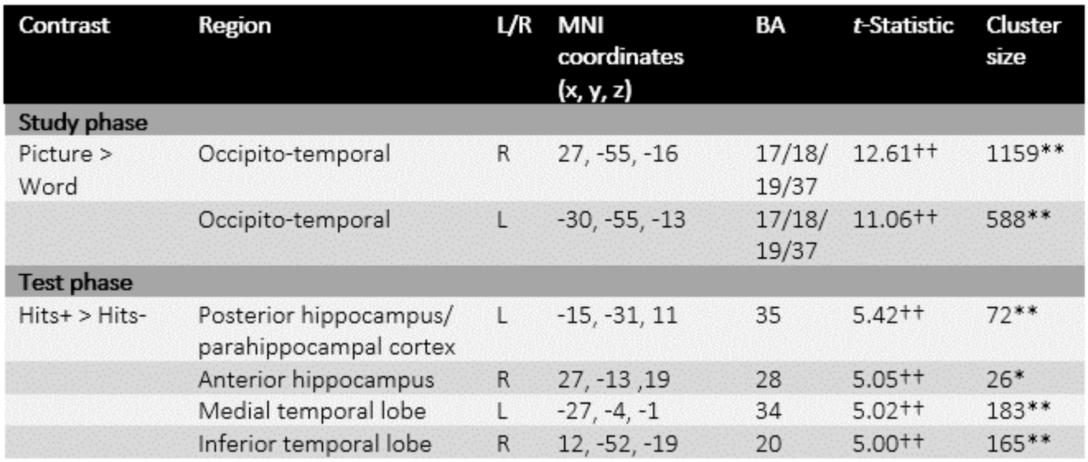
Contrast	Direction (S/E)	Region	L/R	MNI coordinates (x, y, z)	BA	*t*-Statistic	Cluster size
Picture only priming							
Repetition (main)	S	Medial temporal lobe, fusiform gyrus, hippocampus	L	-24, -40, -16	28	3.91†	83**
Interaction repetition x subsequent source memory	-	-	-	-	-	-	-
Word only priming							
Repetition (main)	S	Postcentral/inferior parietal gyrus	L	-39, -37, 53	2	4.15†	64**
	S	Precentral/inferior frontal gyrus	L	-48, 5, 35	6	3.86†	89**
Interaction repetition x subsequent source memory	-	-	-	-	-	-	-
Picture/Word priming							
Repetition (main)	-	-	-	-	-	-	-
Interaction repetition x subsequent source memory	E	Precuneus	R	9, -64, 41	7	3.86†	26*

Note. S = suppression, E = enhancement, L = left, R = right, BA = approximate Brodmann Area. MNI coordinates refer to peak voxel coordinates.
* $p_{cluster} < 0.05$ (uncorrected)
** $p_{cluster} < 0.05$ (*FWE*-corrected)
† $p_{peak} < 0.001$ (uncorrected)
†† $p_{peak} < 0.05$ (*FWE*-corrected)

4.3.2.2 Control analyses

Two control analyses were carried out to demonstrate the reliability of the data. The results for those whole-brain contrasts are presented in Table 4.7. First, during the study phase, the picture only and word only encoding conditions were contrasted to test the hypothesis that picture stimuli, relative to word stimuli, would activate the occipito-temporal cortex. Two large clusters were found in the predicted regions, one large cluster in right occipito-temporal regions and a second one in the left occipito-temporal areas. The second control analysis contrasted hits+ and hits- judgements at test and, as predicted, activation for hits+ judgements was higher than for hits- judgements within the recollection network, with four clusters being identified in left and right hemispheres.

Table 4.7. *Mass-univariate control analyses (experiment 2, fMRI), constrasting mean activation to picture and word stimuli during the study phase and mean activation to hits+ and hits- judgements during the test phase.*



Contrast	Region	L/R	MNI coordinates (x, y, z)	BA	*t*-Statistic	Cluster size
Study phase						
Picture > Word	Occipito-temporal	R	27, -55, -16	17/18/ 19/37	12.61††	1159**
	Occipito-temporal	L	-30, -55, -13	17/18/ 19/37	11.06††	588**
Test phase						
Hits+ > Hits-	Posterior hippocampus/ parahippocampal cortex	L	-15, -31, 11	35	5.42††	72**
	Anterior hippocampus	R	27, -13 ,19	28	5.05††	26*
	Medial temporal lobe	L	-27, -4, -1	34	5.02††	183**
	Inferior temporal lobe	R	12, -52, -19	20	5.00††	165**

Note. S = suppression, E = enhancement, L = left, R = right, BA = approximate Brodmann Area. MNI coordinates refer to peak voxel coordinates.
* $p_{cluster} < 0.05$ (uncorrected)
** $p_{cluster} < 0.05$ (*FWE*-corrected)
† $p_{peak} < 0.001$ (uncorrected)
†† $p_{peak} < 0.05$ (*FWE*-corrected)

4.3.3 Representational similarity analysis

Pattern similarity was calculated for encoding similarity across repeated study episodes and for encoding-retrieval similarity (ERS). For encoding similarity, pattern similarity was computed between consecutive repetitions, i.e., Presentations 1 & 2, Presentations 2 & 3 and Presentations 3 & 4, and the resulting similarity indices were averaged. For ERS, pattern similarity was calculated between each encoding presentation and the retrieval presentation, resulting in four similarity indices that were averaged (see Figure 4.16).

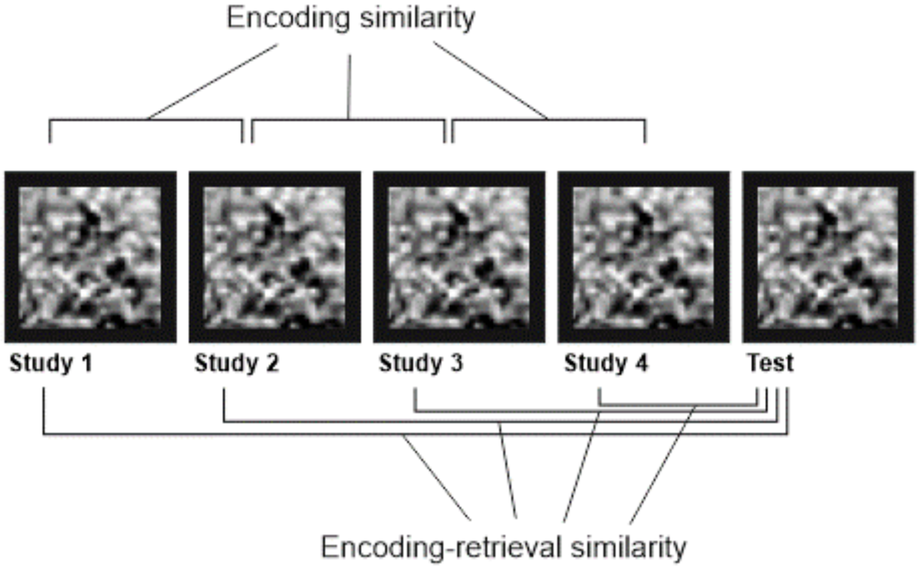
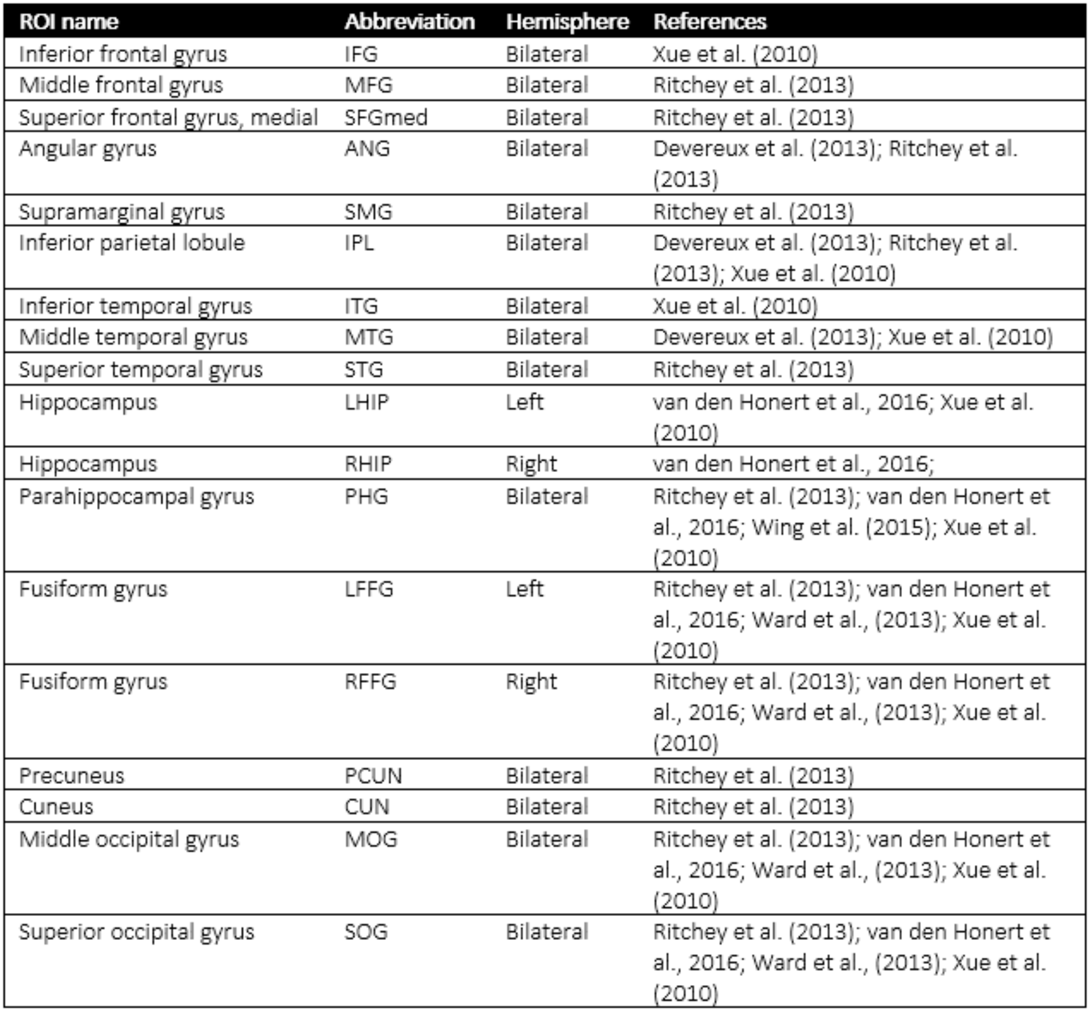


Figure 4.16. Encoding similiarty and encoding-retrieval similarity (ERS) in experiment 2 were computed by correlating beta values from the specified presentation pairs.

A total of 18 ROIs were chosen from the automated anatomical labelling (AAL) atlas (Tzourio-Mazoyer et al., 2002). With exceptions for the hippocampus and the fusiform gyrus, ROIs were bilateral to limit the number of multiple comparisons. Reasons for including separate left and right ROIs for the fusiform gyrus were that the visual word form area is located in the left fusiform gyrus only (L. Cohen et al., 2000; McCandliss, Cohen, & Dehaene, 2003), therefore, differences in picture and word encoding may not be bilateral. For the hippocampus previous research reported memory effects in left but not right hippocampus (Xue et al., 2010). The 18 ROIs are presented in Table 4.8 along with references justifying their inclusion. ROI analyses were followed up with whole-brain searchlight analyses. One participant had to be excluded from RSAs, because of insufficient trial numbers in one condition, meaning that identity mismatch could not be calculated, resulting in $N = 17$.

Table 4.8. *Regions of interest included in the representational similarity analyses performed on data from experiment 2 (fMRI), along with subsequently used abbreviations, hemisphere information and references for inclusion.*



ROI name	Abbreviation	Hemisphere	References
Inferior frontal gyrus	IFG	Bilateral	Xue et al. (2010)
Middle frontal gyrus	MFG	Bilateral	Ritchey et al. (2013)
Superior frontal gyrus, medial	SFGmed	Bilateral	Ritchey et al. (2013)
Angular gyrus	ANG	Bilateral	Devereux et al. (2013); Ritchey et al. (2013)
Supramarginal gyrus	SMG	Bilateral	Ritchey et al. (2013)
Inferior parietal lobule	IPL	Bilateral	Devereux et al. (2013); Ritchey et al. (2013); Xue et al. (2010)
Inferior temporal gyrus	ITG	Bilateral	Xue et al. (2010)
Middle temporal gyrus	MTG	Bilateral	Devereux et al. (2013); Xue et al. (2010)
Superior temporal gyrus	STG	Bilateral	Ritchey et al. (2013)
Hippocampus	LHIP	Left	van den Honert et al., 2016; Xue et al. (2010)
Hippocampus	RHIP	Right	van den Honert et al., 2016;
Parahippocampal gyrus	PHG	Bilateral	Ritchey et al. (2013); van den Honert et al., 2016; Wing et al. (2015); Xue et al. (2010)
Fusiform gyrus	LFFG	Left	Ritchey et al. (2013); van den Honert et al., 2016; Ward et al., (2013); Xue et al. (2010)
Fusiform gyrus	RFFG	Right	Ritchey et al. (2013); van den Honert et al., 2016; Ward et al., (2013); Xue et al. (2010)
Precuneus	PCUN	Bilateral	Ritchey et al. (2013)
Cuneus	CUN	Bilateral	Ritchey et al. (2013)
Middle occipital gyrus	MOG	Bilateral	Ritchey et al. (2013); van den Honert et al., 2016; Ward et al., (2013); Xue et al. (2010)
Superior occipital gyrus	SOG	Bilateral	Ritchey et al. (2013); van den Honert et al., 2016; Ward et al., (2013); Xue et al. (2010)

Separate encoding similarity and ERS indices were computed for each of the six conditions (see Figure 4.17). Encoding similarity and ERS patterns were analysed for modality-independent subsequent source memory effects, modality-specific subsequent source memory effects and effects of encoding modality, only including trials for which the source could later be retrieved, i.e., hits+. For each contrast, a measure of item-level similarity and a measure of item-specific similarity are reported (see 2.5.2.2 for details). Each contrast was analysed using paired-samples t-tests. T-statistics and significance levels (uncorrected and *FDR*-corrected for the 18 ROIs) are reported.

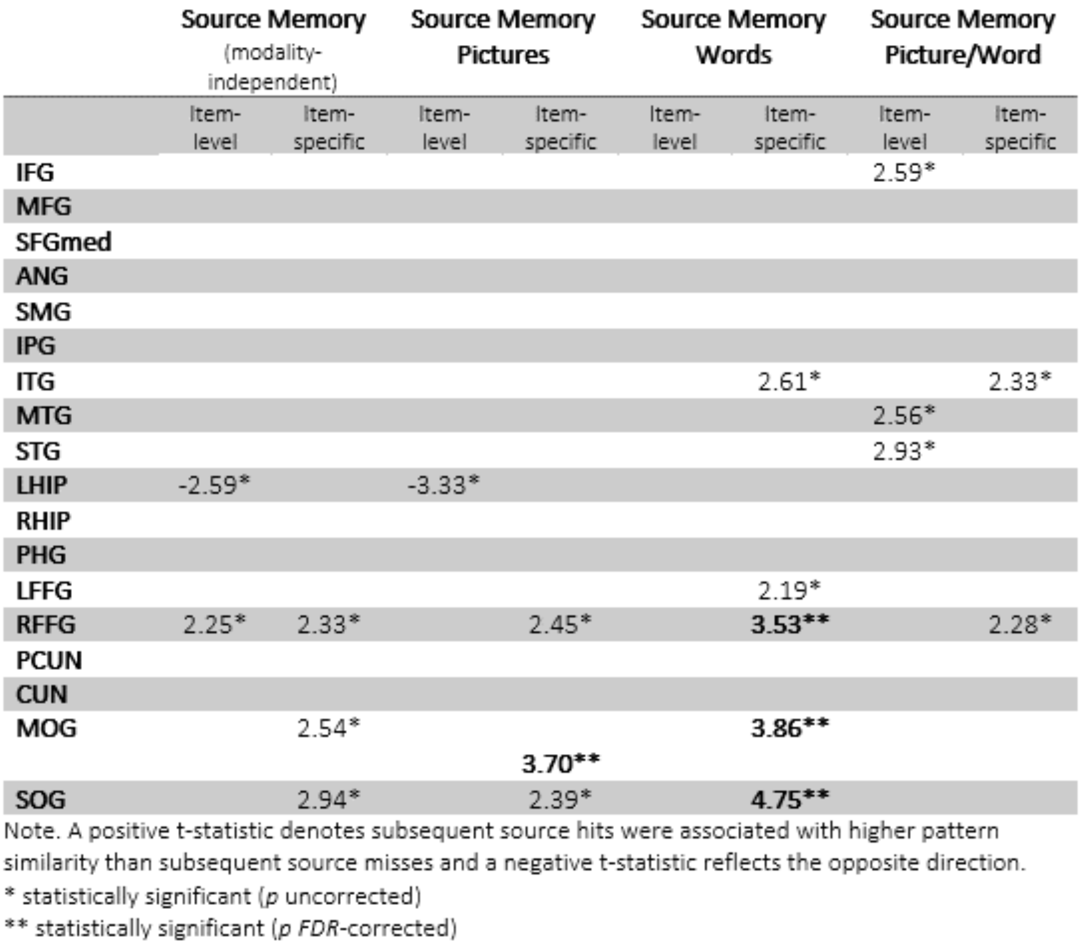
Figure 4.17. Identity matrix displaying the six conditions included in analyses of data from experiment 2 (fMRI), for which similarity scores were calculated. Item-level and item-specific similarity are reported in the present investigation.

4.3.3.1 Encoding similarity

Effects of subsequent source memory

Results for modality-independent and modality-specific differences in similarity patterns relating to subsequent source memory are reported in Table 4.9. Modality-independent subsequent source memory effects were found in the left hippocampus, right fusiform gyrus and middle and superior occipital gyri, though none of those effects survived FDR-correction. At the item-level, the hippocampus represented items, for which the source was later remembered, less similarly than those for which the item was remembered but the source could not be identified. The right fusiform gyrus, on the other hand, showed higher similarity for subsequent hits+ than hits- trials. This was found to be the case for item-level similarity as well as for item-specific similarity, reflecting that subsequent hits+ items were represented more similarly to themselves than to other items of the same category compared to subsequent hits- trials. Similar item-specific similarity effects were also found in middle and superior occipital gyri.

Table 4.9. *Summary of t-statistics (experiment 2, fMRI) for multiple pairwise t-tests contrasting encoding similarity to subsequent hits+ and hits- judgements.*



	Source Memory (modality-independent)		**Source Memory Pictures**		**Source Memory Words**		**Source Memory Picture/Word**	
	Item-level	Item-specific	Item-level	Item-specific	Item-level	Item-specific	Item-level	Item-specific
IFG							2.59*	
MFG								
SFGmed								
ANG								
SMG								
IPG								
ITG						2.61*		2.33*
MTG							2.56*	
STG							2.93*	
LHIP	-2.59*		-3.33*					
RHIP								
PHG								
LFFG						2.19*		
RFFG	2.25*	2.33*		2.45*		**3.53****		2.28*
PCUN								
CUN								
MOG		2.54*		**3.70****		**3.86****		
SOG		2.94*		2.39*		**4.75****		

Note. A positive t-statistic denotes subsequent source hits were associated with higher pattern similarity than subsequent source misses and a negative t-statistic reflects the opposite direction.
* statistically significant (*p* uncorrected)
** statistically significant (*p FDR*-corrected)

A number of modality-specific subsequent source memory effects were reported, with some surviving FDR-correction. Item-specific similarity was higher for subsequent picture only hits+ than hits- trials in the middle occipital gyrus and a similar trend was observed in superior occipital and right fusiform gyri. These three regions were also found to represent word hits+ trials more similarly to themselves than to other word stimuli compared to subsequent hits- trials, along with the same trends in left fusiform and inferior temporal gyri. Notably, these effects in the occipital regions were only found in the uni-modal encoding conditions and not when perceptual features changed across repetitions. Additional weaker modality-specific effects emerged as well. The modality-independent effect in the left hippocampus was also found in the picture only encoding condition, possible driving the modality-independent effect. Finally, in the alternated picture&word condition, hits+ trials were found to be represented more similarly than hits- trials in the inferior frontal and temporal gyri at the item-level. Item-specific similarity was also higher for subsequent hits+ than hits- trials in inferior temporal and right fusiform gyri.

Exploratory searchlight analyses did not reveal any additional effects for the contrasts displayed in Table 4.9.

Effects of encoding modality

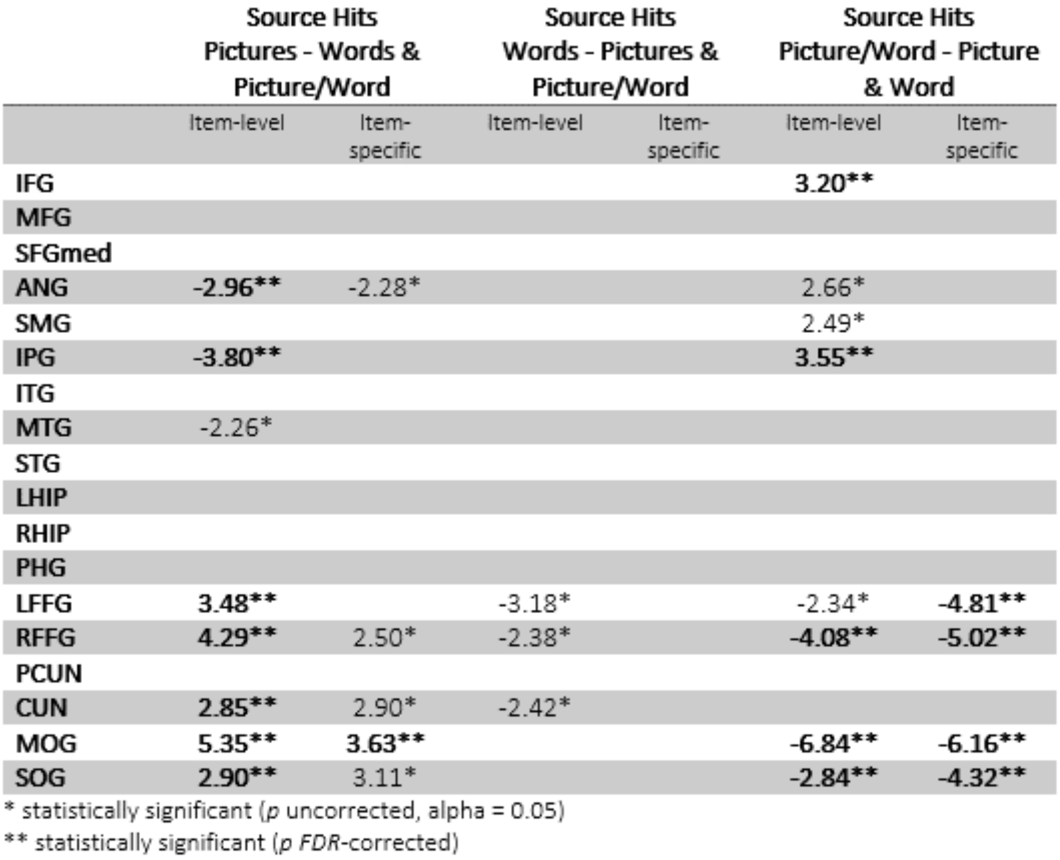
In addition to modality-independent and –specific subsequent source memory effects, this research was concerned with the effects of encoding modality on similarity patterns. For this analysis, only subsequent hits+ trials were included to investigate effects of encoding modality in subsequent recollection judgements. Three contrasts contrasted each encoding modality with the other two: picture only compared to an average of word only and picture&word, word only compared to an average of picture only and picture&word and, finally, picture&word compared to an average of picture only and word only (uni-modal compared to multi-modal encoding). The results are presented in Table 4.10.

Strong effects of higher similarity between presentations of items encoded as pictures only compared to the other two conditions were found in left and right fusiform, middle and superior occipital gyri as well as the cuneus at the item-level. Item-specific picture reinstatement was also observed in the middle occipital gyrus and trends showed in right fusiform and bilateral superior occipital gyri and the cuneus. Additionally, picture only items were represented less similarly than items encoded in the other two encoding conditions in angular and inferior parietal gyri at the item-level. The same effect was also observed in the middle temporal gyrus but did not survive multiple comparison corrections. Item-specific similarity in the angular gyrus was also lower for picture only trials than for trials in the other two conditions.

Items in the word only condition were represented less similarly than items encoded in the other two conditions in left and right fusiform gyri and the cuneus. However, these effects did not survive multiple comparisons and are likely reflecting the finding that pictures were represented more similarly in those regions.

Contrasting stimuli presented in the multi-modal picture&word condition and those presented in the uni-modal conditions revealed strong item-level and item-specific negative effects in left and right fusiform and bilateral middle and superior occipital gyri. These regions represented multi-modally encoded stimuli less similarly than uni-modally encoded stimuli. The inferior frontal and inferior parietal gyri, on the other hand, were observed to show higher item-level pattern similarity for the multi-modally encoded than the uni-modally encoded items, with the same trends also observed in angular and supramarginal gyri.

Table 4.10. *Summary of t-statistics (experiment 2, fMRI) for multiple pairwise t-tests contrasting encoding modalities only including subsequent hits+ judgements.*



	Source Hits Pictures - Words & Picture/Word		Source Hits Words - Pictures & Picture/Word		Source Hits Picture/Word - Picture & Word	
	Item-level	Item-specific	Item-level	Item-specific	Item-level	Item-specific
IFG					3.20**	
MFG						
SFGmed						
ANG	-2.96**	-2.28*			2.66*	
SMG					2.49*	
IPG	-3.80**				3.55**	
ITG						
MTG	-2.26*					
STG						
LHIP						
RHIP						
PHG						
LFFG	3.48**		-3.18*		-2.34*	-4.81**
RFFG	4.29**	2.50*	-2.38*		-4.08**	-5.02**
PCUN						
CUN	2.85**	2.90*	-2.42*			
MOG	5.35**	3.63**			-6.84**	-6.16**
SOG	2.90**	3.11*			-2.84**	-4.32**

* statistically significant (*p* uncorrected, alpha = 0.05)
** statistically significant (*p FDR*-corrected)

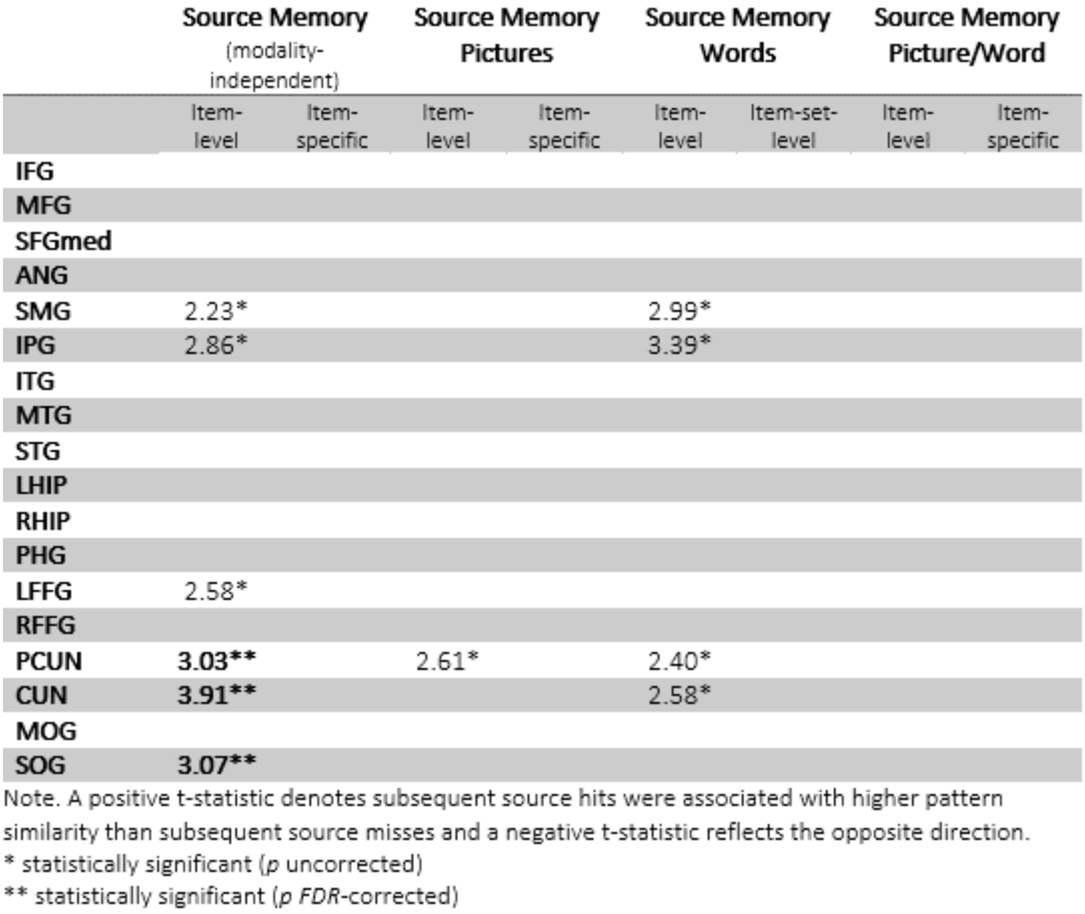
Exploratory searchlight analyses did not reveal any additional effects for the contrasts displayed in Table 4.10.

4.3.3.2 Encoding-retrieval similarity

Effects of source memory

Results for modality-independent and modality-specific differences in ERS patterns discriminating source memory are reported in Table 4.11. Modality-independent source memory effects with higher item-level similarity for hits+ than hits- judgements were observed in precuneus, cuneus and superior occipital gyrus. The same trend was found in supramarginal, inferior parietal and left fusiform gyri, though these effects did not survive correction for multiple comparisons.

Table 4.11. *Summary of t-statistics (experiment 2, fMRI) for multiple pairwise t-tests contrasting encoding-retrieval similarity to subsequent hits+ and hits- judgements.*



	Source Memory (modality-independent)		**Source Memory Pictures**		**Source Memory Words**		**Source Memory Picture/Word**	
	Item-level	Item-specific	Item-level	Item-specific	Item-level	Item-set-level	Item-level	Item-specific
IFG								
MFG								
SFGmed								
ANG								
SMG	2.23*				2.99*			
IPG	2.86*				3.39*			
ITG								
MTG								
STG								
LHIP								
RHIP								
PHG								
LFFG	2.58*							
RFFG								
PCUN	**3.03****		2.61*		2.40*			
CUN	**3.91****				2.58*			
MOG								
SOG	**3.07****							

Note. A positive t-statistic denotes subsequent source hits were associated with higher pattern similarity than subsequent source misses and a negative t-statistic reflects the opposite direction.
* statistically significant (*p* uncorrected)
** statistically significant (*p FDR*-corrected)

Modality-specific ERS source memory effects were less pronounced than for encoding similarity and none survived multiple comparisons correction. A trend in the precuneus suggested that pictures only hits+ judgements were represented more similarly (at the item-level) than hits- judgements. Source memory effects in the word only encoding condition were found in supramarginal and inferior parietal gyri and precuneus and cuneus, regions that already showed higher similarity between encoding and retrieval for modality-independent hits+ than hits- judgements. The mean ERS scores are displayed in Figure 4.18, showing that the modality-independent ERS differences for hits+ and hits- judgements are not entirely driven by the word encoding condition, but rather, differences in hits+ and hits- ERS are observed across all three encoding modalities, though not statistically significant.

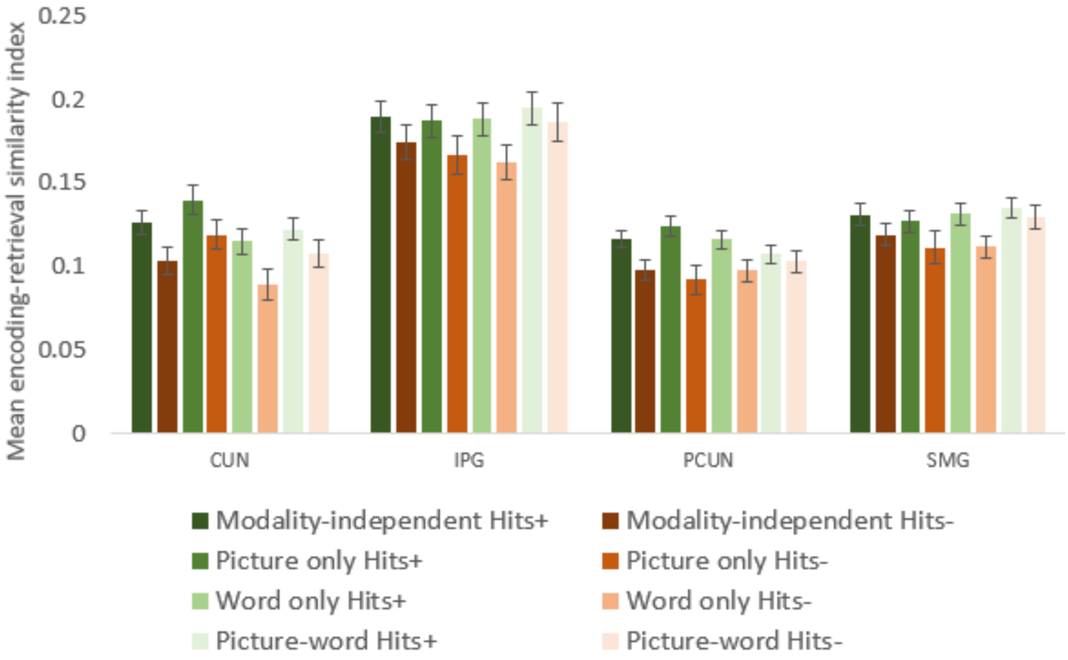
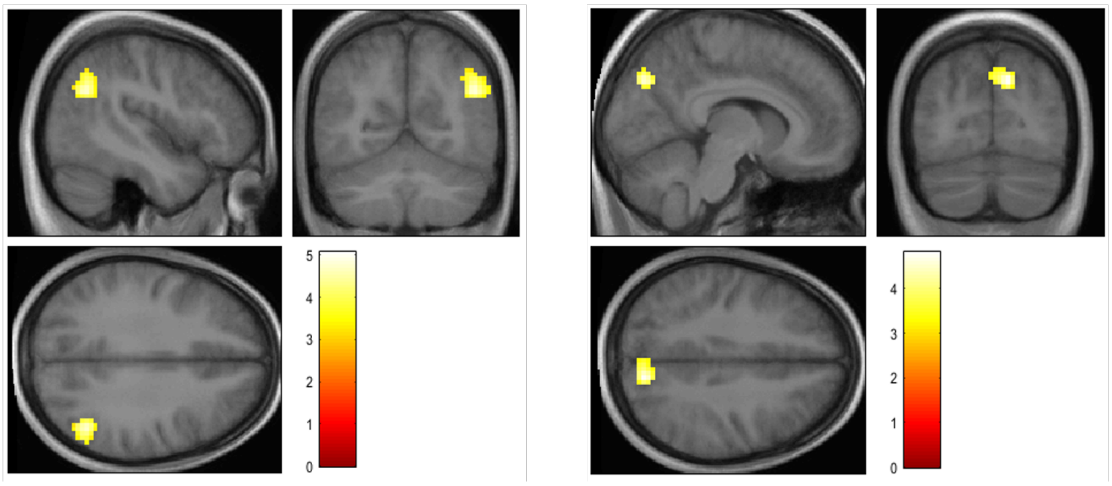


Figure 4.18. Experiment 2 (fMRI): Mean encoding-retrieval similarity scores for modality-independent and modality-dependent hits+ and hits- judgements.

Exploratory searchlight analyses revealed similar effects as the ROI analyses and two clusters were found to be significant even after *FWE*-correction that were not significant after multiple comparison corrections in the ROI analyses (displayed in Figure 4.19). For the item-level, modality-independent contrast between hits+ and hits- judgements, a cluster (k = 123) emerged in the right inferior parietal lobule with its peak voxel in the angular gyrus (MNI coordinates x = 48, y = -61, z = 29), p = .003 (*FWE*-corrected). A second significant cluster (k = 64) was found for the item-level, picture only encoding contrast between hits+ and hits- judgements within the cuneus and precuneus (peak voxel MNI coordinates x = 12, y = -76, z = 35), *p* = .048 (*FWE*-corrected). Both these effects had been reported as trends in the ROI analyses but were shown to survive multiple comparison correction only in the searchlight analyses.


a) Modality-independent ERS source memory effect

Hits+ > Hits-

b) Picture only modality-specific ERS source memory effect

Hits+ > Hits-

Figure 4.19. Encoding-retrieval similarity searchlight source memory effects in experiment 2 (fMRI) for a hits+ > hits- contrast in a) modality-independent and b) picture only modality-specific searchlight analysis contrasts. Peak voxel threshold was at $p < .001$ uncorrected, cluster threshold at $p < .05$ FWE-corrected.

Effects of encoding modality

For the effects of encoding modality, only a t-contrast between picture only and word only encoding was of interest. The alternated picture&word encoding condition was omitted from these analyses, because ERS indices were computed by averaging across the four encoding-retrieval pairs (study 1 – test, study 2 – test, study 3 – test, study 4 – test), so that any ERS results relevant to this condition would only occur when looking at the encoding-retrieval pairs separately.

The ROI analyses testing ERS effects for differences between items encoded as pictures only and items encoded as words only did not reveal any effects that survived *FDR*-correction. However, trends were observed at the item-level in the cuneus, $t = 2.75$, $p < .05$ (uncorrected), and superior occipital gyrus, $t = 2.32$, $p < .05$

(uncorrected), with picture only items being more similar than word only items, indicating reinstatement of pictorial information in the absence of the actual picture stimulus at test.

Additional searchlight analyses revealed two clusters that were significant after *FWE*-correction (displayed in Figure 4.20). Both clusters were found for the item-level similarity contrast between picture only and word only encoding modalities with higher similarity for items repeatedly encoded as pictures than those repeatedly encoded as words. A larger cluster ($k = 321$) was found to be significant in the right occipital areas including parts of middle and superior occipital gyri and the cuneus (BA 19), $p < .001$ (*FWE*-corrected; peak voxel at MNI coordinates x = 33, y = -37, z = -31). A slightly smaller cluster ($k = 127$) was found in the right inferior temporal lobe regions, $p = .003$ (*FWE*-corrected; peak voxel at MNI coordinates x = 18, y = -91, z = 23).

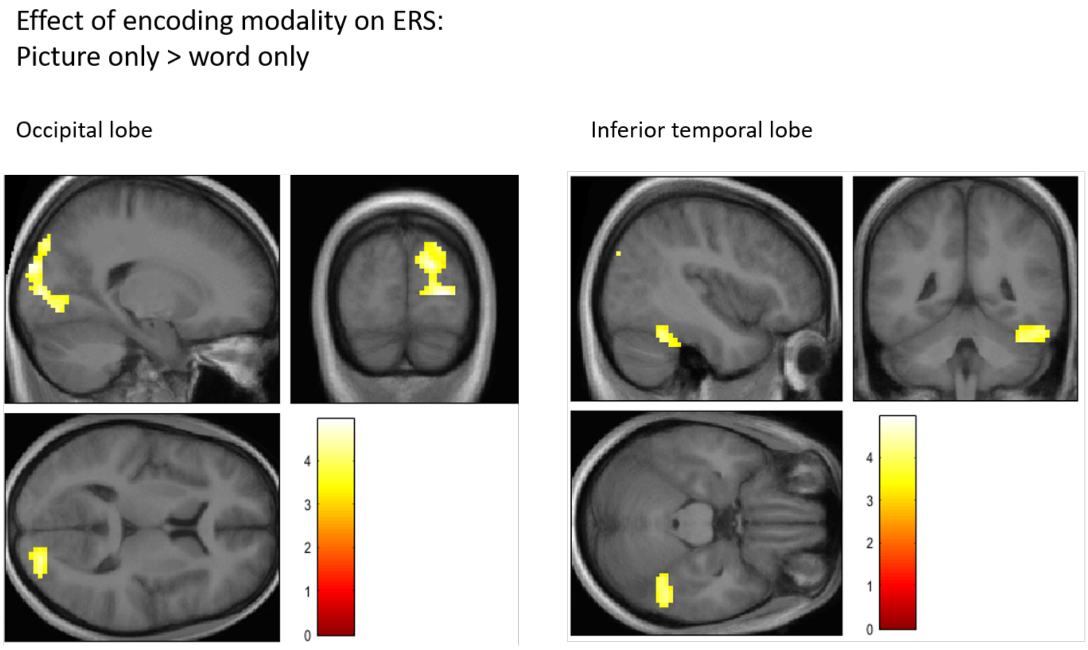


*Figure 4.20.*Encoding-retrieval similarity searchlight results from experiment 2 (fMRI), showing picture only encoding to be more similar than word only encoding in occipital and inferior temporal regions. Peak voxel threshold was at $p < .001$ uncorrect, cluster threshold at $p < .05$ FWE-corrected.

4.4 Discussion

Behavioural results were largely consistent with the behavioural results from the EEG experiment (discussed in 3.4.1). Item and source memory performance was generally high. The picture superiority effect was absent, as the picture only encoding condition was associated with more misses than the other two conditions. Finally, as reported in the EEG version of this experiment, RTs during the study phase were faster to picture only stimuli than to stimuli from the other two encoding modalities.

4.4.1 fMRI mass-univariate analysis results

Functional MRI data were analysed with respect to repetition-related changes in the three encoding modalities and whether those repetition effects predicted subsequent source memory performance. Repetition suppression effects were found in both uni-modal encoding conditions but they did not interact with subsequent source memory. For the alternated picture-word encoding condition, mean BOLD signal was found to increase with repetitions and this increase was higher in subsequent hits+ than hits- judgements. Additionally, control analyses supported the hypotheses with higher activation to picture than word stimuli in the predicted regions and higher activation to hits+ than hits- judgements at test in areas within the medial temporal lobe.

In line with previous research (see Grill-Spector et al., 2006; Schacter et al., 2007), repetition suppression effects were found in brain regions that are typically implicated in the processing of perceptual and semantic information. Word only repetition effects occurred in left pre- and post-central gyri, extending into inferior parietal and frontal gyri, respectively. Moreover, picture only repetition effects were observed in the medial temporal lobe, including the hippocampus and fusiform gyrus. Both modality-specific repetition suppression effects overlap with regions showing word- and picture-based repetition suppression identified by a recent meta-analysis (H. Kim, 2017). These repetition suppression effects are likely reflecting enhanced semantic and perceptual processing efficiency (Buckner et al., 1998; Grill-Spector et al., 2006; Henson & Rugg, 2003; Schacter et al., 2007; Wig et al., 2005). A repetition enhancement trend was only observed in the multi-modal picture-word encoding condition in posterior parietal regions with peak voxels in the precuneus.

This effect was stronger for subsequent hits+ than hits- trials. Previous research has more often reported a link between repetition enhancement and subsequent memory performance (Heusser et al., 2013; Kremers et al., 2014; van den Honert et al., 2016; Vannini et al., 2013) than a link between repetition suppression and subsequent memory performance (but see Xue et al., 2011). It appears that repetition enhancement effects are most likely observed during conceptual repetition, though they havealso been reported in word repetition studies, probing semantic priming (reviewed in Segaert et al., 2013). For example, Heusser and colleagues (2003) reported repetition enhancement only in a cross-modal encoding condition and only this repetition enhancement effect was related to subsequent memory performance. Here, repetition enhancement effects were reported in inferior parietal regions, which are generally considered to a) be part of a wider episodic recollection network (Cabeza et al., 2012; J. D. Johnson & Rugg, 2007; King et al., 2015; Rugg & King, 2017; Rugg & Vilberg, 2013) and b) involved in amodal, conceptual stimulus processing and multi-modal feature integration (Bonnici, Richter, Yazar, & Simons, 2016; Chou, Chen, Wu, & Booth, 2009; Fairhall & Caramazza, 2013; Seghier, 2013). Therefore, the subsequent source memory-dependent increase in mean activation in the multi-modal picture-word condition may reflect retrieval operations during the incidental encoding phase (H. Kim, 2017; Segaert et al., 2013), which facilitate later source memory recognition for the alternated picture&word condition. This interpretation is consistent with previous suggestions of the posterior parietal cortex being activated during the study phase and implicated in long-term memory formation (Elman, Rosner, Cohn-Sheehy, Cerreta, & Shimamura, 2013). Perhaps such retrieval operations were not necessary in order to subsequently recollect source information in the uni-modal encoding conditions. However, as repetition enhancement effects did not survive corrections for multiple comparisons, any interpretations of these effects are somewhat tentative until the effects have been replicated in hypothesis-driven future research. There is no obvious overlap between the here reported repetition effects and those observed during the scalp EEG recordings (presented in Chapter 3). However, as neither the fMRI repetition suppression effects nor the repetition-related changes in EEG amplitudes interacted with subsequent source memory performance, it may be suggested that changes in LPC and FN400 amplitudes are more likely reflecting repetition suppression than enhancement. Therefore, fMRI repetition suppression and EEG repetition-related amplitude changes may be related to implicit rather than explicit measures of memory, as demonstrated in the EEG chapter (see Chapter 3) and existing fMRI literature (e.g., van den Honert et al., 2016; Ward et al., 2013). Additionally, the repetition suppression effects in the picture only encoding modality were mainly observed in MTL regions, which have previously been proposed to generate the LPC (Guillem et al., 1999; Halgren et al., 1994). However, a fundamental difference remains between the effects yielded with those two neuroimaging techniques: fMRI repetition suppression effects were shown to be modality-dependent, whereas the EEG effects did not interact with encoding modality. On that basis, it remains unclear whether repetition effects measured with EEG and fMRI reflect similar neural mechanisms.

4.4.2 Representational similarity analysis

Encoding similarity and ERS patterns were investigated to identify modality-independent and modality-specific source memory effects as well as effects of encoding modality in hits+ trials. Due to low frequencies of misses, item memory contrasts were not considered. ROIs were chosen based on previous literature. Results from exploratory searchlight analyses were reported when those provided additional insights. Across multiple encoding presentations, item-specific pattern reinstatement in occipital regions was associated with superior source memory outcome, but only in the uni-modal encoding conditions (picture only, word only). Moreover, item-level and item-specific similarity patterns were higher for pictures compared to the other two encoding conditions in occipito-temporal regions but less similar in inferior parietal regions, including the angular gyrus. The inferior parietal gyrus was found to represent items encoded in the multi-modal picture&word condition more similarly across encoding when compared to the uni-modal encoding conditions. The reverse effects with lower pattern similarity for multi-modally compared to uni-modally encoded items were observed in occipito-temporal regions. Item-level ERS patterns were found to discriminate between hits+ and hits- judgements, with higher hits+ similarity in parietal and occipital regions. Reinstatement of pictorial information from the study phase in the absence of pictorial stimuli at test were shown at the item-level in occipital and right inferior temporal lobes, however, this did not extend to item-specific pattern reinstatement. Additional trends, i.e., contrasts that were only significant before corrections for multiple comparisons, will be discussed.

Encoding similarity – subsequent memory

Strong subsequent source memory effects were found in middle and superior occipital gyri when items were encoded uni-modally. Subsequent source hits were associated with higher encoding similarity than items, which were recognised, but the source could not be retrieved. Higher pattern similarity likely reflects perceptual reinstatement of the same patterns across repeated encoding presentations and this reinstatement was stronger for subsequent hits+ than hits- judgements. This result is in line with a previous investigation into pattern similarity and source memory (van den Honert et al., 2016) and resembles previous findings for item memory similarity patterns (e.g., Ward et al., 2013; Xue et al., 2010). However, to the author's knowledge, no previous research has demonstrated this subsequent source memory effect at the item-specific level, i.e., that for subsequent hits+ judgements items are more similarly represented to themselves than other items from the same category when compared to hits- judgements. In the present paradigm, participants had to later remember whether they encountered a concept repeatedly as a picture, repeatedly as a word or as both, pictures and words. In order to successfully retrieve the source, it is likely that the items had to be represented more similarly to themselves than to other items. Additionally, the early visual regions were expected to be sensitive to perceptual feature overlap (e.g., Ress & Heeger, 2003) and have previously been shown to represent items more similarly to themselves than to other items of the same category (Ritchey et al., 2013). Therefore, it is no surprise that this effect was significant only in the uni-modal encoding conditions. Moreover, these results provide evidence for the reactivation view (Benjamin & Tullis, 2010; Thios & D'Agostino, 1976) in that item-specific reactivation across repeated encoding support subsequent memory and more specifically subsequent source memory. Interestingly, a trend was observed in the right fusiform gyrus that, in addition to item-specific hits+ similarity being higher than item-specific hits- similarity in the uni-modal encoding conditions, this trend was also observed in the multi-modal picture&word condition. Research has indicated that the ventral temporal cortex, including the fusiform gyrus, may be representing semantic information (Chao, Haxby, & Martin, 1999; Mechelli, Sartori, Orlandi, & Price, 2006). Moreover, a study on patients with semantic dementia has shown that the right anterior fusiform gyrus was implicated in associative semantic knowledge (Mion et al., 2010). Thus, this region may be important for organising item-specific semantic information, whilst also incorporating source information for later successful source retrieval. However, because this effect did not survive multiple comparison corrections, it will have to be replicated in order to make stronger inferences about the role of the right fusiform gyrus in source memory encoding.

Similar to the trend in the right fusiform gyrus, item-specific similarity in the inferior temporal gyrus and item-level similarity in inferior frontal and middle and superior temporal gyri and were higher for subsequent hits+ judgements than hits- judgements in the multi-modal picture&word condition, although these effects were not significant after correction for multiple comparisons. Inferior and middle temporal gyri have been proposed to represent concepts irrespective of the modality they are presented in (Fairhall & Caramazza, 2013), which in line with the ventral cortex representing semantic knowledge (Chao et al., 1999; Mechelli et al., 2006). It is therefore not surprising that these regions would be sensitive to conceptual repetition. In order for participants to later remember that they saw the concept in both modalities, some form of conceptual reinstatement may have been necessary, explaining why these similarity patterns were higher for subsequent hits+ than hits- judgements. Furthermore, the inferior frontal gyrus has been shown to be part of the semantic system (Binder, Desai, Graves, & Conant, 2009) and to be activated more when task difficulty increased (Binder, Medler, Desai, Conant, & Liebenthal, 2005; Desai, Conant, Waldron, & Binder, 2006; R. L. C. Mitchell, 2005). Though the explicit task was held constant in this experiment, the multi-modal picture&word encoding condition may have required additional conceptual integration in order to subsequently remember that the item was studied as both, a picture and a word. Finally, another interesting trend emerged in the left hippocampus. Item-level similarity was lower for subsequent hits+ than hits- judgements. This trend was observed in the modality-independent and the picture only encoding conditions, with the latter one possibly driving the modality-independent result. The finding of less similarity for hits+ than hits- judgements is in contrast to previous research on similarity effects between subsequent item hits and misses (Xue et al., 2010). However, it may be that source memory information is represented differently to item memory. Although the hippocampus is proposed to bind information together (e.g., Josselyn et al., 2015; Moscovitch, 1992), thereby potentially creating more similar representations, this structure is also suggested to represent and extract unique encoding features (Nadel & Moscovitch, 1997; Norman, 2010; O'Reilly et al., 2014) and prevent interferences with past events (O'Reilly & McClelland, 1994). Previous research has indeed shown more hippocampal dissimilarity between items that were subsequently remembered (LaRocque et al., 2013). Moreover, recent research has shown that representations in the hippocampus only became more similar after a consolidation period of a week (Tompary & Davachi, 2017), highlighting that initial hippocampal representations are more dynamic and can be updated with each additional learning episode (Mack, Love, & Preston, 2016). Finally, the present result may also reflect hippocampal pattern separation signals that have previously been reported during encoding (Bakker et al., 2009; Chanales, Oza, Favila, & Kuhl, 2017; Leutgeb, Leutgeb, Moser, & Moser, 2007) and linked to memory performance (Favila, Chanales, & Kuhl, 2016; Karlsson Wirebring et al., 2015).

Encoding similarity – encoding modality

Encoding similarity patterns clearly dissociated occipito-temporal and inferior parietal regions. Bilateral fusiform and occipital gyri as well as the precuneus showed strong sensitivity to stimuli repeatedly encoded as pictures but showed the reverse effect for stimuli encoded as pictures and words alternately. On the other hand, inferior parietal regions were found to be sensitive to feature integration across repetitions, i.e., the multi-modal encoding condition, but similarity patterns were found to be lower for the picture only encoding condition compared to the other two conditions. Occipito-temporal regions have been shown to be involved in the processing of perceptual features of pictorial stimuli (Grady et al., 1998; Vandenberghe et al., 1996), it is therefore not surprising that reactivation of pictures was higher compared to the other two conditions. Interestingly, these similarity patterns are shown to be disrupted when the perceptual but not conceptual features of the stimulus change between repetitions, as indicated by lower similarity in the picture&word encoding conditions when compared to the two uni-modal conditions. While pattern similarity in occipital regions, across exemplar repetitions of scenes, has been shown to be relatively unaffected by small perceptual feature changes (van den Honert et al., 2016), this appears to not be the case for conceptual repetitions of items presented as pictures and words alternately. The picture&word multi-modal encoding effect observed in the inferior parietal gyrus, with the same trends shown in adjacent angular and supramarginal gyri, provides further evidence for a role of those parietal regions in the amodal integration of semantic features (Chou et al., 2009; Devereux et al., 2013) or multi-modal feature integration (Bonnici et al., 2016; Yazar, Bergström, & Simons, 2017). The posterior parietal cortex has been suggested to act as a convergence zone by activation and binding episodic features, which are stored in different neocortical areas (Shimamura, 2011). A review on recent findings involving the ventral lateral parietal cortex, and in particular the angular gyrus, summarised that MVPA-based investigations have repeatedly demonstrated that this brain region represents categories of information differently and that the observed patterns can even distinguish between individual events (Rugg & King, 2017). Moreover, the angular gyrus' sensitivity to multi-modal memories was previously shown during episodic retrieval (Bonnici et al., 2016), indicating that some form of retrieval was taking place during the study phase of the present repeated incidental encoding paradigm. Additionally, the angular gyrus was shown to represent object categories conceptually rather than modality-specifically (Fairhall & Caramazza, 2013). Taken together, the inferior parietal regions, including the angular and supramarginal gyri appear to integrate and represent semantic information about stimuli irrespective of perceptual features associated with different encoding modalities. The present findings indicate that pattern similarity in these regions increases when feature integration demands increase, consistent with previous research.

ERS – source memory

Item-level similarity between the study and test phases (ERS) was generally found to be higher for hits+ than hits- judgements. Moreover, with the exception of a few trends, this effect was largely modality-independent. This source memory effect was observed in the precuneus, cuneus and superior occipital gyrus with additional trends, not surviving multiple comparison corrections, in left fusiform gyrus and bilateral supramarginal and inferior parietal gyri. However, additional searchlight analyses showed that the inferior parietal regions did show higher item-level similarity for hits+ than hits- judgements even after *FWE*-corrections. These results are generally in line with previous research on ERS patterns relating to item memory contrasts, i.e., comparing item memory hits and misses (Ritchey et al., 2013; Wing et al., 2015). Furthermore, the ERS results provide support for theoretical frameworks that suggest similar operations to take place during successful encoding and retrieval of information, such as the *encoding specificity principle* (Tulving, 1983; Tulving & Thomson, 1973) and the *transfer-appropriate processing* account (Morris et al., 1977). However, the observed effects in inferior parietal regions may be specific to objective recollection, as decoding accuracy sometimes failed to discriminate between different subjective ratings of vividness or remembering (Kuhl & Chun, 2014; Thakral, Wang, & Rugg, 2017). Moreover, source memory effects in ERS patterns were found to be largely modality-independent, which is surprising given that content-sensitive recollection has been demonstrated in univariate investigations during the test phase (J. D. Johnson & Rugg, 2007; Khader, Burke, et al., 2005; reviewed in Rugg et al., 2008). On the other hand, results from univariate fMRI analyses have also shown that differences in mean activation due to memory performance was largely modality-independent (Duarte et al., 2011; Persson & Söderlund, 2015). In contrast to those univariate investigations, however, the modality in which items were presented in the present study was not held constant across encoding and retrieval. It is possible that the ERS source memory effects presented here reflect conceptual recollection of items and their associated source, i.e., encoding modality, because conceptual recollection was encouraged by the present paradigm. This interpretation is consistent with the role of inferior parietal regions in conceptual, amodal item representation.

An interesting trend in the precuneus indicated that item-level similarity was higher for hits+ than hits- judgements in the picture only encoding condition. As a reminder, in this condition, participants repeatedly studied pictures of items, which were cued with the corresponding word during the test phase, when participants made item and source judgements. The precuneus has previously been linked to memory-related imagery (Cavanna & Trimble, 2006; Fletcher et al., 1995) and imagination. For example, when participants encoded words paired with either viewed or imagined pictures, activation of the precuneus during test was related to the retrieval of words previously paired with imagined pictures (Lundstrom et al., 2003; Lundstrom, Ingvar, & Petersson, 2005), suggesting that participants re-imagined or reinstated the picture from the study phase. However, a bar graph displaying the mean ERS indices for the cuneus, precuneus, supramarginal and inferior parietal gyri illustrated that ERS was higher for hits+ than hits- judgements across all modalities, indicating that the observed ERS effects were largely modality-independent.

ERS – encoding modality at test

Finally, effects of encoding modality on ERS patterns were tested. The multi-modal picture&word encoding condition was excluded from these contrasts, as the four encoding-retrieval pairs were averaged to obtain a single ERS index and thus, information relevant to that particular encoding condition would have been averaged over. Higher item-level ERS for items encoded as pictures compared to those encoded as words was revealed by searchlight analyses (in addition to weaker effects in the ROI analyses) in right occipital areas as well as right inferior temporal lobe regions. These results indicate that pictorial information from the study phase is reactivated during the test phase even in the absence of the original pictorial stimulus, which is only cued with its verbal counterpart at test. Rich pictorial information has previously been shown to be represented in occipito-temporal regions during remembering (e.g., Kensinger & Schacter, 2007; MacEvoy & Epstein, 2009, 2011; Wing et al., 2015). However, existing research on reinstatement has typically presented stimuli in the same modality during study and test phase (Kensinger & Schacter, 2007). Alternatively, participants were shown the same label at test that accompanied a scene during the study phase and explicitly asked to reactivate the scene rather than make item and source memory judgements (Wing et al., 2015). The unique experimental design of the present investigation required participants to retrieve information regarding perceptual stimulus features, i.e., pictorial information, when only prompted with the word for the concept. Thereby, excluding any perceptual overlap between study and test phase in the picture only encoding condition. Finally, in the present experiment, no statistically significant reinstatement effects were observed at the item-specific level. Item-specific reactivation has previously been reported in early visuo-sensory regions (Bosch et al., 2014), however, item-specificity was simply calculated on a trial-by-trial basis, much like the item-level similarity in the present study, rather than comparing specific items to reactivation patterns of other but similar items. Moreover, the stimuli used in that experiment did not require any semantic processing and the to-be-retrieved information was related to the orientation of a visual stimulus, i.e., the visual stimulus was presented at both encoding and retrieval. Item-specific reinstatement of pictorial information from the study phase may have taken place but the searchlight analysis lacked power and/or the ROIs were poorly defined to detect the effect. It is, however, also likely that the present results of item-level but not item-specific reinstatement indicate that more general picture information was reinstated. Indeed, a follow-up analysis of an identical contrast (similarity higher for items encoded as pictures only than those encoded as words only, only including hits+ judgements) but for set-level similarity revealed two clusters that largely overlapped with the item-level similarity results, adding further evidence that this reinstatement effect was not item-specific but reflecting instead reinstatement of general picture information.

Taken together, the univariate fMRI analyses revealed an interesting trend in posterior parietal regions: a linear increase in mean BOLD signal within the posterior parietal regions, indexing repetition enhancement, was observed in the multi-modal picture-word encoding condition and this linear increase was stronger in subsequent hits+ than hits- judgements. This effect was suggested to reflect necessary retrieval operations to take place during encoding in order to bind information together and subsequently be able to retrieve the associated source during the test phase. The effects of implicit and explicit retrieval during incidental encoding paradigms are highly debated (see Voss & Paller, 2008a) and further research will be needed to identify the degree of explicit retrieval operations taking place in these paradigms and their impact on subsequent item and source memory. These findings from univariate analyses inform past and future research concerning the neural correlates of repeated encoding and have given rise to novel research questions. The focus of this thesis, however, is to shed light on neural similarity patterns and reactivation processes during memory formation and between memory formation and retrieval as assessed by RSA. Similarity analyses showed that item-specific pattern reinstatement across encoding episodes predicted subsequent source memory for uni-modal encoding in the occipital gyri. Pattern similarity between encoding and retrieval was found to be less item-specific but instead item-level similarity patterns were higher across superior occipital and posterior parietal regions for hits+ than hits- judgements. When considering the effects of encoding modality in the context of correct source judgements, strong effects were found between all three encoding conditions. Across encoding presentations, occipito-temporal item-level and item-specific pattern similarity was higher for pictures compared to the other two encoding conditions, word only and picture&word encoding, reflecting the picture-sensitivity of these regions. Inferior parietal regions were found to represent items more similarly when they were alternately presented as pictures and words across the study phase compared to when they were encoded uni-modally. This result likely reflects conceptual processing and integration of overlapping semantic features. Finally, while ERS source memory effects appeared to be largely modality-independent, evidence for reinstatement of pictorial information from the study phase was found in occipital and right inferior temporal regions. These effects generally support an important role for reactivation in source memory formation and retrieval. While reactivation across repeated encoding presentations was found to be item-specific in some cases, reinstatement was only reported at the item-level for ERS patterns, indicating the reactivation of individual items at retrieval was not higher than the reactivation of other items from the same category.

Chapter 5 – Encoding context, repetition and memory (EEG)

5.1 Introduction

A large body of research has shown that the nature of the encoding task affects subsequent memory performance (e.g., Fletcher et al., 2003; Friedman et al., 1996; Paller & Kutas, 1992; Paller et al., 1987). These results were typically yielded when comparing semantic and non-semantic encoding task, generally supporting Craik and Lockhardt's levels of processing framework (Craik & Lockhart, 1972), showing that deep/semantic encoding is associated with better memory performance than shallow/non-semantic encoding. Moreover, in the context of repetition, some early research on word repetition priming indicated that the task had to be kept constant in order to yield reliable repetition priming effects (Ratcliff, Hockley, & McKoon, 1985, Experiment 2), while others reported priming effects even across tasks (Clarke & Morton, 1983; Jacoby, 1983; Jacoby & Dallas, 1981; Scarborough et al., 1979). Another line of research has investigated the effects of retroactive interference by presenting stimuli in different contexts, e.g., different encoding tasks (e.g., Kim et al., 2017; Koen & Rugg, 2016). Retroactive interference is generally measured by employing an AB/AC paradigm (Postman & Underwood, 1973), where a stimulus A is first presented in a context B, followed by presenting A in another, interfering context C. These paradigms typically report worse context memory compared to stimuli that were presented only once, in a single context (Anderson & Neely, 1996; Hupbach, Gomez, Hardt, & Nadel, 2007; Kim et al., 2017; McGovern, 1964). When the same stimulus is repeated in a different context, it is thought to reactivate the memory associated with the first context (McClelland et al., 1995; Norman & O'Reilly, 2003) and integrate the novel context in order to generalise across the two contexts (Richter, Chanales, & Kuhl, 2016; Schlichting & Preston, 2015; Schlichting, Zeithamova, & Preston, 2014; Shohamy & Wagner, 2008; Zeithamova & Preston, 2010). This generalisation, facilitated by reactivation, then weakens subsequent context memory. These suggestions are in line with the competition trace theory (Yassa & Reagh, 2013), which suggests that repetition improves item memory or familiarity at the cost of episodic details, such as context memory. Contrary to the competition trace theory and the reactivation view, the multiple trace theory proposes that each stimulus presentation is encoded uniquely, thereby providing multiple traces of the same items (Hintzman, 1986; Hintzman & Block, 1971; Nadel & Moscovitch, 1997), and enabling subsequent retrieval of episodic details. Taken together, it may be suggested that, when an item is encoded in different task contexts, either reactivation occurs, which is associated with worse context memory, or multiple traces are created facilitating superior context memory. This would mean that subsequent context memory could be predicted based on the underlying operations that take place during encoding. While research has investigated the effect of different encoding tasks on subsequent memory performance and on repetition effects, either separately or in an interference paradigm, very few studies have directly compared the behavioural and neural differences between repeatedly performing the same task and performing different tasks, i.e., encoding repeated stimuli in the same context or different contexts. Such a paradigm will allow a direct comparison between the reactivation hypothesis (McClelland et al., 1995) and the multiple trace theory (Nadel & Moscovitch, 1997). Participants will repeatedly encode one-half of a set of stimuli in the same context, which is hypothesised to involve reactivation. The other half of the stimuli will be encoded in different contexts, which is hypothesised to involve one of two different operations, reactivation or the creation of multiple traces. Reactivation is hypothesised to be associated with subsequent hits- judgements, while the creation of multiple traces is predicted to be associated with subsequent hits+ judgements.

Event-related potentials

ERP research investigating Dm effects in semantic and non-semantic encoding tasks have reported the difference between subsequent hits and misses to be larger in semantic encoding tasks (Friedman et al., 1996; Paller & Kutas, 1992; Paller et al., 1987; Sanquist et al., 1980). Others noted qualitative differences in Dm effects between semantic and non-semantic tasks (Otten & Rugg, 2001a). Dm effects occurred under both encoding instructions, however, the semantic task was associated with enhanced positivity Dm effects, while the non-semantic task led to Dm effects with less positivity for subsequent hits relative to misses. Moreover, repetition effects have been reported in a semantic encoding task but not in a non-semantic task (Friedman et al., 1996). Taken together, differences relating to encoding tasks were generally interpreted to reflect different encoding orientations being associated with differences in underlying neural processes that are engaged during study (Paller & Wagner, 2002). To the author's knowledge, no previous ERP experiments have investigated the effects of repeatedly performing the same encoding task compared to performing different encoding tasks for the same stimulus. Rather than comparing the effects of different task instructions, this chapter is concerned with the effect of same and different task encoding on subsequent source memory and repetition. Additionally, in Chapter 3 (section 3.3.1.2.2), exploratory single-trial analyses revealed a repetition effect, which was largely independent of subsequent source memory and encoding modality. This repetition effect was shown to be related to item-repetition but only for a parietal cluster of electrodes and only between presentations 1 and 2. This chapter also aims to replicate those results and extend them to different encoding task conditions.

ERPs measured from the test phase have also been shown to be sensitive to encoding task manipulations. For example, in a between-groups design, participants encoded pictures and words of objects and performed one of two encoding tasks (artist/function) depending on the group they were in (Johnson et al., 1997). At test, participants either performed an old/new recognition task or a source identification task, where they indicated whether they had studied the object as a picture or a word or not studied it at all (new). All stimuli were presented as words at test. During retrieval ERP mean amplitudes at frontal and parietal sites discriminated items according to how they were encoded during the study phase. These results were not directly mapped to FN400 and LPC effects, although it appears that an early negative frontal deflection around 450ms, reminiscent of the FN400, was associated with the artist task, while an early (onset around 300 ms) but longer-lasting parietal effect, possibly reflecting the LPC, was related to the function encoding task. These findings were interpreted to reflect that differential information relating to an item is distributed across the neocortex (Johnson et al., 1997). In another experiment (Johnson et al., 2008), participants encoded words under two different encoding tasks. In one task, they were presented with the word superimposed on a scene and the task was to image the item at a location within the scene. In another task, words were presented on a blank background and participants were asked to generate a sentence based on the word. At retrieval, an R-K test assessed recollection. Differential recollection effects were found for the two encoding tasks. Recollection

ERPs to items encoded in the sentence condition were associated with more positive waveforms over anterior electrode sites than ERPs to items encoded in the scene condition. This effect was observed from about 300 – 1000 ms post stimulus onset. From about 800 ms onwards, the same effect, with opposite polarity, was observed over posterior electrode sites. Because of the temporal overlap between the study content dependent effects and previously well-established recollection effects, namely, the LPC, these findings were suggested to reflect reinstatement of information from the study phase during recollection (Johnson et al., 2008). However, in a retroactive interference paradigm, it was reported that ERPs measured at test were not sensitive to the encoding conditions, i.e., no test ERP differences were reported for stimuli that were initially encoded in the retroactive interference condition compared to two control encoding conditions (Tendolkar, Doyle, & Rugg, 1997). Taken together, it appears that the LPC at test is sensitive to the nature of the encoding task though perhaps not to retroactive interference.

The present experiment employed a subsequent memory paradigm in which each stimulus, written names of famous people, was presented four times during encoding. Half of the stimuli were repeated under the same semantic encoding task instructions, while the other half was repeated across four different semantic encoding task instructions (“Is this person female?”, “Is this person currently active in show business?”, “Is this person British?” and “Do you like this person?”). Therefore, famous names were either repeatedly encoded in the same context or in distinct contexts. At test, participants performed an old/new judgement task, assessing item memory, followed by a source memory question probing participants’ memory for the encoding task they performed during the study phase. This experimental paradigm allows direct comparisons of the reactivation hypothesis and the encoding variability view when considering the behavioural data. Based on previous studies on retroactive interference, source memory is predicted to be worse for the different compared to the same encoding task condition. Moreover, to the author’s knowledge, a paradigm that directly compares the two types of repeated encoding has not been employed in ERP research. This experiment aims to establish and investigate the neural correlates of repeated memory encoding under the same or different encoding task instructions with respect to subsequent source memory performance. Based on the behavioural accounts introduced in this chapter, repetition effects are predicted to differ between the two encoding task conditions. Moreover, ERPs to subsequent hits+ and hits- judgements are predicted to differ in the different encoding task condition. That is because same and different context encoding are hypothesised to engage different processes across repetitions but, furthermore, the process engaged during different task encoding is expected to predict subsequent source memory performance, with reactivation being associated with worse source/context memory. As reactivation during the different context encoding is predicted to be associated with worse source memory but potentially higher familiarity, the FN400 is predicted to reflect this process. At test, the LPC is typically associated with recollection. Furthermore, in Chapter 3 of the present manuscript, the LPC at test was modulated by encoding modality. Therefore, the LPC is hypothesised to be sensitive to the encoding task manipulation in the present paradigm. If the LPC indexes recollection and reinstatement of associated details, it may be that a larger amount of details, as would be the case for the different encoding task condition, will be reflected in larger LPC amplitudes.

5.2 Method

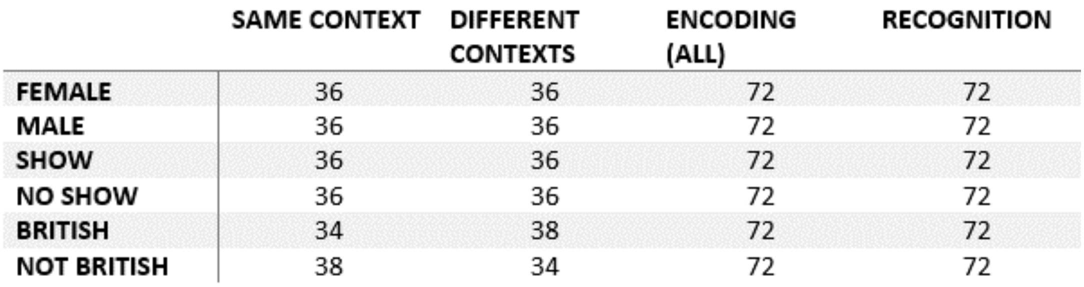
5.2.1 Participants

Twenty-four right-handed adult volunteers (13 females) participated in the experiment. Participants were aged 18 to 25 years ($M_{\text{age}} = 20 \pm 2$) and had completed an average of 15±2 years of education. In addition to general inclusion criteria (see 2.1), all participants were British, because stimuli were selected based on a behavioural pilot study only including British participants. Data from one participant were excluded from all analyses due to failing to follow task instructions. Data from another two participants were excluded from EEG analyses due to poor EEG data quality, resulting in 21 included participants (13 females).

5.2.2 Materials

Stimuli were a total of 288 (written) names of famous people (e.g., Keith Richards, Michelle Obama). Stimuli were selected from a total of 350 famous names based on a behavioural pilot study to identify the most well-known famous people amongst a sample of participants with similar characteristics as the sample in the present experiment. Famous names were matched across all tasks and conditions in accordance with the four encoding tasks (gender, currently active in show business or not, British or not; see Table 5.12). During the study phase, half of the stimuli were repeatedly presented as written words in the centre of a black background. Words were presented in white Courier New 36 font. A personal memories questionnaire was administered upon completion of the test phase. The personal memories questionnaire (see Appendix C) required participants to rate the famous names presented during the study phase in terms of the amount and quality of personal memories they held for them, ranging from 0 (no personal memory) to 4 (very vivid personal memories), with the instruction to leave the row blank if the participant did not know the famous person at all.

Table 5.12. *Frequencies of famous names stimuli, used in experiment 3 (EEG), referring to males/females, currently active in show business/not active, British/not British in the two encoding conditions (same/different context) and across study and test phase.*



	SAME CONTEXT	DIFFERENT CONTEXTS	ENCODING (ALL)	RECOGNITION
FEMALE	36	36	72	72
MALE	36	36	72	72
SHOW	36	36	72	72
NO SHOW	36	36	72	72
BRITISH	34	38	72	72
NOT BRITISH	38	34	72	72

5.2.3 Task & procedure

In the study phase, participants performed four different categorisation tasks on the names they were presented with. At the beginning of each block, they were presented with a question they had to answer with regards to the stimuli. The four questions were “Is this person female?”, “Is this person currently active in show business?”, “Is this person British?” and “Do you like this person?”. Task order was pseudo-randomised across participants. Participants were encouraged to guess the answer in cases where they were not familiar with the famous name or when they did not know the answer. They were instructed to press one of two buttons corresponding to whether their answer to the question was “yes” or “no”.

Additionally, participants were encouraged to only blink when the word “blink” appeared on the screen. During the encoding phase, each stimulus was presented four times. Half of the stimuli were presented once in each of the four tasks (*different task condition*), the other half was presented repeatedly within only one of the four encoding tasks (*same task condition*). With four repetitions per stimulus this resulted in a total of 576 encoding trials. The average inter-trial interval (ITI) in both experiments was 4100 ms. The experimental procedure is illustrated in Figure 5.21. At the end of the encoding phase, participants performed a trail-making distractor task.

During the test phase, participants performed an unexpected recognition-source memory test. In this task, all old stimuli from the encoding phase were presented along with the remaining set of new stimuli. Both lists were matched in terms of gender, whether famous people were currently active in show business or not and whether they were British or not. All stimuli were presented as white written words in Courier New 36 font on black background. Participants gave an old/new response depending on whether or not they thought the name had been presented during the encoding phase. Participants were cued with a name and instructed to indicate whether this stimulus had been presented in any of the previous tasks by pressing one of eight buttons on the response pad corresponding to the following responses: “definitely old”, “perhaps old”, “perhaps new”, and “definitely new”. “Old” responses were followed by a source memory question asking participants in which task the famous name had been previously been categorised with the response options “all four tasks”, “gender task”, “show business task”, “British task”, “like task” and “I don’t know”. Stimuli were presented for 1500 ms, followed by a fixation cross for 1000 ms. Depending on participants’ old/new response, either a fixation cross appeared for 1500 ms or the source memory question appeared for 1500 ms. Another fixation cross of random duration (800 – 1200ms, average ITI= 5000 ms) then indicated the beginning of the next trial.

Once participants had completed the recognition task, they filled in a personal memories questionnaire. The data form this questionnaire were not included in any subsequent analyses as the relevance of those data went beyond the scope of the present research.

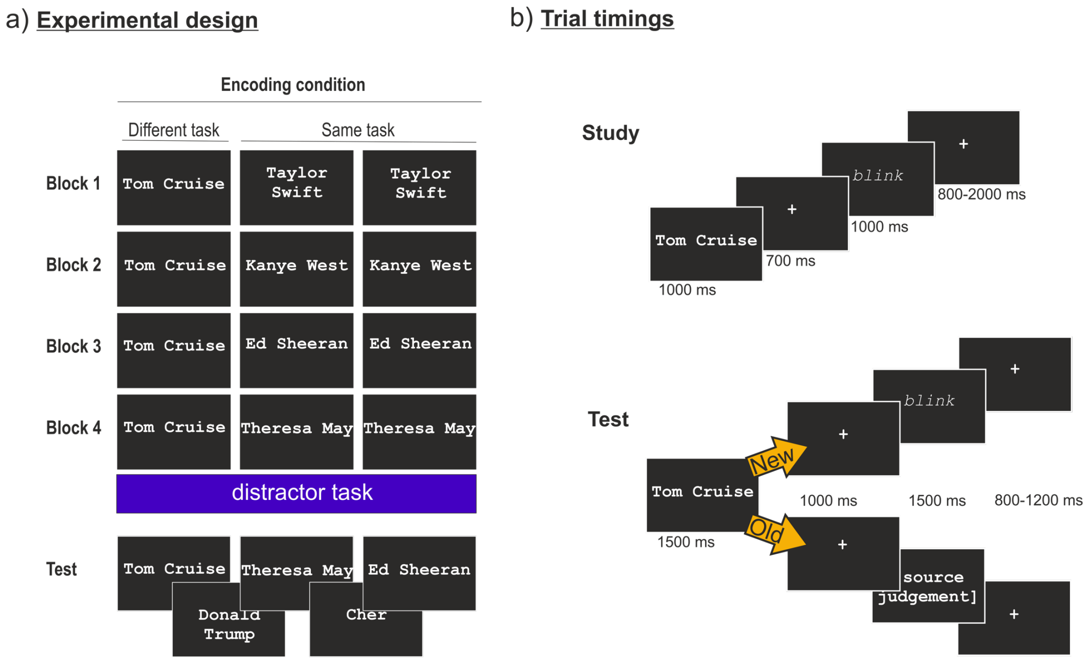


Figure 5.21. Experiment 3 (EEG): a) The experimental paradigm with four encoding presentations of each stimulus during the study phase; participants encoded half of the stimuli in a different task condition, i.e., performing a different task at each presentation of the stimulus, the other half were encoded in a same task condition, i.e., participants repeatedly performed the same semantic encoding task; in a test phase, participants made old/new judgements followed by source judgements; b) trial timings.

5.3 Results

The repeated-measures design included three factors of interest at study and two at test: memory performance (hits+, hits-; behavioural analyses also include misses), repetition (presentation 1,2,3,4; only at study) and encoding context (different, same). Because of lower frequencies of hits+ judgements compared to Chapter 3, hits+ trials included all correct item and correct source judgements irrespective of confidence ratings. Hits- trials were characterised as old/new hits, irrespective of confidence rating, followed by an incorrect source memory response or no response, indicating the source could not be retrieved. As item memory performance was high, misses are only included in behavioural analyses. Because of a lack of low confidence responses, confidence was not included in further analyses. Participants' responses to the item memory question indicated that they were more often highly confident of their response ($M_{\%\mathrm{HC}} = 96 \pm 8$) than responding with low confidence ($M_{\%\mathrm{LC}} = 4 \pm 8$), $t_{20} = 26.912$, $p < .001$.

5.3.1 Behavioural results

5.3.1.1 Reaction times at study

Reaction times during the study phase were analysed in a 3 x 2 x 4 repeated-measures ANOVA with the factors memory performance (hits+, hits-, misses), encoding context (same, different) and presentation (1, 2, 3, 4). Reaction times are displayed in Figure 5.22. The ANOVA revealed main effects of encoding context $F_{1,20} = 108.614$, $p < .001$, and presentation, $F_{2,36} = 20.152$, $p < .001$. No statistically significant interactions involved subsequent memory performance. RTs under the same encoding task condition were faster than RTs under the different encoding task condition. Furthermore, RTs decreased across presentations (all $p < .006$ with the exception of presentation 3 and presentation 4, where this difference was non-significant, $p > .05$).

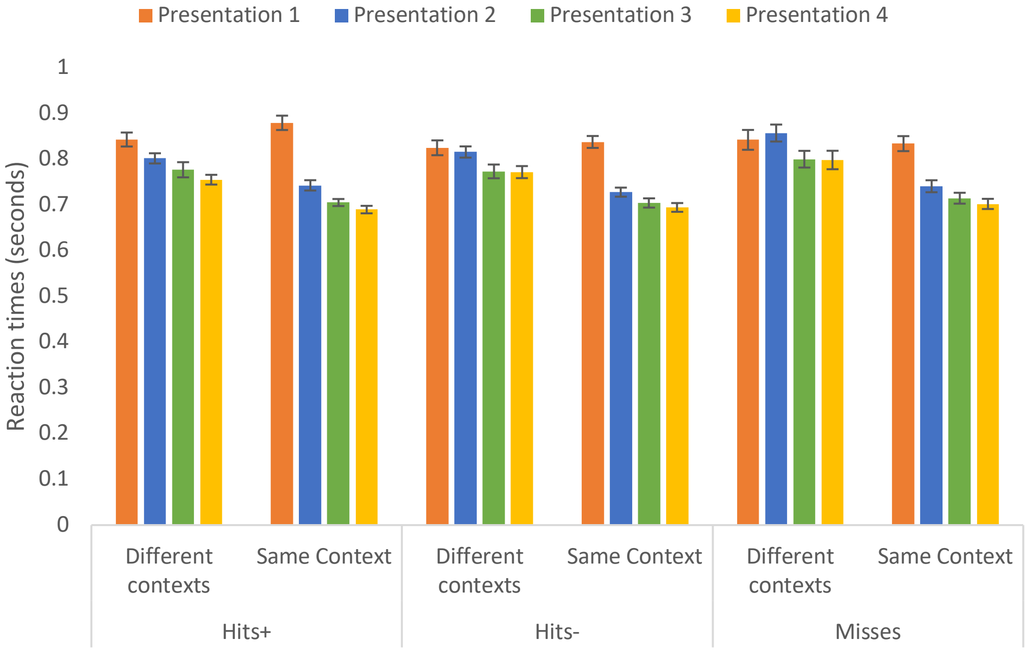
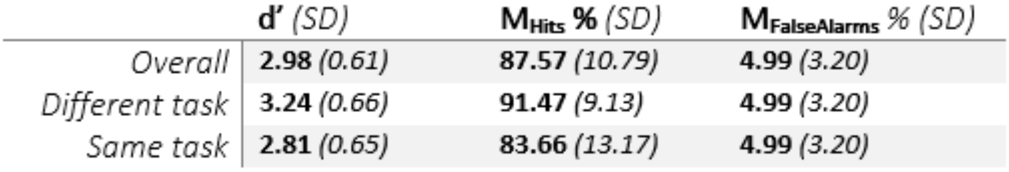


Figure 5.22. Reaction times (in seconds) in experiment 3 (EEG) for all four presentations during the study phase, separately for subsequent memory performance and encoding contexts. Error bars denote standard error.

5.3.1.2 Discriminability analysis

Discriminability scores (*d'*) were calculated based on the frequencies of hits and false alarms. The normalised probabilities of overall hits and false alarms were compared in a paired-samples t-test. The t-test showed that participants' performance in the recognition memory task was statistically significantly above chance, t_{20} = 22.529, $p < .001$. Mean and standard deviations of *d'* scores and percentages of hits and false alarms are illustrated in Table 5.13. Those individual *d'* scores indicate that recognition memory performance was higher in the different encoding task condition (verging on a ceiling effect).

Table 5.13. *Experiment 3 (EEG): The mean d' scores and mean % of Hits and False Alarms with standard deviations (italicized, in parentheses) for overall memory performance and across the two encoding conditions.*



	d' *(SD)*	**M_{Hits} %** *(SD)*	**$M_{FalseAlarms}$** % *(SD)*
Overall	**2.98** *(0.61)*	**87.57** *(10.79)*	**4.99** *(3.20)*
Different task	**3.24** *(0.66)*	**91.47** *(9.13)*	**4.99** *(3.20)*
Same task	**2.81** *(0.65)*	**83.66** *(13.17)*	**4.99** *(3.20)*

5.3.1.3 Behavioural performance at test

Frequencies of hits+, hits- and misses (memory performance) were analysed in terms of encoding context (same vs. different) in a 3 x 2 repeated-measures ANOVA. Descriptive statistics of the data included in the analysis are displayed in Figure 5.23. The ANOVA revealed a main effect of memory, $F_{2.40}$ = 52.441, $p <$ .001 and an interaction between memory performance and encoding context, $F_{1,24}$ = 29.551, $p < .001$. A post-hoc test revealed that all three levels of memory performance differed significantly from each other in terms of frequencies, all $p <$ .002. The majority of responses resulted in hits- judgements (correct item memory, incorrect source memory), fewer responses resulted in hits+ judgements (correct item and correct source memory) and the least responses resulted in misses. Following up on the interaction between memory performance and encoding context showed that encoding under the same encoding task condition was associated with more hits+ judgements than the different encoding task condition, $p < .001$. The same encoding task condition was, however, also associated with more misses than the different encoding task condition, $p < .001$. Finally, the different encoding task condition was associated with more hits- judgements than the same encoding task condition, $p < .001$.

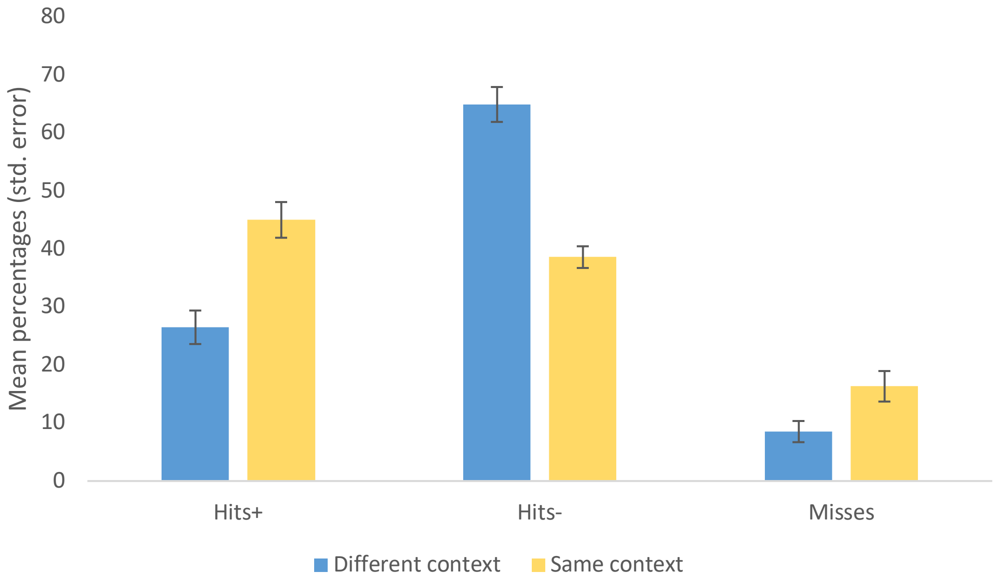


Figure 5.23. Behavioural performance in experiment 3 (EEG). Mean percentages and standard error of the three levels of memory performance (hits+, hits-, misses) and encoding context (same, different). Error bars denote standard errors.

5.3.1.4 Reaction times at test

RTs measures during the test phase were analysed in two separate repeated-measures ANOVAs. First, RTs to the item memory (old/new) task were examined in a 3 x 2 ANOVA with the factors memory performance and encoding task condition. In a second analysis, RTs to the source memory task were analysed. In this 2 x 2 repeated-measures ANOVA, the factors were memory performance (only two levels, as misses were not followed up with a source memory question) and encoding task condition.

The ANOVA analysing item memory RTs at test revealed a main effect of encoding context, $F_{1,20} = 15.444$, $p = .001$. Item memory responses were made faster to items previously encoded under the different encoding task condition compared to the same encoding task condition. No main effect of memory performance on RTs was found for the item memory responses, $F_{1,22} = 1.867$, $p = .186$, however, simple effects analyses indicated that hits+ judgements to the old/new question were made faster than hits- judgements, $p = .001$.

The ANOVA analysing RTs to the source memory question revealed main effects of source memory performance, $F_{1,20} = 15.178$, $p = .001$, and encoding context, $F_{1,20} = 8.497$, $p = .009$. Correct source responses were given faster than incorrect source responses and as similar to item memory RTs, source memory responses were made faster to items previously encoded under the different encoding task condition compared to the same encoding task condition.

5.3.2 ERP analysis

Based on the literature, two ERP components were selected. The early frontal FN400-like EPR was measured between 300 -500 ms post stimulus onset at electrode sites F1/F2, F3/F4, FC1/FC2 and FC3/FC4. The late parietal LPC-like ERP was measured between 500 - 700 ms post stimulus onset at electrode sites P1/P2, P3/P4, P5/P6 and PO3/PO4. Additionally, the frontal and the parietal component were also measured between 700 – 900 ms, as exploratory analyses in Chapter 3 (see 3.3.2.3) revealed effects related to explicit source memory performance in this time window.

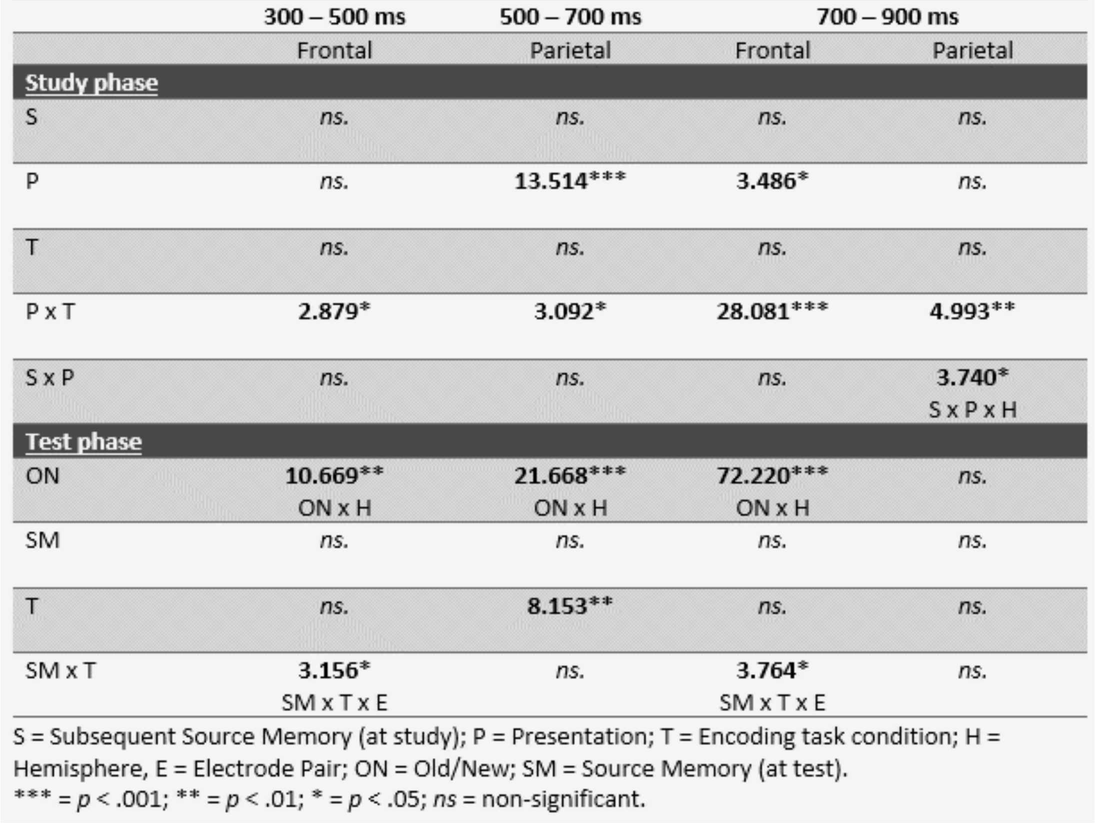
ERP analyses at study investigated the interactions between the factors subsequent source memory, repetition and encoding task condition. ERP analyses at test focused on main effects and interactions for the factors source memory and encoding task condition. Finally, single-trial analyses were performed to replicate the results from chapter 3 (3.3.2.2) in the present paradigm.

ERP analyses were conducted at study and test and the results are presented in Table 5.14. Data from the study phase were analysed separately for the FN400 between 300 – 500 ms, the LPC from 500 – 700 ms and for both, a frontal and a parietal component made up of the same electrodes as the FN400 and LPC, during a time window from 700 to 900 ms post stimulus onset. Data were submitted to separate 2 x 4 x 2 x 2 x 4 repeated-measures ANOVAs, with the factors subsequent source memory (hits+, hits-), presentation, (1,2,3,4), encoding task condition (same, different), hemisphere (left, right) and electrode pair. Measures during the test phase from the same components and time windows were submitted to ANOVAs investigating the old/new effect as well as effects of source memory and encoding task condition at test. First, separate 2 x 2 x 4 repeated-measures ANOVAs were carried out with the factors old/new (only high confidence trials included), hemisphere and electrode pair. To investigate main effects and interactions of the factors source memory and encoding task condition, data were also submitted to separate 2 x 2 x 2 x 4 repeated-measures ANOVAs, with the factors source memory (hits+, hits-), encoding task condition (same, different), hemisphere (left, right) and electrode pair.

Repeated-measures ANOVA results from study and test phase are presented in Table 5.14.

5.3.2.1 Study phase ERP analyses

Table 5.14. *Experiment 3: ERP analysis results (F statistics and significance level) from repeated-measures ANOVAs at study and test phase.*



	300 – 500 ms	500 – 700 ms	700 – 900 ms	
	Frontal	Parietal	Frontal	Parietal
Study phase				
S	*ns.*	*ns.*	*ns.*	*ns.*
P	*ns.*	**13.514*****	**3.486***	*ns.*
T	*ns.*	*ns.*	*ns.*	*ns.*
P x T	**2.879***	**3.092***	**28.081*****	**4.993****
S x P	*ns.*	*ns.*	*ns.*	**3.740*** S x P x H
Test phase				
ON	**10.669**** ON x H	**21.668***** ON x H	**72.220***** ON x H	*ns.*
SM	*ns.*	*ns.*	*ns.*	*ns.*
T	*ns.*	**8.153****	*ns.*	*ns.*
SM x T	**3.156*** SM x T x E	*ns.*	**3.764*** SM x T x E	*ns.*

S = Subsequent Source Memory (at study); P = Presentation; T = Encoding task condition; H = Hemisphere, E = Electrode Pair; ON = Old/New; SM = Source Memory (at test).
*** = $p < .001$; ** = $p < .01$; * = $p < .05$; *ns* = non-significant.

Frontal (300 – 500 ms)

For the early frontal FN400-like component, the only significant effect was found for the interaction between presentation and encoding task condition. As illustrated in Figure 5.24a, in the same encoding task condition, the increase in negativity appears to be gradual across presentations with a significant difference between presentations 1 and 4, $p = .008$. In the different task condition, however, the first and third presentation were found to be more negative than the second presentation, $p = .021$, $p = .009$, respectively. Overall, Figure 5.24b indicates that presentations 1 and 3 are more negative than presentations 2 and 4. Simple effects analyses also revealed a task difference at presentation 1, $p = .031$, which signifies that any interpretation of these encoding task-related differences in repetition effects will have to be made with caution.

Parietal (500 – 700 ms)

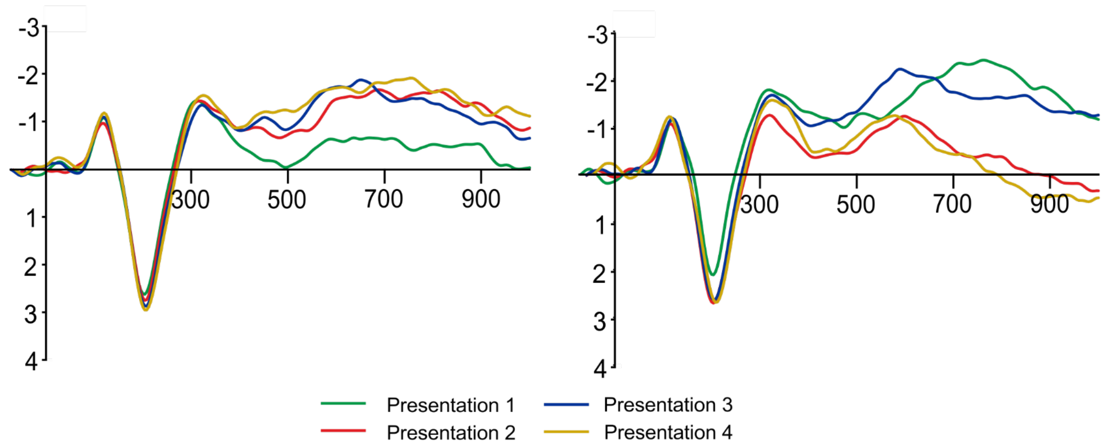
For the LPC-like component between 500 – 700 ms, a main effect of presentation as well as an interaction between encoding task condition and presentation were found to be statistically significant. The main effect of presentation reflected a linear increase in positivity across presentations with first presentation significantly less positive than subsequent presentations, all $p < .008$. Figure 5.24c displays the repetition effect in the same task condition and Figure 5.24d presents the repetition effect in the different task condition. Although both encoding conditions display a linear increase in positivity, the main effect of presentation extends to the same task condition with presentation 1 being significantly less positive than subsequent presentations, all $p < .002$. For the different task condition only presentation 1 and presentation 4 differ statistically significantly from each, $p = .019$. As for the FN400, simple effects analyses also revealed the same difference between encoding tasks at presentation 1, $p = .044$.

Frontal (700 – 900 ms)

For the frontal component between 700 and 900 ms post stimulus onset, the repeated-measures ANOVA revealed a main effect of presentation and an interaction between encoding task condition and presentation. Following-up on the main effect of presentation revealed no statistically significant pairwise comparisons, all $p > .064$. Simple effects analyses, following up on the interaction, found an increase in negativity in the same task condition, though not as gradual as in the earlier FN400 time window. Mean amplitudes at presentation 1 were less negative than at presentation 2, $p = .012$, and presentation 4, $p = .004$. This pattern is illustrated in Figure 5.24a. The pattern in the different task condition is less clear with presentations 1 and 3 differing from 2 and 4 by being associated with more negative mean amplitudes, all $p < .003$. This is illustrated in Figure 5.24b. As previously, a task difference was found at presentation 1 with the different task condition being associated with more negative mean amplitudes than the same task condition, *p* < .001.

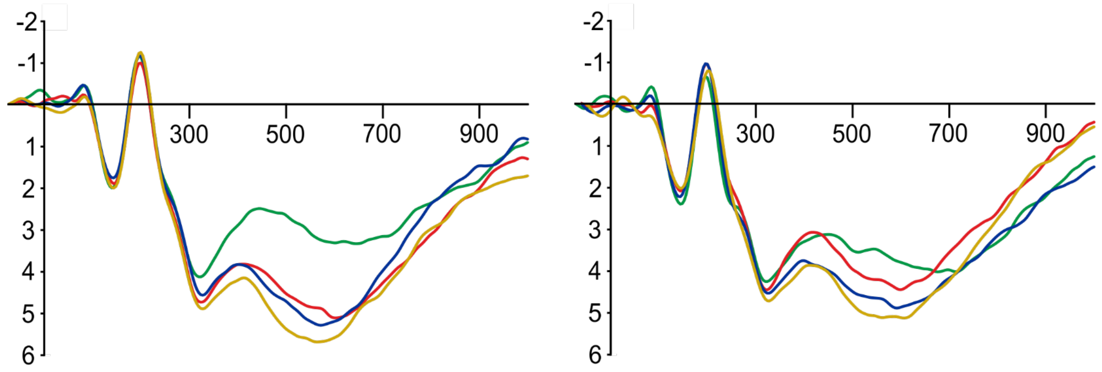
Parietal (700 – 900 ms)

Finally, the parietal component between 700 and 900 ms was associated with interactions between encoding task condition and presentation as well as between subsequent source memory, presentation and hemisphere. Follow-up analyses on the interaction between encoding task condition and presentation revealed no clear repetition patterns, illustrated in Figure 5.24. In the same task condition, ERPs to presentation 4 were more positive than to presentations 1 and 3, *p* = .018 and *p* = .030, respectively. Additionally, presentation 2 elicited a more positive ERP waveform than presentation 1, *p* =.037. For the different task condition, presentation 1 elicited the most positive ERP waveform, which were statistically significantly larger than those at presentation 2, *p* = .028. The two encoding task conditions also differed in mean amplitudes at presentation 1, *p* = .001. Simple effects analyses following up on the interaction between subsequent source memory, presentation and hemisphere revealed a trend, *p* = .071, for subsequent hits- judgements to be associated with more positive ERP waveforms than hits+ judgement but only at presentation 1 in left hemisphere electrodes, as illustrated in Figure 5.25.



a) Frontal: same encoding task condition

b) Frontal: different encoding task condition



c) Parietal: same encoding task condition

d) Parietal: different encoding task condition

e) Scalp topographies

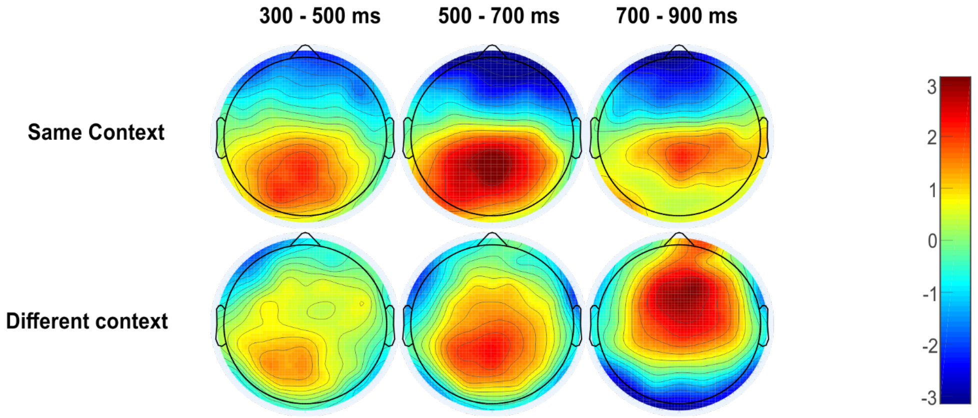


Figure 5.24. Experiment 3 (EEG): Grand average ERPs (N = 21) to presentations 1, 2, 3 and 4 in the same and different encoding task conditions in a) the fronto-central component, measured between 300 – 500 ms and 700 – 900 ms, averaged across electrode sites F1/F2, F3/F4, FC1/FC2 and FC3/FC4, d) the parietal component, measured between 500 – 700 ms and 700 – 900 ms, averaged across electrode sites P1/P2, P3/P4, P5/P6 and PO3/PO4 and e) scalp topographies of a contrast between mean amplitudes at Presentation 4 minus Presentation 1, separately for same and different context encoding.

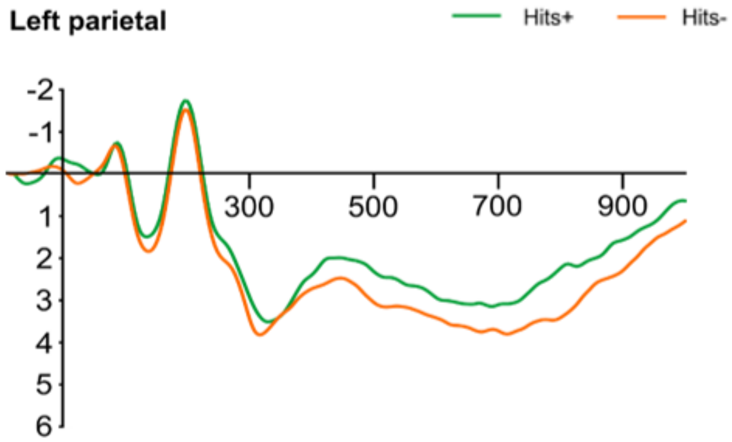


Figure 5.25. Experiment 3 (EEG): Grand average ERPs (N = 21) to subsequent hits+ and hits- judgements at presentation 1, averaged over encoding contexts, illustrating the subsequent source memory effect, averaged across electrode sites P1, P3, P5 and PO3.

5.3.2.2 Test phase ERP analyses

Frontal (300 – 500 ms)

During the test phase, the repeated-measures ANOVA on the FN400 data revealed an old/new effect that interacted with hemisphere as well as an interaction between encoding task, source memory and electrode pair. The old/new effect was found to only be statistically significant in the right hemisphere with old stimuli eliciting more negative waveforms than new stimuli, $p = .039$. Simple effects analyses, following up on the interaction between encoding task, source memory and electrode pair revealed no significant simple comparisons or meaningful trends (displayed in Figure 5.28a,b).

Parietal (500 – 700 ms)

For the LPC, the old/new effect was found to interact with hemisphere. Additionally, a main effect of encoding task was revealed along with a trend for the source memory effect, $F_{1,20} = 3.463$, $p = .078$. The old/new effect was significant in the left hemisphere, $p < .001$, with old stimuli eliciting more positive waveforms than new stimuli, illustrated in Figure 5.28c,d. The main effect of task was characterised by stimuli encoded in the different task condition being associated with more positive LPC mean amplitudes than those stimuli encoded in the same task condition (displayed in Figure 5.26a). Additionally, a trend was found for hits+

judgements to elicit more positive LPC waveforms than hits- judgements, as illustrated in Figure 5.26b.

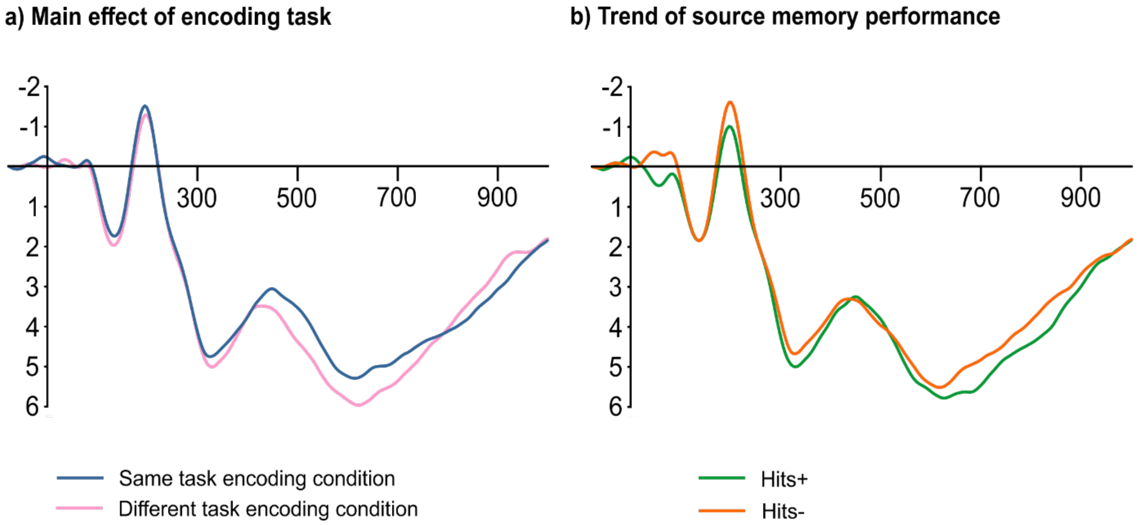


Figure 5.26. Experiment 3 (EEG): Grand average ERPs (N = 21), illustrating LPC effects, measured between 500 – 700 ms, averaged across parietal electrode sites P1/P2, P3/P4, P5/P6, PO3/PO4, for a) the main effect of encoding context measured at test and b) a trend indicating a main effect of source memory.

Frontal (700 – 900 ms)

The frontal component in the late time window between 700 and 900 ms was associated with an interaction between old/new and hemisphere as well as an interaction between encoding task, source memory and electrodes (see Figure 5.27). Simple effects analyses following up on the interaction between encoding task, source memory and electrode showed a difference in encoding task condition but only in hits- trials. At electrode pairs F1/F2, FC1/FC2, FC3/FC4, stimuli encoded under the same task condition elicited more negative ERPs than stimuli encoded across different tasks, all $p < .049$. The old/new effect was significant in both hemispheres, $p < .001$, but qualitative differences were shown. In the left hemisphere, new stimuli were associated more negative waveforms than old stimuli, whereas in right hemisphere old stimuli elicited more negative waveforms than new stimuli. This is illustrated in Figure 5.28a,b.

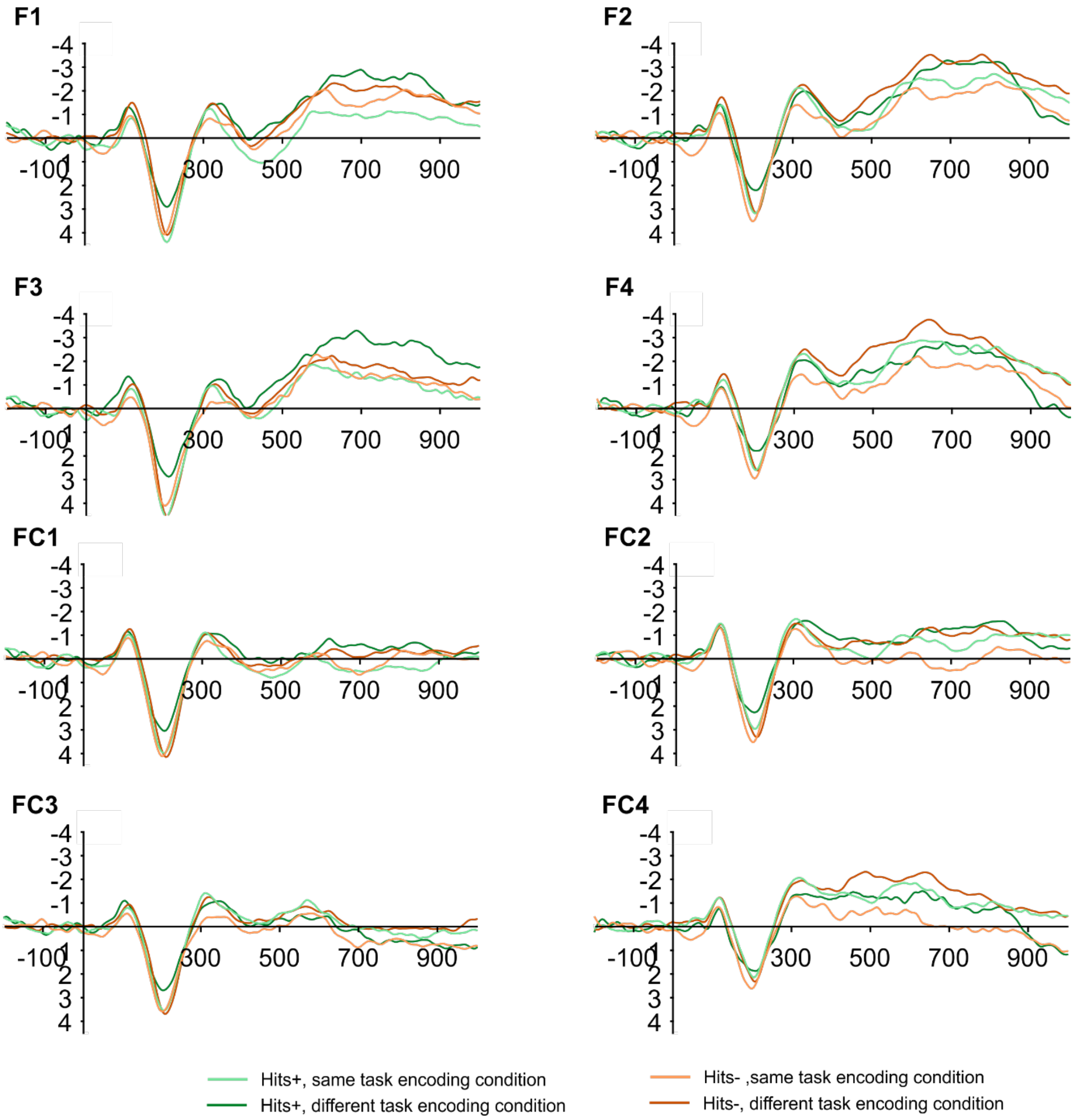


Figure 5.27. Experiment 3 (EEG): Grand average ERPs (N = 21), illustrating the interaction between source memory performance, encoding task condition and electrode site, measured over frontal electrode sites, between 700 – 900 ms.

Parietal (700 – 900 ms)

No statistically significant main effects or interactions were revealed for the parietal component between 700 and 900 ms post stimulus onset.

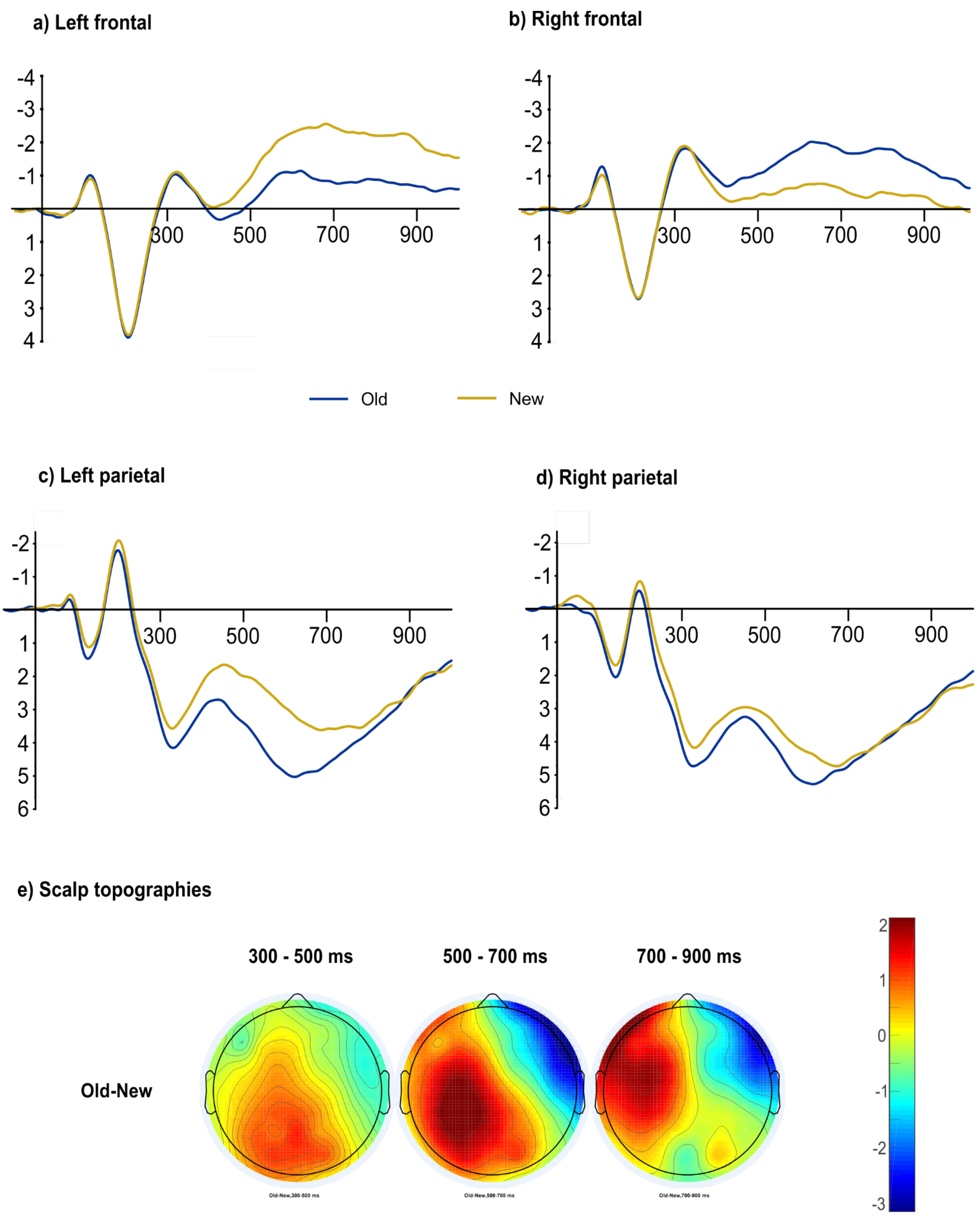


Figure 5.28. Experiment 3 (EEG): Grand average ERPs (N = 21) to high confidence correct old and new judgements during the test phase in a) the left fronto-central component, measured between 300 – 500 ms, averaged across electrode sites F1, F3, FC1 and FC3, b) the right fronto-central component averaged across electrode sites F2, F4, FC2 and FC4, c) the left parietal component, measured between 500 – 700 ms, averaged across electrode sites P1, P3, P5 and PO3, d) the right parietal component, averaged across electrode sites PP2, P4, P6 and PO4 and e) scalp topographies of the contrast old (high confidence hits) minus new (high confidence correct rejections).

5.3.2.3 Single-trial analyses (study phase, repetition effects)

In order to replicate the results from Chapter 3 (section 3.3.1.2.2) and expand those findings to different encoding task conditions, the same mass-univariate ERP approach (Groppe et al., 2011a) was applied to identify and isolate the repetition effect as observed in the planned analyses. Therefore, presentation 1 and presentation 4 were submitted to a repeated-measures, two-tailed cluster-based permutation test. As for the other EEG dataset, 201 data points were measured between 200 and 1000 ms from a subset of 21 frontal and 21 parietal electrode sites, which resulted in 8442 comparisons with 24 t-score degrees of freedom. 2500 permutations were performed. No reliable frontal/negative cluster could be identified. A parietal/positive cluster, i.e., a positivity increase in mean amplitudes from presentation 1 to 4, was identified at electrode sites CP1, CP2, CP3, CP4, CP5, P1, P2, P3, CPz and Pz between 448 and 712 ms post stimulus onset.

Positivity enhancement across repetitions

Mean amplitudes were extracted for each single trial. The aim of the first analysis was to replicate the finding that only the parietal repetition effect between presentations 1 and 2 was related to item-specific repetition. For each stimulus and each consecutive presentation pair (Presentation 1 and 2, Presentation 2 and 3, Presentation 3 and 4), positivity enhancement was calculated by subtracting the earlier from the later presentation. A control value for enhancement was computed by calculating the same differences except that the amplitude values from the trial occurring right before the actual stimulus repetition were used. Paired-samples t-tests were used to test whether stimulus-related repetition effects differed from the control. Positivity enhancement was found to be significantly larger than in the control condition between presentation 1 and 2 but only in the same task condition, $t_{20} = 4.971$, $p < .001$. Additionally, positivity enhancement in subsequent hits+ judgements, $t_{20} = 3.017$, $p = .007$, and in the same task condition, $t_{20} = 5.559$, $p < .001$, were found to be larger than the control enhancement values. Based on those findings, direct comparisons between the conditions (subsequent hits+ vs hits- trials, same vs different task) were carried out for the overall enhancement and the enhancement between presentation 1 and 2. For the contrast between hits+ and hits-, an overall enhancement effect indicated that hits+ were associated with more increase than hits-, $t_{20} = 2.150$, $p = .044$. A similar trend was observed between presentation 1 and 2, $t_{20} = 1.760$, $p = .094$. The difference between same and different task condition indicated that the same task was associated with a larger increase than the different task condition, though this was only statistically significant between presentation 1 and 2, $t_{20} = 2.506$, $p = .021$, but not for the overall effect across all consecutive presentation pairs, $t_{20} = 1.707$, $p = .103$.

Amplitude enhancement effects and implicit memory (RTs)

To replicate the finding that item-specific positivity enhancement is related to decreases in RTs (section 3.3.1.2.2), the amplitude differences between consecutive presentation pairs calculated for the previous analysis were correlated across trials with differences in RTs between consecutive presentation pairs. The correlation coefficients obtained for each participant were then submitted to a one-sample t-test, which showed that the relationship between positivity enhancement and RT decreases across repetitions was statistically significant, $t_{20} = 5.439$, $p < .001$.

Control analysis: LPC enhancement and repetition lag

Due to methodological constraints in the present experimental paradigm, the same task condition was always associated with shorter repetition lags than the different encoding task condition. While this systematic bias cannot be entirely controlled for, correlations between amplitude enhancement and repetition lag were computed from the single-trial data to assess whether changes in mean amplitudes were associated with differences in repetition lag. For each participant, mean increase in LPC amplitudes between repetitions was correlated with repetition lag. The correlation coefficients were then submitted to a one-sample t-test. The correlations between LPC enhancement and repetition lag were not significantly different from zero, $t_{1,20} = .424$, $p = .676$. This result indicates that differences in repetition lag were not associated with differences in repetition enhancement as observed in the parietal cluster between 448 and 712 ms post stimulus onset.

5.4 Discussion

The present experiment investigated the effects of two different encoding task conditions on subsequent memory performance and repetition. Participants repeatedly encoded items either in the same context, i.e., same encoding task instructions or in different contexts, i.e., different encoding task instructions. From theories regarding the mechanisms underlying different encoding strategies, differences between those two encoding task conditions were hypothesised. It was proposed that same task encoding would be associated with the reactivation of the same item and contextual cues across repetitions, leading to superior source memory for the encoding context. In the different task condition, however, subsequent source memory performance was expected to be lower than in the same task condition, because of those same reactivation processes leading to interference. Therefore, two different mechanisms were proposed to underlie encoding in the different task condition and these mechanisms would predict subsequent source memory. While behavioural data generally supported our predictions, the EEG data presented in this chapter only partly support the hypotheses regarding reactivation and multiple traces in the different encoding task condition. Those are more appropriately addressed in the following chapter, Chapter 6, as RSA is often used as a measure of reactivation. Finally, while the differences between encoding task conditions are interpreted as arising from repeatedly encoding stimuli under the same or different task instructions, one confounding factor is important to keep in mind. Due to methodological constraints in the present paradigm, stimuli repeated in the same task condition were associated with shorter repetition lags and were therefore repeated closer in time to each other than stimuli that were repeated in different task condition. A control analysis indicated that differences in repetition lag did not relate to differences in mean amplitude enhancement across repetitions.

5.4.1 Behavioural results

Most judgements during the recognition-source task led to hits- judgements, followed by hits+ judgements and the fewest responses resulted in misses. Furthermore, an interaction was shown between the three levels of memory performance and the encoding context condition. Encoding stimuli in the different context condition was associated with fewer hits+ judgements, more hits- judgements and fewer misses than encoding stimuli in the same context condition. The pattern of this interaction suggests that encoding items in different contexts may lead to superior item memory performance than repeatedly encoding items in the same context; however, this comes at a decrement of additional details that can be remembered. This is in line with results from retroactive interference paradigms (Anderson & Neely, 1996; Hupbach et al., 2007; Kim et al., 2017), suggesting that items were more likely to be generalised across contexts at the cost of contextual source information. Interestingly, the different encoding task condition was not only associated with worse source memory as predicted by retroactive interference, it was also associated with better item memory, i.e., more hits- judgements and fewer misses than the same encoding task condition. This suggests that encoding stimuli in different contexts compared to mere repetition in the same context, strengthens item memory, which supports the encoding variability view (Bower, 1972; Hintzman, 1986; Martin, 1968; Nadel & Moscovitch, 1997). During the study phase, RTs were found to index repetition priming by decreasing across multiple presentations. Moreover, RTs to stimuli encoded in the same task condition were faster than RTs to stimuli encoded in the different task condition, indicating shorter processing time in the same task condition than the different encoding task condition. The reverse effect was observed during the test phase. RTs to both, item and source memory, questions were revealed to be faster to stimuli encoded in the different task condition compared to stimuli encoded in the same task condition. Finally, RTs resulting in hits+ judgements were faster than those resulting in hits- judgements. The behavioural results provide support for the hypothesis that the encoding of stimuli in different contexts is associated with better item memory at the cost of contextual details.

5.4.2 ERP results

Mean amplitudes for an early frontal FN400-like component (300 – 500 ms), a parietal LPC-like component (500 – 700 ms), a late frontal component (700 – 900 ms) and a later LPC-like component (700 – 900 ms) were extracted and analysed. Note that the LPC is commonly measured in 200 ms time windows within the 400 – 900 ms range (see Rugg & Curran, 2007), therefore, both of the chosen time windows are likely to reflect an LPC. The later, and especially for a frontal component less typical time window, was chosen based on the ERP results presented in Chapter 3.3.1.2., as effects relating to explicit memory performance were found to occur somewhat later than in the predicted time windows, while repetition effects appeared to occur earlier. ERP analyses at study revealed interactions between encoding task condition and presentation in all time windows and components. However, as will be discussed, any interpretations are tentative as the two encoding task conditions were also found to differ at presentation 1, suggesting the two repetition effects might not be directly comparable. In the later time window, LPC amplitudes were found to discriminate subsequent source memory performance but only at presentation 1 and only in the left hemisphere. During the test phase a right-hemispheric FN400 old/new effect, a left-hemispheric LPC old/new effect and a late frontal old/new effect were revealed. Additionally, the LPC at test was found to discriminate old stimuli according to their associated encoding task condition (same or different task) and a trend was shown for LPC amplitudes to differ quantitatively for hits+ and hits- judgements. Finally, single-trial analyses revealed item-repetition effects in a parietal cluster between 448 – 712 ms post-stimulus onset between presentation 1 and 2 and only in the same task condition. Item-specific repetition enhancement of LPC amplitudes was higher for subsequent hits+ trials compared to hits- trials. Item-related repetition priming, as reflected in RT reductions, was associated with amplitude increases in positivity across presentations, replicating the results from section 3.3.1.2.2.

Study phase – ERP analyses

During the study phase, only one effect was related to subsequent source memory performance. In the LPC-like component, between 500 and 700 ms post stimulus onset, subsequent hits- judgements elicited more positive ERP waveforms than subsequent hits+ judgements but only at the first presentation and only in the left hemisphere. This is in line with quantitative differences relating to episodic recollection at test (reviewed in Friedman & Johnson, 2000; Rugg & Curran, 2007; Wilding & Ranganath, 2012) and has previously also been reported during the study phase in experiments investigating subsequent source memory (Groh-Bordin et al., 2006; Yovel & Paller, 2004). The finding that this effect only occurred in the left hemisphere is consistent with reports of a late left parietal component related to old/new as well as recollection judgements (e.g., Rugg & Yonelinas, 2003). In Chapter 3, it was speculated that multiple repetitions during encoding might change the characteristics of the typically observed Dm effects, which is reflected in this effect only occurring at the first presentation in the present investigation. However, despite overlaps in time window and electrode sites with well-established recollection effects at test, here, the direction of the effect indicated a qualitative difference from this recollection effect (e.g., Yovel & Paller, 2004). Unlike the typically reported LPC effect relating to episodic recollection, subsequent hits- judgements elicited more positive mean amplitudes than subsequent hits+ judgements in the present investigation. A similar effect, with the same direction, was reported in Chapter 3. Taken together, while LPC mean amplitudes at study and at test appear to discriminate source memory performance, the qualitative differences, as indexed by opposite directions of this effect at study and test, warrant further research into the ERP correlates of source memory encoding and retrieval. It remains to be determined to which extent LPC source memory effects overlap between study and test phase.

In addition to the subsequent source memory effect observed over parietal electrode sites from 500 – 700 ms, an interaction between encoding context and repetition was reported in both components and time windows. LPC-like mean amplitudes between 500 – 700 ms post stimulus onset were shown to increase in positivity across repetitions in both encoding conditions. Here, the interaction reflected a much more gradual increase in the different encoding task condition, with only presentations 1 and 4 differing statistically significantly from each other. The same encoding task condition was associated with a strong novelty effect between presentations 1 and 2 and only small, non-significant increases in positivity thereafter. Analogously, for the early frontal FN400-like component repeated encoding in the same context was associated with a gradual increase in negativity. However, the repetition pattern observed in the different task condition was somewhat surprising in that presentations 1 and 3 were associated with more negative mean amplitudes than presentation 2 and 4. Moreover, all of the interactions between encoding context and repetition were reported along with a task difference at presentation 1. This finding signals that the repetition effects associated with the two encoding task conditions may not be directly comparable. The differences in repetition effects between encoding task conditions may be partly explained by differences in repetition lag between the two conditions. However, that does not account for the task difference at presentation 1 and would affect the repetitions but not the first presentation of a stimulus. Gradual increases in parietal positivity and frontal negativity have been reported in previous studies (Renoult et al., 2012; Van Strien et al., 2005) including the present thesis (see Chapter 3.3.2.1). However, the pattern relating to repetitions in the different context conditions, observed in an FN400-like component, may indicate an effect of different task instructions. Although all encoding task instructions required some form of semantic elaboration, the gender task, for example, may have involved less elaboration than judging whether a famous person was currently active in show business or not. ERP differences have been observed between semantic and non-semantic tasks (Friedman et al., 1996; Otten & Rugg, 2001a; Paller & Kutas, 1992; Paller et al., 1987; Sanquist et al., 1980), which likely extends to different levels of depth of semantic elaboration required by the encoding task (Craik & Lockhart, 1972). The pseudo-randomisation applied to the task order in the present experimental design presented tasks either in the order 1, 2, 3, 4 or 3, 4, 1, 2 (1 = gender task, 2 = show business task, 3 = British task, 4 = like task). In the same task condition, stimuli were repeated in either one of the four tasks, thus averaging tasks to investigate repetition effects would likely diminish any possible effects relating to the different task instructions. For the different task condition, however, the present results observed in the FN400 component would suggest task-related differences that distinguish the gender and the British task from the show business and the like task. Notably, such potential effects are not reflected in LPC mean amplitudes at study. Although interactions between encoding task condition and repetition were predicted based on behavioural hypotheses, there was no indication of a difference between subsequent hits+ and hits- trials in the different task condition, as reflected by ERP mean amplitudes. Due to the methodological confounds discussed here, how repeated stimulus encoding in different contexts affects ERP mean amplitudes is not entirely clear. However, these results encourage further research into how different levels of semantic elaboration potentially affect mean amplitudes. Using a paradigm with well-controlled semantic encoding tasks, presenting stimuli repeatedly in same and different contexts, with same repetition lags in both conditions, will lead to further, more interpretable insights into the ERP correlates of encoding variability.

Test phase – ERP analyses

During the test phase, frontal and parietal old/new effects were reported for the early and later time window. LPC mean amplitudes were found to differentiate stimuli that were initially encoded in the same context from those encoded in different contexts. Additionally, a trend was observed for LPC amplitudes to be more positive for hits+ than hits- judgements. In the traditional FN400 time window, an old/new effect was observed in the right hemisphere, with old stimuli eliciting more negative waveforms than new stimuli. For the LPC, measured between 500 and 700 ms post stimulus onset, left-hemispheric mean amplitudes to old stimuli were found to be more positive than to correct rejections. Both these results are in line with a large body of previous research reporting an early right frontal and a late left parietal old/new effect (reviewed in Friedman & Johnson, 2000; Paller & Wagner, 2002; Voss & Paller, 2008b, 2017; Wagner et al., 1999; Wilding & Ranganath, 2012). More surprisingly, an interaction between old/new and hemisphere was observed in the frontal component during the later time window, between 700 – 900 ms. This interaction reflected a qualitative difference in the old/new effect between left and right hemisphere. Larger negative deflections in the left hemisphere were associated with high confidence correct rejections (i.e., new stimuli), while larger negative deflections in the right hemisphere were elicited by stimuli correctly judged as old with high confidence. Generally, FN400 amplitudes between 300 – 500 ms have been shown to be more negative-going for correct rejections compared to hits (Addante, Ranganath, & Yonelinas, 2012; Cansino & Trejo-Morales, 2008; Mollison & Curran, 2012; Wilding, 2000), which is in line with the waveforms observed over left-hemispheric electrode sites, although this old/new effect was not statistically significant in the early time window. For a later frontal ERP (around 800 – 1500 ms), mean amplitudes have been reported to be more negative to correct rejections than hits (Cansino & Trejo-Morales, 2008; Wilding, 1999; Wilding & Rugg, 1996, 1997), supporting the presence of a later frontal component distinguishing old and new stimuli. This is consistent with the patterns observed over left frontal electrode sites. However, the nature of this interaction between old/new and hemisphere remains unexplained. Because of those qualitative differences between the hemispheres, it may be suggested that different neural processes contribute to the old/new effect observed in left and right hemisphere.

The LPC at test has previously been associated with episodic recollection (e.g., Friedman & Johnson, 2000; Rugg & Curran, 2007). Similar to previous studies (Addante, Ranganath, & Yonelinas, 2012; Cansino & Trejo-Morales, 2008; Mollison & Curran, 2012, experiment 1), the present investigation observed LPC amplitudes to hits+ judgements to be more positive-going than to hits- judgements (although this effect was only a trend and did not reach statistical significance). In addition to the LPC's role in recollection, it has also been reported to reflect reinstatement of information from the study phase during recollection (Johnson et al., 2008). Therefore, LPC amplitudes were hypothesised to be sensitive to the two different encoding task conditions. In the present experiment, positive parietal deflections, measured between 500 to 700 ms post stimulus onset, were observed to be larger for stimuli, which were initially encoded across different contexts compared to stimuli, which were encoded repeatedly in the same context. While such an effect may indicate the reinstatement of processes or information relating to the study phase, it is noteworthy that the main effect of encoding task, measured at test, did not interaction with source memory performance. In Chapter 3, LPC amplitudes at test were shown to differ based on the modality stimuli were encoded in. However, due to low hits- frequencies, it was not possible to look at an interaction between source memory performance and encoding modality at test. Instead, only recollected, i.e., hits+ judgements, were included in the analysis. Both these findings provide support for LPC amplitudes to reflect distinct information from the encoding phase, but it is not clear yet, whether those differences index reinstatement. However, previous investigations of reinstatement have suggested that recollection may not be necessary for reinstatement, as reinstatement processes were also observed during familiarity judgements (e.g., Johnson et al., 2009). Another interesting aspect of this result was that stimuli encoded in the different task condition elicited larger LPC amplitudes than those repeatedly encoded in the same context. LPC amplitudes have previously been suggested to index the amount of available episodic details, as it was shown to reflect the number of correct source judgements in a graded fashion (Wilding, 2000). Therefore, the LPC difference between the two encoding task conditions, as observed in the present experiment, may reflect the larger amount of retrieval cues, and thereby associated information, in the different encoding task condition compared to the same task condition.

Exploratory single-trial analyses (repetition effects)

Single-trial analyses were carried out on data from the study phase, in order to replicate the results from Chapter 3. The only reliable repetition effect that could be identified occurred in a parietal electrode cluster, showing an increase in positivity across presentations between around 450 to 700 ms post stimulus onset. The absence of a reliable repetition effect at frontal electrode sites is also reflected in the unexpected patterns in ERP results. Single-trial mean amplitudes were extracted in this parietal cluster and repetition-related amplitude enhancements were calculated for each consecutive presentation pair of each stimulus. As in Chapter 3, a control enhancement value was computed by calculating the repetition enhancement for each stimulus but this time using the trial that occurred immediately before the item repetition. When comparing item-specific and control enhancement values, it was found that only the difference between first and second presentation over parietal electrode sites was related to stimulus-specific repetition. However, this was only found in the same task condition and did not extend to the different encoding task condition. This generally indicates that repetition effects may occur independently of encoding modality, as shown in Chapter 3, but are dependant on encoding context (same vs different). Moreover, overall (i.e., averaged over all presentation pairs) positivity enhancement was shown to differ from the control enhancement and overall enhancement in subsequent hits+ judgements was found to differ from the control value. This indicates that positivity enhancement in the same task condition and positivity enhancement in subsequent hits+ judgements indexed item-specific repetition. These results are partly in line with the results from Chapter 3, i.e., item-specific repetition occurred between presentations 1 and 2, when participants repeatedly performed the same task. However, it further extends those results to all presentation pairs in the same encoding task condition and in subsequent hits+ judgements. One possibility for these discrepancies is that the repetition effect in Chapter 3 occurred earlier than the subsequent source memory effect, whereas in the present experiment, the timing of repetition and explicit memory effects overlap more. These results encouraged direct comparisons of subsequent source memory performance as well as the two encoding task conditions. Those comparisons showed that item-specific positivity enhancement was higher for the same than the different encoding task condition between presentations 1 and 2. Moreover, subsequent hits+ judgements were overall found to be associated with larger item-specific positivity enhancements across this parietal cluster than subsequent hits- judgements. Taken together, these results suggest that single-trial positivity enhancement is only related to item-repetition in the same encoding task condition, providing further support that the neural mechanisms underlying same and different task encoding differ. Moreover, subsequent source memory performance could be predicted based on single-trial repetition enhancement occurring in a similar time window and electrode sites as the LPC, typically measured at test. This results is somewhat reminiscent of previous ERP research, showing that a repetition-related increase in positivity over parietal electrode sites further correlated with subsequent memory performance (Griffin et al., 2013; Groh-Bordin et al., 2007; Olichney et al., 2000). The authors suggested this increase to index increases in memory strength (Groh-Bordin et al., 2006; Van Strien et al., 2005), which is consistent with the proposed behavioural benefits of repeated encoding (e.g., Crowder, 1976; Glenberg et al., 1977; Opitz, 2010) and the LPC's association with episodic memory. Additionally, item-specific amplitude enhancements across repetitions were found to be related to decreases in RTs across item-repetitions, as demonstrated in Chapter 3 and previous fMRI research (van den Honert et al., 2016; Ward et al., 2013).

Overall, the two encoding task conditions were associated with differences in memory performance as well as with distinct ERP correlates. The behavioural data provides strong support for the hypothesis that repeated encoding across different contexts improves item memory at the cost of context memory. ERP analyses revealed distinct repetition effects for same and different task encoding. Although patterns for the FN400 were less clear, LPC amplitudes were shown to be sensitive to repetition in both encoding task conditions. LPC waveforms to different task encoding reflected a more gradual increase in mean amplitudes, while the repetitions in the same task were particularly sensitive to a novelty effect between presentation 1 and 2. Furthermore, item-specific parietal repetition enhancement effects were found to only be reliable in the same encoding task condition. Interestingly, these item-specific repetition-related increases were also shown to predict subsequent source memory in the time window and electrode sites typically associated with an

LPC when measured at test. Finally, further evidence was provided for the LPC at test to be modulated by information from the study phase, possibly reflecting reinstatement effects.

Chapter 6 – Encoding context, repetition and memory (fMRI)

6.1 Introduction

The present fMRI experiment is concerned with similar questions as the EEG experiment presented in Chapter 5. From behavioural theories and data, it was hypothesised that repeated stimulus encoding in same and different context encoding conditions are associated with dissociable underlying mechanisms. It was proposed that repeatedly encoding a stimulus in the same context was associated with reactivation of the same item and context, thereby strengthening the memory. This proposal is largely in line with the reactivation view (Benjamin & Tullis, 2010; Thios & D'Agostino, 1976) and a large body of literature corroborating the notion that neural reactivation is associated with superior subsequent memory performance (e.g., Levy & Wagner, 2013; Staresina, Alink, Kriegeskorte, & Henson, 2013; van den Honert et al., 2016; Xue et al., 2010). However, comparatively little is known about the mechanisms supporting memory formation when stimuli are repeatedly encoded in different contexts. The encoding variability view and multiple trace theory (Hintzman, 1986; Hintzman & Block, 1971; Nadel & Moscovitch, 1997) suggest that item memory is strengthened by creating unique traces for each stimulus presentation, leading to a larger variety in retrieval cues. Retroactive interference paradigms have generally shown that source memory is worsened when stimuli are repeatedly presented in different contexts (Anderson & Neely, 1996; Hupbach et al., 2007; Kim et al., 2017; McGovern, 1964). However, that sheds little light on mechanisms involved when the different contexts are successfully encoded. Therefore, it was predicted that different neural mechanisms underlie memory encoding in a different encoding task condition. It was suggested that either reactivation occurs, which is associated with worse context memory, or that multiple traces are created facilitating superior context memory. Subsequent source memory performance can then be predicted based on the cognitive and neural operations involved during different context encoding. Questions regarding the underlying degree of reactivation can be directly assessed by using RSA to compute pattern similarity as an index of reactivation.

Mass-univariate fMRI investigations

Similar to ERP research, fMRI research has established dissociable correlates of semantic and non-semantic encoding (e.g., Fletcher et al., 2003; Otten & Rugg, 2001b). In the study by Fletcher and colleagues (2003), semantic encoding, relative to non-semantic encoding, was shown to be associated with greater mean activation in left lateral PFC as well as left MTL. Non-semantic encoding, on the other hand, was associated with greater activity in right medial PFC. Another experiment reported non-semantic, successful encoding during a syllable judgement task to be associated with higher activations in bilateral intraparietal sulcus and fusiform gyrus as well as right PFC and left occipital gyrus (Otten & Rugg, 2001b). These examples illustrate that activation predicting subsequent memory performance is further influenced by the encoding task. More specifically, mean activation is influenced by whether a semantic or a non-semantic encoding task is employed, as signaled by activation in different brain networks predicting later memory. These findings have also been extended to subsequent source memory contrasts, with task-independent subsequent source memory effects in ventral extrastriate visual cortex while task-dependent effects showed a double-dissociation within posterior regions (Park, Uncapher, & Rugg, 2008). Namely, the semantic animacy task was associated with subsequent source memory effects in left middle occipital and fusiform gyri, left cuneus and right superior temporal gyrus. The non-semantic syllable judgement task, on the other hand, was found to show subsequent source memory effect in right inferior occipital and temporal gyri (Park et al., 2008). However, rather than comparing two different classes of encoding tasks, to the author's knowledge, no univariate fMRI investigations have examined the effects of repeatedly encoding stimuli in the same or different semantic encoding tasks. The paucity of such research may partly be explained by the notion that questions regarding reactivation may be more appropriately assessed by investigating distributed neural patterns, i.e., employing multivariate approaches, rather than examinations of mean activation (see Rissman & Wagner, 2012). However, given the relative novelty of the present experimental paradigm, differences in mean activation between the two encoding task conditions as well as underlying repetition-related changes might provide additional insights into same and different context encoding. The EEG results presented in chapter 5 indicated interactions between encoding condition and repetition, which was interpreted as reflecting distinct mechanisms underlying stimulus encoding in the two conditions. From the EEG and fMRI results relating to encoding modality (chapter 3 and 4), it was speculated that EEG repetition effects are more likely to reflect repetition suppression than enhancement, because, like repetition suppression, they did not predict subsequent source memory performance. However, the EEG repetition effects in chapter 5 did predict subsequent source memory performance. LPC amplitudes enhancement across repetitions was stronger for subsequent hits+ than hits- judgements. Therefore, it may be hypothesised that fMRI repetition suppression predicts subsequent source memory outcome in this particular design.

Representation Similarity Analysis

Evidence from studies investigating pattern similarity across repeated encoding in different contexts has resulted in mixed support of the reactivation view and the multiple trace theory, with the majority of studies, however, demonstrating evidence for reactivation. For example, it was demonstrated that pattern similarity for items, which were repeated in different contexts, correlated with subsequent recognition memory performance (Lohnas & Davachi, 2017). Higher similarity in right dorsolateral PFC, right fusiform gyrus, right anterior hippocampus and posterior medial cortex was associated with higher hit rates during the test phase. Moreover, for subsequently recognised stimuli, repeated in the different task condition, pattern similarity in these regions was higher compared to stimuli, which were repeated in a same task condition. This finding also extended to bilateral perirhinal regions, although there was no correlation with hit rates observed here. Importantly, while these results provide valuable insights into same and different task encoding, the authors did not contrast hits and misses or different states of remembering, i.e., source memory outcome or remembering and knowing. In a similar experiment, participants encoded items in different encoding contexts (Do et al., 2016). Items were sorted according to subsequent memory performance, which corresponded to correct source, when participants were able to recollect both tasks that were performed during encoding, partially forgotten, i.e., participants remembered studying the item but could only recollect one task, and completely forgotten, when items were judged as new. Subsequent correct source judgements were then compared to the other two memory conditions. Higher pattern similarity was reported for subsequent recollection in left inferior parietal lobule, bilateral dorsolateral occipital cortex and right fusiform gyrus. The authors suggested that those findings reflected reactivation of memory representations that was not influenced by the context variability between the encoding episodes. Contrary to predictions based on the reactivation hypothesis, a study employing a retroactive interference paradigm reported higher pattern similarity between item repetitions in lateral occipital cortex to be associated with worse source memory for the task the items were encoded in (Kim et al., 2017). It was suggested that reactivation of items occurring in different contexts, as reflected in higher pattern similarity in lateral occipital cortex, impairs subsequent context memory. Although not discussed by the authors, the results observed in the lateral occipital cortex may suggest that another process, such as multiple traces for multiple encoding episodes, is related to subsequent correct context memory. Taken together, these results indicated that different task encoding might be associated with reactivation. However, none of the previous studies has directly compared subsequent hits+ and hits- judgements within a same task condition and a different task condition.

Moreover, to the author's knowledge, no previous research has addressed differences in same and different task encoding in the context of encoding-retrieval similarity, i.e., reinstatement. Univariate investigations have shown that successful recollection of items that were initially studied in different encoding tasks relied on the core recollection network irrespective of the encoding that was previously performed (Johnson, Suzuki, & Rugg, 2013). In addition to that, task-dependent reinstatement effects were observed outside of this recollection network and were shown to overlap with task-dependent mean activation measured during the study phase. These results suggest that both, content-independent recollection and content-specific reinstatement operate to facilitate successful episodic retrieval (Johnson et al., 2013). However, as previously emphasised, measures of mean activation are less suitable than RSA for investigations of reactivation and reinstatement. Showing overlaps in mean activation between study and test does not extend to idiosyncratic patterns representing single items and is typically regarded a less sensitive measure compared to similarity patterns (Jimura & Poldrack, 2012).

The present fMRI experiment employed the same experimental design as the EEG experiment presented in Chapter 5, with slight modifications due to practical constraints, including a slightly lower number of stimuli included and omitting the distractor task. A subsequent memory paradigm was used with four spaced repetitions of each stimulus, followed by a surprise source-recognition task. Participants studied each stimulus four times. Stimuli were studied in one of two encoding context conditions: repeatedly performing the same encoding task (referred to in-text as *same context* or *same encoding task condition*) or performing a different encoding task at each presentation of the stimulus (referred to in-text as *different context* or *different encoding task condition*). At test, participants made item memory judgements (old/new), followed by source memory judgements relating to encoding context (‘*which encoding task?*’). The present experimental procedure was primarily designed to address differences in similarity patterns relating source memory effects when stimuli are either repeated in the same context or repeated in differing contexts. Behavioural results are expected to replicate the findings presented in Chapter 5, i.e., same relative to different context encoding is hypothesised to be associated with more hits+ judgements but fewer hits- judgements (more item misses). Due to the relative novelty of the present experimental design, mass-univariate whole-brain analyses are performed investigating mean activation in the two encoding task conditions. Additionally, the univariate analyses are concerned with repetition-related changes in same and different context encoding and whether these changes predict subsequent source memory performance. RSA is predicted to reveal distinct source memory effects for the two encoding task conditions. Based on the theoretical hypothesis proposed in Chapter 5 and reiterated here, an interaction between encoding task condition and subsequent source memory would be expected. In the same encoding task condition, the degree of reactivation is predicted to be higher for subsequent hits+ than hits- judgements. In the different encoding task condition, on the other hand, higher levels of reactivation are hypothesised to imply more generalisation across contexts and therefore be associated with subsequent hits- judgements. Analogous patterns of results are predicted for ERS patterns, in that the retrieval of a single context relies on reactivation/reinstatement of study phase information, whereas the retrieval of multiple contexts relies on more complex reinstatement processes. Due to conflicting results reported in the very few studies investigating questions regarding same and different context encoding, no region-specific hypotheses were made. Instead, ROI analyses were conducted in previously selected regions (see Table 6.19), followed by whole-brain searchlight analyses.

6.2 Method

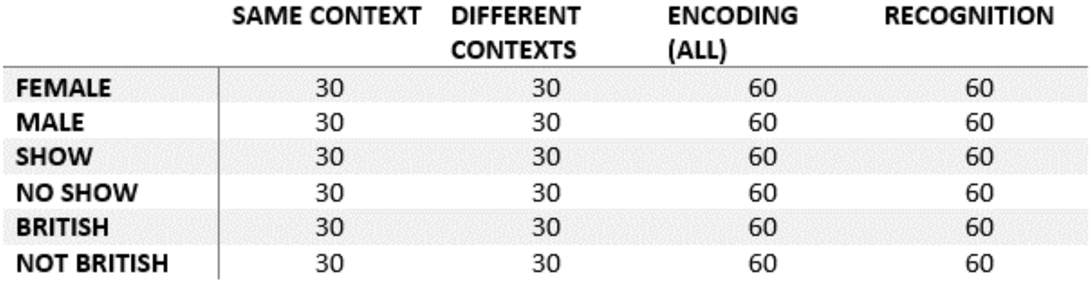
6.2.1 Participants

Twenty British healthy adult volunteers (12 females) were recruited. Participants were aged 18 to 36 years old (M_{age} = 24 ±6), with an average of 16 ±3 years of education. Data of one participant were excluded due to technical faults during scanning and data from another two participants were excluded due to excessive movement during the scan, resulting in *N* = 17 (10 females).

6.2.2 Materials

Stimuli were a subset of 240 stimuli chosen from the 288 names of famous people (e.g., Keith Richards, Michelle Obama) used in the EEG version of this experiment. Famous names were matched across all tasks and conditions in accordance with the four encoding tasks (gender, currently active in show business or not, British or not; see Table 6.15). During the study phase, half of the stimuli were repeatedly presented as written words in white Courier New 36 font, in the centre of a black background.

Table 6.15. *Experiment 4 (fMRI): Number of stimuli per condition, referring to males/females, currently active in show business/not active, British/not British in the two encoding conditions (same/different context) and across study and test phase.*



	SAME CONTEXT	DIFFERENT CONTEXTS	ENCODING (ALL)	RECOGNITION
FEMALE	30	30	60	60
MALE	30	30	60	60
SHOW	30	30	60	60
NO SHOW	30	30	60	60
BRITISH	30	30	60	60
NOT BRITISH	30	30	60	60

6.2.3 Task & procedure

In the study phase, participants performed four different categorisation tasks. At the beginning of each block, they were presented with a question they had to answer about the famous names. The four questions were “Is this person female?”, “Is this person currently active in show business?”, “Is this person British?” and “Do you like this person?”. Task order was pseudo-randomised across participants. Participants were encouraged to guess the answer in cases where they were not familiar with the famous name or when they did not know the answer. Participants were instructed to press one of two buttons corresponding to whether their answer to the question was “yes” or “no”. During the encoding phase, each stimulus was presented four times. Half of the stimuli were presented once in each of the four tasks (*different context*), the other half was presented repeatedly within only one of the four encoding tasks (*same context*). With four repetitions per stimulus this resulted in a total of 480 encoding trials in the fMRI experiment. The average inter-trial interval (ITI) was 4100 ms. The experimental procedure is illustrated in Figure 6.29. At the end of the encoding phase, participants had a short break during which they could rest their eyes.

During the test phase, participants performed an unexpected recognition-source memory test. In this task, all old stimuli from the encoding phase were presented along with the remaining set of new stimuli. Both lists were matched in terms of gender, whether famous people were currently active in show business or not and whether they were British or not. All stimuli were presented as white written words in Courier New 36 font on black background. Participants gave an old/new response depending on whether or not they thought the name had been presented during the encoding stage. Participants were presented with a name and instructed to indicate whether this name had been presented in any of the previous tasks by pressing one of four buttons on the response pad corresponding to the following responses: “definitely old”, “perhaps old”, “perhaps new”, and “definitely new”. “Old” responses were followed by a source memory question asking participants in which task the famous name had previously been categorised with the response options “all four tasks”, “gender task”, “show business task”, “British task”, “like task” and “I don’t know”. Stimuli were presented for 1500 ms, followed by a fixation cross for 1000 ms. Depending on the participants’ old/new response, either a fixation cross or the source memory question appeared for 1500 ms. Another fixation cross of random duration (800 – 1200 ms, average ITI= 5000 ms) then indicated the beginning of the next trial.

Once participants had completed the recognition task, they filled in a personal memories questionnaire. As for the EEG version of this experimental design, data form this questionnaire were not included in any subsequent analyses, as the relevance of those data went beyond the scope of the present research.

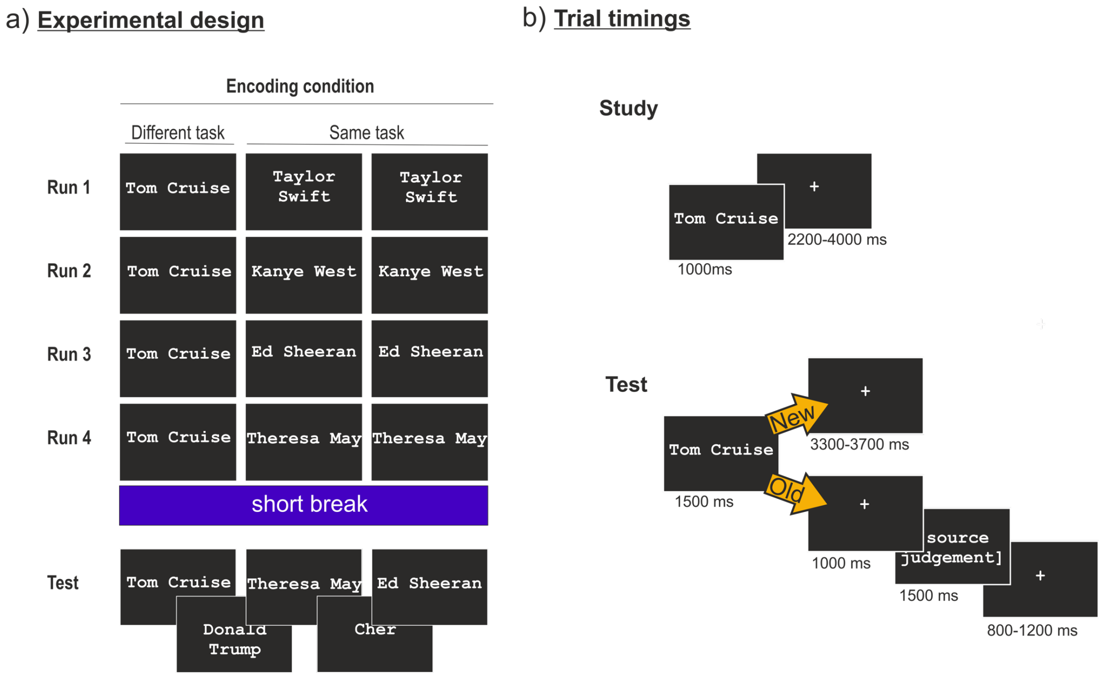


Figure 6.29. Experiment 4 (fMRI): a) The experimental paradigm with four encoding presentations of each stimulus during the study phase; participants encoded half of the stimuli in a different task condition, i.e., performing a different task at each presentation of the stimulus, the other half were encoded in a same task condition, i.e., participants repeatedly performed the same semantic encoding task; in a test phase, participants made old/new judgements followed by source judgements; b) trial timings.

6.3 Results

The repeated-measures design included three factors of interest at study and two at test: subsequent memory (hits+, hits-; behavioural analyses also include misses), repetition (presentation 1,2,3,4; only at study) and encoding context (different, same). Hits+ trials included all correct item and correct source memory judgements irrespective of confidence ratings. Hits- trials were characterised as old/new hits followed by an incorrect source memory response or no response, indicating the source could not be retrieved. Participants' responses to the item memory question indicated that they were more often highly confident of their response ($M_{\%HC} = 95 \pm 5$) than responding with low confidence ($M_{\%LC} = 5 \pm 5$), $t_{16} = 38.392$, $p < .001$. Therefore, confidence judgements were not included in any of the analyses.

6.3.1 Behavioural results

6.3.1.1 Reaction times at study

RTs during the encoding phase were analysed in a 3 x 2 x 4 repeated-measures ANOVA with the factors memory performance (hits+, hits-, misses), encoding condition (same task, different task) and presentation (1, 2, 3, 4). No differences in RTs were found that related to subsequent memory performance. The ANOVA revealed main effects of encoding context, $F_{1,13} = 44.333$, $p < .001$, and presentation, $F_{3,39} = 4.348$, $p = .010$. Follow-up analyses revealed that RTs were faster to stimuli encoded in the same context compared to those encoded in different contexts (see Figure 6.30). RTs were also found to overall decrease across presentations, but this difference was only statistically significant between presentation 1 and 3 ($p = .049$). Although the interaction between presentation and encoding context was statistically non-significant after Greenhouse-Geisser correction for sphericity violations, $p = .062$, the reaction times displayed in Figure 6.30 indicate that repetition priming only occurred in the same encoding task condition.

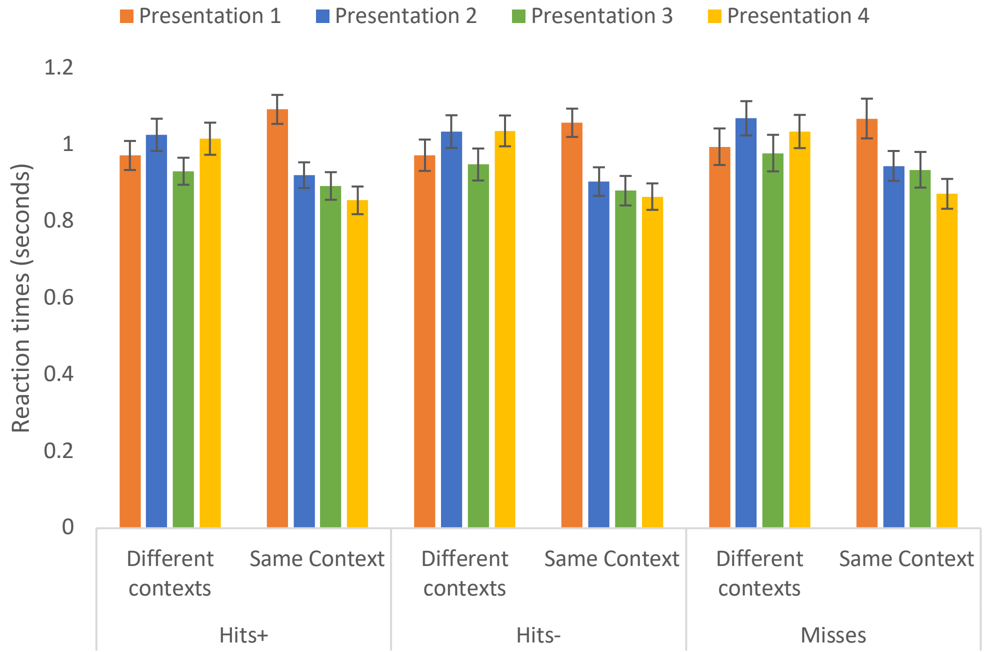
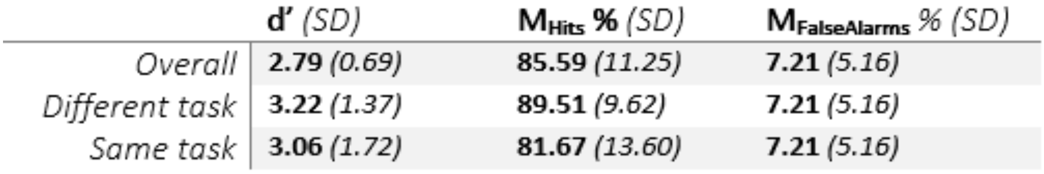


Figure 6.30. Reaction times (in seconds) in experiment 4 (fMRI) for all four presentations during the study phase, separately for subsequent memory performance and encoding contexts. Error bars denote standard error.

6.3.1.2 Discriminability analysis

Discriminability scores were calculated and normalised probabilities of overall hits and false alarms were compared in a paired-samples t-test. The t-test showed that participants' performance in the recognition memory task was above chance, $t_{16} = 17.180$, $p < .001$. Mean and standard deviations of *d'* scores and percentages of hits and false alarms are displayed in Table 6.16. Those individual *d'* scores indicate that recognition memory performance was higher in the different encoding task condition.

Table 6.16. Experiment 4 (fMRI): *The mean d' scores and mean % of Hits and False Alarms with standard deviations (in brackets) for overall memory performance and across the three modality conditions, picture only, word only and picture&word.*



	d' *(SD)*	**M_{Hits} %** *(SD)*	**$M_{FalseAlarms}$** *% (SD)*
Overall	**2.79** *(0.69)*	**85.59** *(11.25)*	**7.21** *(5.16)*
Different task	**3.22** *(1.37)*	**89.51** *(9.62)*	**7.21** *(5.16)*
Same task	**3.06** *(1.72)*	**81.67** *(13.60)*	**7.21** *(5.16)*

6.3.1.3 Behavioural performance at test

Frequencies of hits+, hits- and misses (memory performance) were analysed in terms of encoding task condition (same, different) in a 3 x 2 repeated-measures ANOVA. Descriptive statistics are displayed in Figure 6.31. The ANOVA revealed a main effect of memory, $F_{2,32} = 33.543$, $p < .001$ and an interaction between memory performance and encoding context, $F_{2,32} = 3.602$, $p = .039$. A post-hoc test revealed that all three levels of memory performance differed from each other in terms of frequencies, all $p < .015$. The majority of responses resulted in hits- judgements (correct item memory, incorrect source memory), fewer responses resulted in hits+ judgements (correct item and correct source memory) and the least responses resulted in misses. Following up on the interaction between memory performance and encoding context showed that encoding under the different encoding task condition was associated with more hits- judgements than the same encoding task condition, $p = .038$. The same encoding task condition was associated with more misses than the different encoding task condition, $p < .001$.

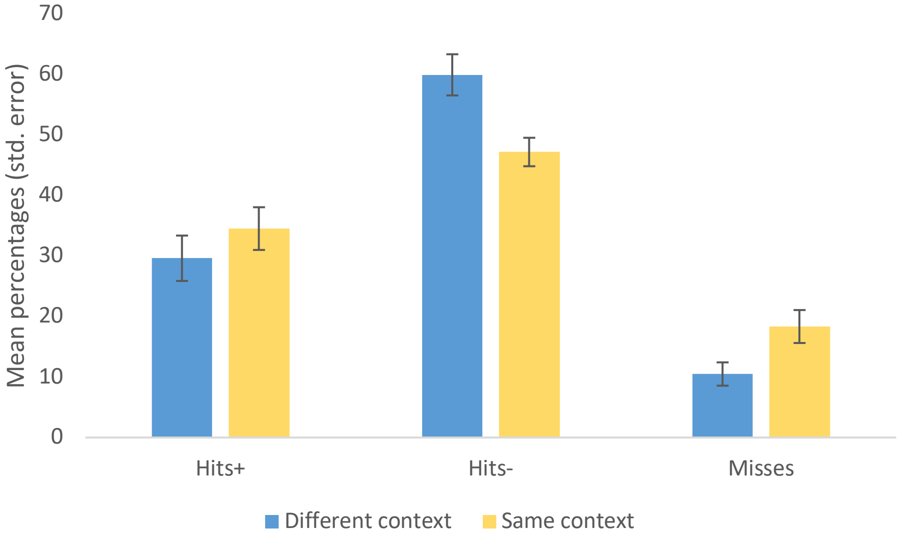


Figure 6.31. The mean percentages and standard error of the three levels of memory performance (hits+, hits-, misses) and encoding context (different, same).

6.3.1.4 Reaction times at test

RTs measures during the test phase were analysed in two separate repeated-measures ANOVAs. First, RTs to the item memory (old/new) task were examined in a 3 x 2 ANOVA with the factors memory performance and encoding task condition. In a second analysis, RTs to the source memory task were analysed. In this 2 x 2 repeated-measures ANOVA, the factors were memory performance (only two levels because misses were not followed up with a source memory question) and encoding task condition.

The ANOVA analysing item memory RTs revealed no significant main effects or interactions. However, to follow-up the RT results from the EEG experiment presented in Chapter 5, two trends were observed for RTs to be faster to stimuli encoded in the different task condition than the same task condition, $p = .077$, and for RTs to hits+ judgements to be faster than to hits- judgements, $p = .094$.

The ANOVA analysing RTs to the source memory question revealed a main effect of source memory performance, $F_{1,16} = 18.484$, $p = .001$. Correct source responses were given faster than incorrect source responses. Additionally, a trend was revealed for RTs to stimuli encoded in the same task condition to be faster than RTs to stimuli encoded in the different task condition, $F_{1,16} = 4.142$, $p = .059$.

6.3.2 fMRI mass-univariate analysis

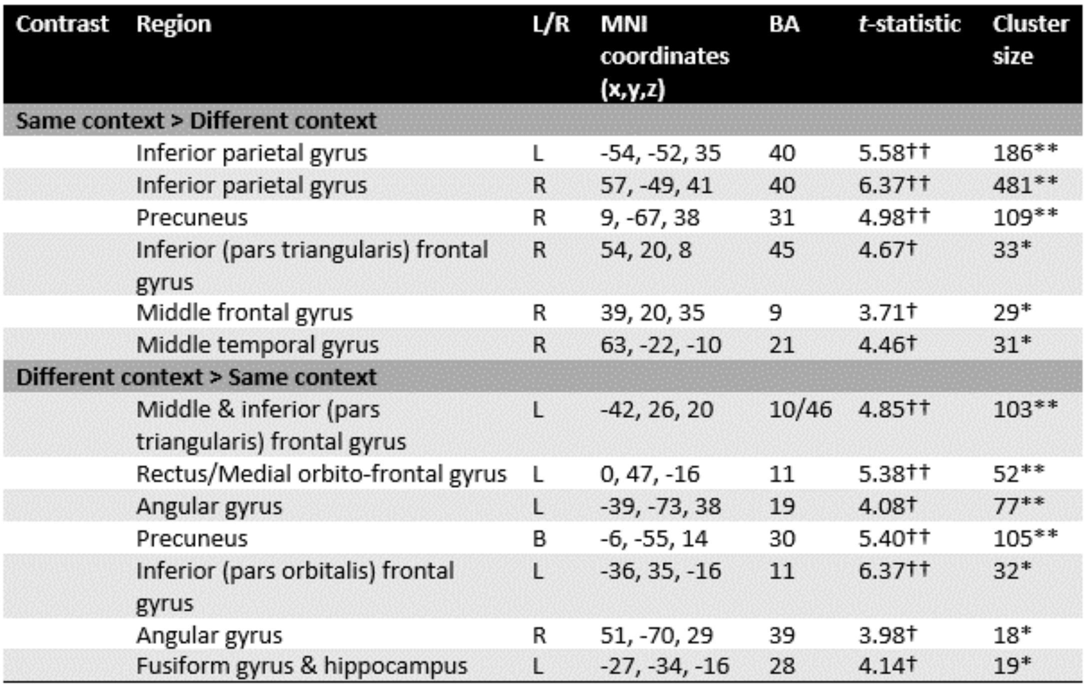
One GLM was constructed with 16 regressors of interest modelling the effects of source memory (hits+, hits-), presentation (1,2,3,4) and encoding context (different, same) during the study phase. A nuisance regressor modelled all trials, which were not included in the analyses, i.e., subsequent misses. Two sets of whole-brain investigations were carried out. The first analysis was concerned with effects of encoding task condition irrespective of repetition and subsequent source memory performance. The second set of analyses examined repetition-related changes in mean activation for the two encoding task conditions separately and whether such changes interacted with subsequent source memory performance.

6.3.2.1 Effects of encoding task condition

Because of the novelty of the present experimental design, differences between the same and different context encoding conditions during the study phase were examined irrespective of subsequent source memory performance and repetition in a first instance. Two whole-brain t-contrasts modelled these differences to identify brain regions in which mean activation was either higher for the same encoding task condition than the different encoding task condition or vice versa.

The results form those two t-contrasts are presented in Table 6.17. Encoding stimuli repeatedly in the same context compared to different contexts was associated with higher mean activation in bilateral inferior parietal gyri and right precueneus. Additional trends in the same direction were observed in right inferior and middle frontal gyri and the middle temporal gyrus, however, these clusters did not survive FWE-corrections. Different context encoding, on the other hand, was found to be associated with higher levels of mean activation in left frontal regions, including inferior, middle and orbito-frontal gyri, and bilateral precuneus compared to same context encoding. Additional trends in the same direction were reported in the right angular gyrus and left medial temporal lobe, including the fusiform gyrus extending into the hippocampus, but did not survive multiple comparison corrections.

Table 6.17. *Mass-univariate study phase analyses (experiment 4, fMRI), contrasting the two encoding task conditions, same and different context encoding, averaged over subsequent hits+ and hits- judgements and over presentations.*



Contrast	Region	L/R	MNI coordinates (x,y,z)	BA	*t*-statistic	Cluster size
Same context > Different context						
	Inferior parietal gyrus	L	-54, -52, 35	40	5.58††	186**
	Inferior parietal gyrus	R	57, -49, 41	40	6.37††	481**
	Precuneus	R	9, -67, 38	31	4.98††	109**
	Inferior (pars triangularis) frontal gyrus	R	54, 20, 8	45	4.67†	33*
	Middle frontal gyrus	R	39, 20, 35	9	3.71†	29*
	Middle temporal gyrus	R	63, -22, -10	21	4.46†	31*
Different context > Same context						
	Middle & inferior (pars triangularis) frontal gyrus	L	-42, 26, 20	10/46	4.85††	103**
	Rectus/Medial orbito-frontal gyrus	L	0, 47, -16	11	5.38††	52**
	Angular gyrus	L	-39, -73, 38	19	4.08†	77**
	Precuneus	B	-6, -55, 14	30	5.40††	105**
	Inferior (pars orbitalis) frontal gyrus	L	-36, 35, -16	11	6.37††	32*
	Angular gyrus	R	51, -70, 29	39	3.98†	18*
	Fusiform gyrus & hippocampus	L	-27, -34, -16	28	4.14†	19*

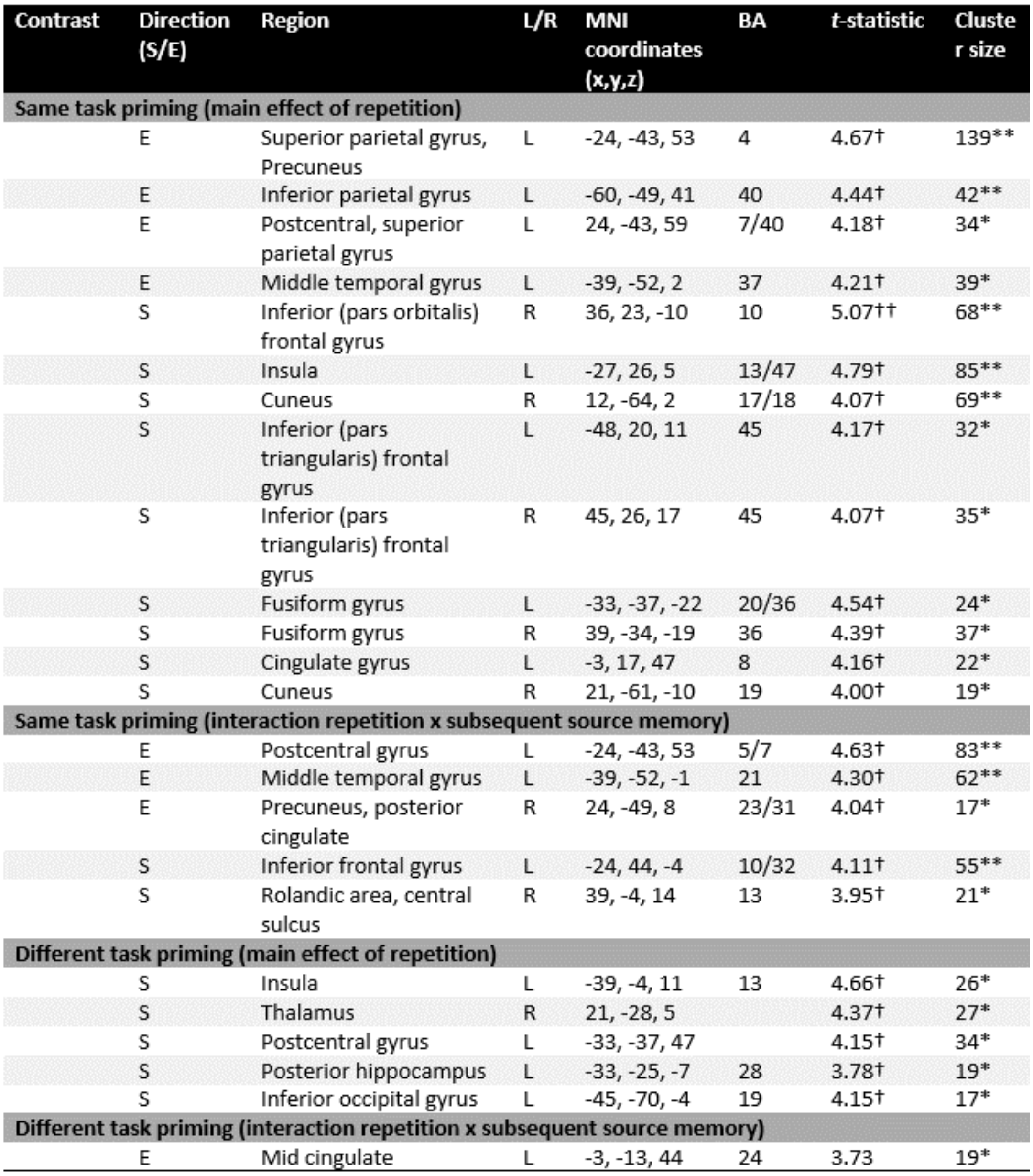
Note. L = left, R = right, B = bilateral, BA = approximate Brodmann Area. MNI coordinates refer to peak voxel coordinates.
* $p_{cluster} < 0.05$ (uncorrected)
** $p_{cluster} < 0.05$ (*FWE*-corrected)
† $p_{peak} < 0.001$ (uncorrected)
†† $p_{peak} < 0.05$ (*FWE*-corrected)

6.3.2.2 Study phase repetition effects

In addition to effects of encoding task condition, the present mass-univariate analyses were concerned with repetition suppression and enhancement effects in the two encoding task conditions and how these related to subsequent source memory performance. To investigate these effects, eight whole-brain t-contrasts were created at a 2nd-level analysis. Similar to Chapter 4, repetition was modelled as a linear change (Grill-Spector & Malach, 2001; Henson et al., 2000; Sayres & Grill-Spector, 2006; Suzuki et al., 2011; Vannini et al., 2013). Four t-contrasts assessed whether repetition suppression and/or enhancement effects were observed in either of the two encoding task conditions. Further t-contrasts modelled differences in repetition-related changes due to subsequent source memory performance.

As outlined in Table 6.18, the majority of repetition-related effects, i.e., repetition suppression and enhancement, were observed in the same encoding task condition. Repetition enhancement effects were found in the left hemisphere in superior and inferior parietal gyri and the precuneus along with trends in the postcentral and middle temporal gyri. Repetition suppression effects relating to same context encoding were reported in the right pars opercularis division of the inferior frontal gyrus, left insula and right cuneus. Additional trends of repetition suppression were observed in bilateral pars triangularis divisions of the inferior frontal gyrus, bilateral fusiform gyri and left cingulate gyrus. Moreover, within the same encoding task condition, subsequent hits+ compared to hits- judgements were associated with more repetition enhancement in left postcentral and middle temporal gyri and right precueneus/posterior cingulate, though the latter effect was only a trend that did not survive corrections for multiple comparisons. On the other hand, subsequent hits+ compared to hits- judgements within same context encoding were also associated with higher repetition suppression in the left inferior frontal gyrus and a similar trend in the right central sulcus. Repetition-related changes in the different encoding task condition did not survive FWE-corrections, however, a number of trends were observed. Stimuli encoded in different contexts were associated with decreases in mean activation, i.e., repetition suppression, in left insula, right thalamus, left postcentral and inferior occipital gyri and in the posterior hippocampus. While no main effects of repetition enhancement were found in the different context encoding condition, a trend indicated repetition enhancement to be higher for subsequent hits+ compared to hits- judgements in the left mid cingulate cortex.

Table 6.18. Mass-univariate results from experiment 4 (fMRI) illustrating regions that show encoding-context specific repetitions effects and interactions between repetition-related changes and subsequent source memory performance, measured during the study phase.



Contrast	Direction (S/E)	Region	L/R	MNI coordinates (x,y,z)	BA	*t*-statistic	Cluster size
Same task priming (main effect of repetition)							
	E	Superior parietal gyrus, Precuneus	L	-24, -43, 53	4	4.67†	139**
	E	Inferior parietal gyrus	L	-60, -49, 41	40	4.44†	42**
	E	Postcentral, superior parietal gyrus	L	24, -43, 59	7/40	4.18†	34*
	E	Middle temporal gyrus	L	-39, -52, 2	37	4.21†	39*
	S	Inferior (pars orbitalis) frontal gyrus	R	36, 23, -10	10	5.07††	68**
	S	Insula	L	-27, 26, 5	13/47	4.79†	85**
	S	Cuneus	R	12, -64, 2	17/18	4.07†	69**
	S	Inferior (pars triangularis) frontal gyrus	L	-48, 20, 11	45	4.17†	32*
	S	Inferior (pars triangularis) frontal gyrus	R	45, 26, 17	45	4.07†	35*
	S	Fusiform gyrus	L	-33, -37, -22	20/36	4.54†	24*
	S	Fusiform gyrus	R	39, -34, -19	36	4.39†	37*
	S	Cingulate gyrus	L	-3, 17, 47	8	4.16†	22*
	S	Cuneus	R	21, -61, -10	19	4.00†	19*
Same task priming (interaction repetition x subsequent source memory)							
	E	Postcentral gyrus	L	-24, -43, 53	5/7	4.63†	83**
	E	Middle temporal gyrus	L	-39, -52, -1	21	4.30†	62**
	E	Precuneus, posterior cingulate	R	24, -49, 8	23/31	4.04†	17*
	S	Inferior frontal gyrus	L	-24, 44, -4	10/32	4.11†	55**
	S	Rolandic area, central sulcus	R	39, -4, 14	13	3.95†	21*
Different task priming (main effect of repetition)							
	S	Insula	L	-39, -4, 11	13	4.66†	26*
	S	Thalamus	R	21, -28, 5		4.37†	27*
	S	Postcentral gyrus	L	-33, -37, 47		4.15†	34*
	S	Posterior hippocampus	L	-33, -25, -7	28	3.78†	19*
	S	Inferior occipital gyrus	L	-45, -70, -4	19	4.15†	17*
Different task priming (interaction repetition x subsequent source memory)							
	E	Mid cingulate	L	-3, -13, 44	24	3.73	19*

Note. L = left, R = right, B = bilateral, BA = approximate Brodmann Area. MNI coordinates refer to peak voxel coordinates.
* $p_{cluster} < 0.05$ (uncorrected)
** $p_{cluster} < 0.05$ (*FWE*-corrected)
† $p_{peak} < 0.001$ (uncorrected)
†† $p_{peak} < 0.05$ (*FWE*-corrected)

6.3.3 Representational similarity analysis

Pattern similarity was calculated for encoding similarity across repeated study episodes (encoding similarity) and for encoding-retrieval similarity (ERS). In Chapter 4, encoding similarity was computed only between consecutive presentation pairs, because of the alternating nature of the picture&word modality condition. In the present investigation, encoding similarity was computed between all possible encoding presentation pairs, i.e., Presentations 1 & 2, Presentations 1 & 3, Presentations 1 & 4, Presentations 2 & 3, Presentations 2 & 4 and Presentations 3 & 4 (see Figure 6.32). ERS patterns were calculated between each encoding presentation and the retrieval presentation. This resulted in six encoding similarity indices that were averaged and four ERS indices, which were also averaged.

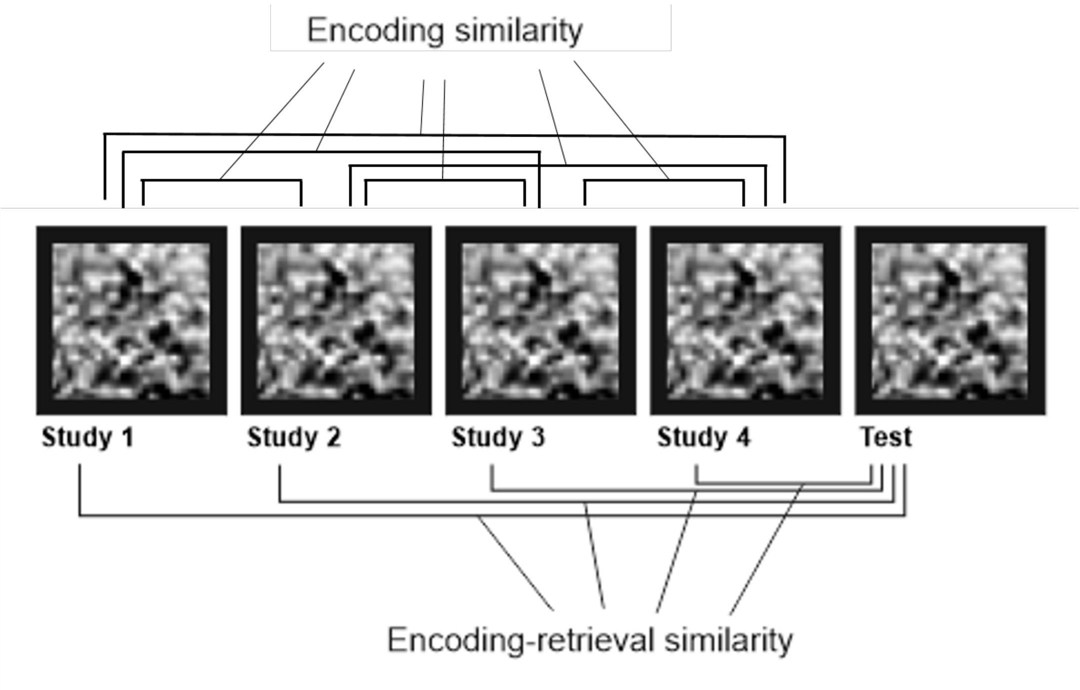
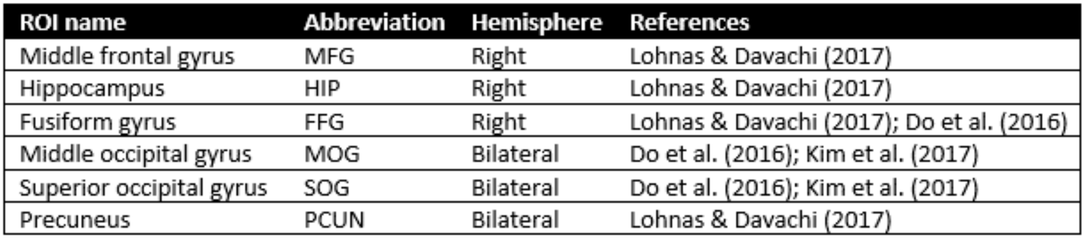


Figure 6.32. Encoding similarity and encoding-retrieval similarity (ERS) in experiment 4 were computed by correlating beta values from the specified presentation pairs.

Six ROIs were chosen from the AAL atlas (Tzourio-Mazoyer et al., 2002) based on previous research addressing similar research questions (see Table 6.19 for information on ROIs and justification for inclusion). ROI analyses were followed up with whole-brain searchlight analyses.

Table 6.19. *Regions of interest for the representational similarity analyses performed on data from experiment 4 (fMRI), detailing subsequently used abbreviations, included hemisphere and references for inclusion.*



ROI name	Abbreviation	Hemisphere	References
Middle frontal gyrus	MFG	Right	Lohnas & Davachi (2017)
Hippocampus	HIP	Right	Lohnas & Davachi (2017)
Fusiform gyrus	FFG	Right	Lohnas & Davachi (2017); Do et al. (2016)
Middle occipital gyrus	MOG	Bilateral	Do et al. (2016); Kim et al. (2017)
Superior occipital gyrus	SOG	Bilateral	Do et al. (2016); Kim et al. (2017)
Precuneus	PCUN	Bilateral	Lohnas & Davachi (2017)

Separate encoding similarity and ERS indices were computed for each of the four conditions (illustrated in Figure 6.33). As already addressed in Chapter 5, the present experimental design was associated with a methodological confound in that repetitions in the same context were always associated with shorter repetition lags than repetitions in different contexts. Precisely, in this fMRI investigation, same task repetitions occurred within the same runs, whereas different task repetitions occurred between runs. This meant that encoding similarity patterns for same and different task encoding could not be contrasted, as between-run similarity would be associated with more variability and, therefore, lower similarity scores than within-run similarity. However, bearing in mind that due to this confound similarity patterns will be lower in the different task condition than the same task condition, this confound does not affect differences in pattern similarity due to source memory performance within the encoding task conditions. Moreover, this confound will also not affect the interaction between source memory performance and encoding task condition. Such an interaction directly tests the hypothesis that in the same task condition, hits+ judgements are associated with more reactivation than hits- judgements; while in the different task condition, hits- judgements are associated with higher levels of reactivation than hits+ judgements. Therefore, encoding similarity and ERS patterns were analysed for source memory effects, separately in the two encoding task conditions, as well as for the interaction between encoding task condition and source memory performance. The source memory effects were assessed separately for same and different task encoding performing paired samples t-tests. The interaction was tested with a repeated-measures ANOVA with the factors source memory (hits+, hits-) and encoding context (same, different). Resulting *t*-statistics for source memory contrasts and *F*-statistics for the interactions as well as significance levels (uncorrected and *FDR*-corrected for the six ROIs) are reported.

In Chapter 4, two different measures of similarity were reported: item-level and item-specific similarity. This was to test the hypothesis that item-specific pictorial information would be reinstated during the test phase in the absence of the picture stimulus. However, item-specific reactivation not of interest to the present hypothesis. Instead, item-level and set-level similarity will reported. To recap, item-level similarity is computed by correlating the beta values for each individual item at one presentation with itself at another presentation, reflecting the degree to which stimulus properties are reactivated. Set-level similarity is calculated by correlating an item at one presentation with all other stimuli of the same category at another presentation, indexing reactivation of more general information or processes that are shared between stimuli of the same category, e.g., all same task hits+ judgements.

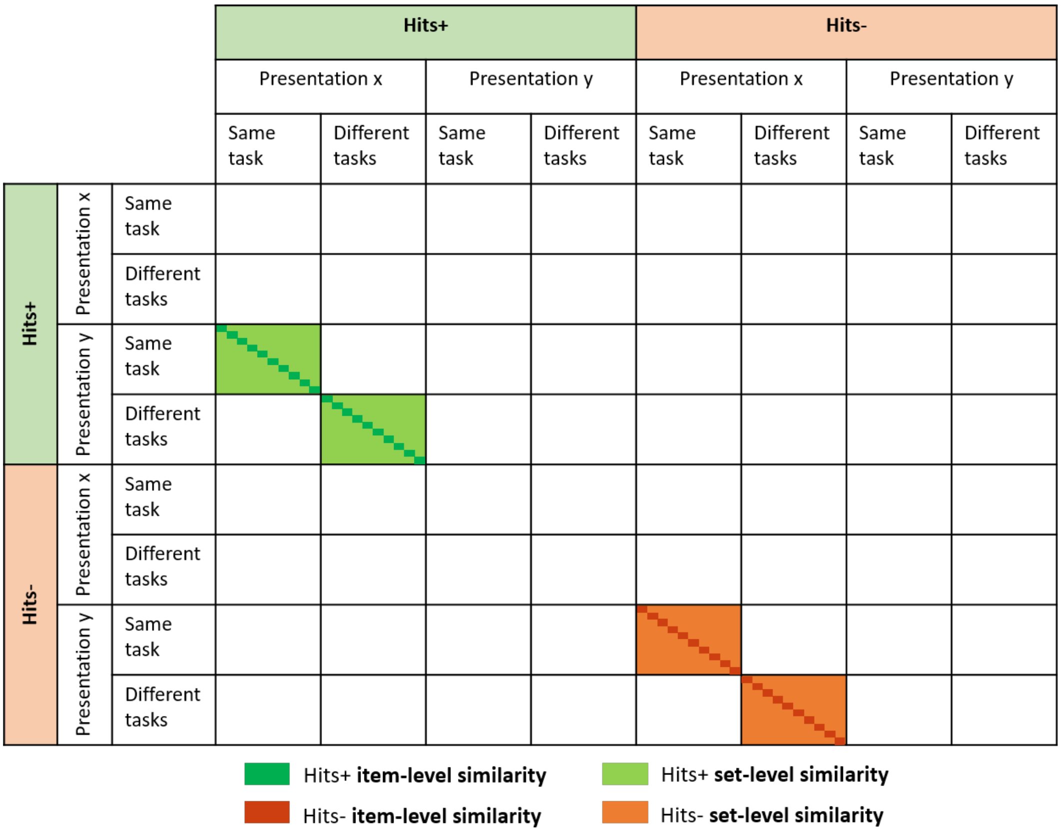
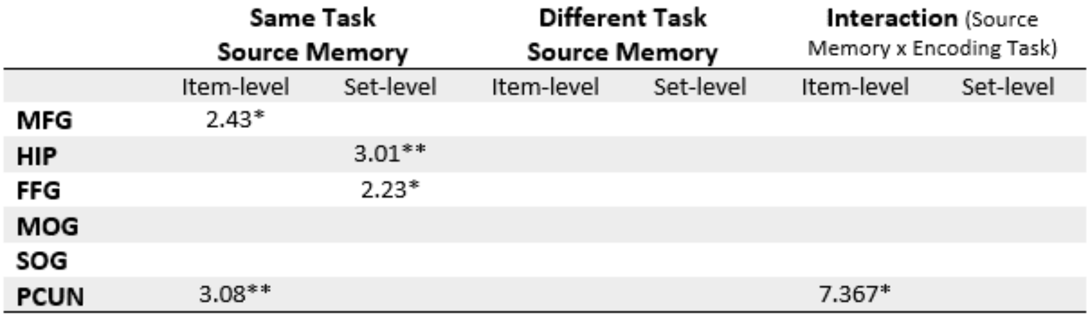


Figure 6.33. Identity matrix displaying the four conditions for which similarity scores were calculated in experiment 4 (fMRI). Item-level and set-level similarity are reported in the present investigation.

6.3.3.1 Encoding similarity

Results relating to statistically significant subsequent source memory effects, separately in the two encoding task conditions, as well as interactions between encoding task condition and source memory performance are reported in Table 6.20. Significant subsequent source memory effects were only found in the same encoding task condition. At the item-level, pattern similarity in the precuneus was higher for subsequent hits+ than hits- judgements. The same trend was observed in the right middle frontal gyrus, but this effect did not survive *FDR*-corrections. Set-level similarity in the right hippocampus was higher for subsequent hits+ compared to hits- trials, with the same trend (not surviving multiple comparison corrections) in the right fusiform gyrus. The interaction between subsequent source memory performance and encoding task condition was found to be significant in the precuneus, though only before corrections for multiple comparisons. Figure 6.34 displays the mean encoding similarity scores (Fisher transformed, item-level similarity).

Table 6.20. *Summary of encoding similarity results across regions of interest (experiment 4, fMRI) from pairwise t-tests contrasting encoding similarity to subsequent hits+ and hits- judgements and repeated-measures ANOVAs testing for interactions between subsequent source memory performance and encoding task condition.*



	Same Task Source Memory		**Different Task Source Memory**		**Interaction** (Source Memory x Encoding Task)	
	Item-level	Set-level	Item-level	Set-level	Item-level	Set-level
MFG	2.43*					
HIP		3.01**				
FFG		2.23*				
MOG						
SOG						
PCUN	3.08**				7.367*	

Note. T-statistics are reported for the same task source memory contrast and the different task source memory contrast. A positive t-statistic denotes subsequent hits+ judgements were associated with higher pattern similarity than subsequent hits- judgements, a negative t-statistic reflects the opposite direction. F-statistics are reported for the interaction (df = 1,16).
* statistically significant (*p* uncorrected)
** statistically significant (*p FDR*-corrected).

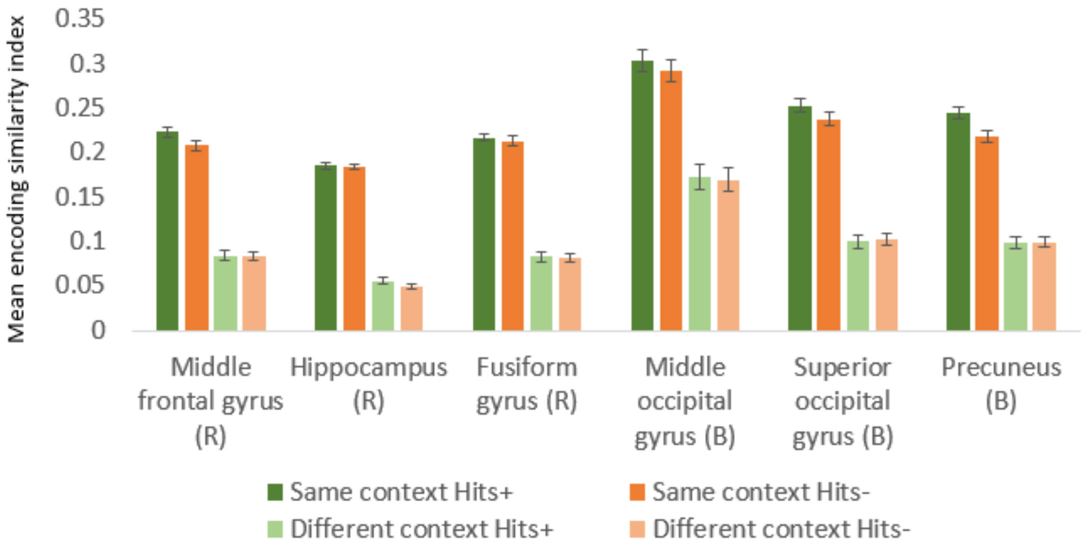


*Figure 6.34.*Experiment 4 (fMRI): Mean encoding item-level similarity scores for subsequent hits+ and hits- judgements separately displayed for the two encoding conditions across the six ROIs. Error bars denote standard errors.

The contrasts used in the ROI analyses were then also submitted to exploratory whole-brain searchlight analyses. The results are presented in Table 6.21. In the same encoding task condition, subsequent hits+ judgements were associated with higher item-level similarity than subsequent hits- judgements in the middle cingulate cortex. A similar trend was observed in the right inferior parietal lobe. For the same contrast, set-level similarity was also found to be higher for subsequent hits+ than hits- judgements in ventromedial prefrontal cortex, left posterior cingulate cortex. Additional trends, although not surviving multiple comparison corrections, were observed in the left middle frontal gyrus, the right fusiform gyrus and the left middle cingulate cortex. No statistically significant subsequent source memory effects were revealed in the different encoding task condition. However, an interaction was found in the left posterior cingulate cortex, which only survived *FWE*-corrections at the set-level. The direction of this interaction was as predicted by the hypotheses. Figure 6.35 illustrates the statistically significant interaction in the posterior cingulate cortex. Set-level similarity in the same task condition is shown to be higher for subsequent hits+ than hits- judgements, while the opposite direction is observed in the different task condition.

Table 6.21. *Summary of searchlight encoding similarity analysis results (experiment 4, fMRI).*

Contrast	Region	L/R	MNI coordinates (x,y,z)	BA	*t*-statistic	Cluster size
Same Task Source Memory (item-level)						
Hits+ > Hits-	Middle cingulate cortex	B	-12, -4, 26	23	3.93†	74**
	Inferior temporal lobe	R	30, -16, -37	20	4.80†	47*
Interaction (item-level)						
	Posterior cingulate cortex	L	-18, -37, 26	23	4.61†	36*
Same Task Source Memory (set-level)						
Hits+ > Hits-	Ventromedial prefrontal cortex	B	3, 14, -16	25	4.39†	87**
	Posterior cingulate cortex	L	-21, -40, 29	23	4.13†	73**
	Middle frontal gyrus (pars orbitalis)	L	-36, 47, -10	10	4.50†	32*
	Fusiform gyrus	R	30, -16, -37	20	4.41†	33*
	Middle cingulate cortex	L	-12, -4, 26	24	4.19†	38*
Interaction (set-level)						
	Posterior cingulate cortex	L	-21, -40, 29	23	4.21†	88**

Note. L = left, R = right, B = bilateral, BA = approximate Brodmann Area. MNI coordinates refer to peak voxel coordinates.
* $p_{cluster} < 0.05$ (uncorrected)
** $p_{cluster} < 0.05$ (*FWE*-corrected)
† $p_{peak} < 0.001$ (uncorrected)
†† $p_{peak} < 0.05$ (*FWE*-corrected)

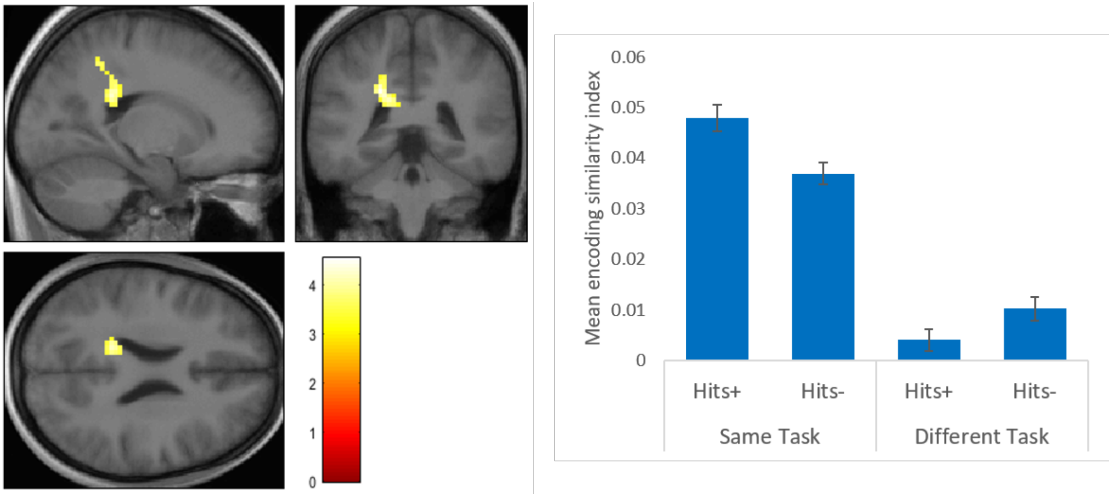
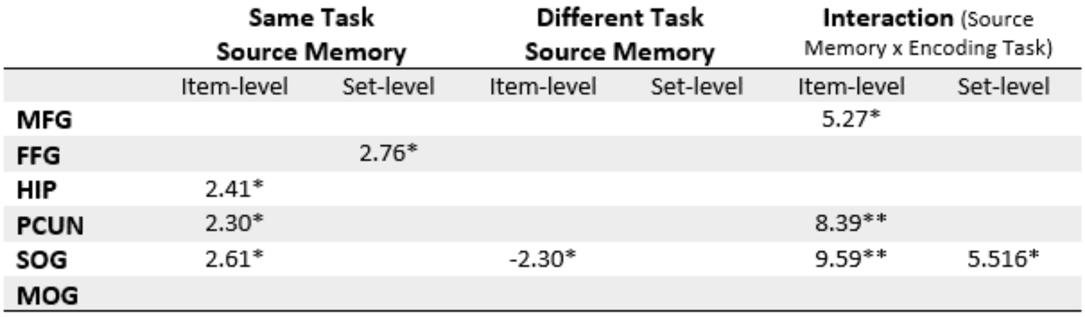


Figure 6.35. Experiment 4 (fMRI): set-level similarity indices in the posterior cingulate cortex.

6.3.3.2 Encoding-retrieval similarity

Results relating to statistically significant source memory effects, separately in the two encoding task conditions, as well as interactions between encoding task condition and source memory performance are reported in Table 6.22. Main effects of source memory performance did not survive corrections for multiple comparisons. However, in the same encoding task condition, trends were observed for hits+ judgements to be associated with higher item-level similarity than hits- judgements in right hippocampus, precuneus and superior occipital gyrus. Additionally, set-level similarity in the right fusiform gyrus was higher for hits+ than hits- judgements. Conversely, in the different encoding task condition, a trend was observed in the superior occipital gyrus for hits- judgements to be associated with higher item-level similarity than hits+ judgements. At the item-level, significant interactions between source memory performance and encoding task condition were observed in the precuneus and superior occipital gyrus. This interaction was also found to be significant in the right middle frontal gyrus before *FDR*-corrections. At the set-level, an interaction was observed in the superior occipital gyrus, although this did not survive multiple comparison corrections. Means of item-level ERS scores are displayed in Figure 6.36, illustrating the significant interactions to be in the predicted direction.

Table 6.22. *Summary of encoding-retrieval similarity results (experiment 4, fMRI) from pairwise t-tests contrasting encoding similarity to hits+ and hits- judgements and repeated-measures ANOVAs testing for interactions between subsequent source memory performance and encoding task condition.*



	Same Task Source Memory		**Different Task Source Memory**		**Interaction** (Source Memory x Encoding Task)	
	Item-level	Set-level	Item-level	Set-level	Item-level	Set-level
MFG					5.27*	
FFG		2.76*				
HIP	2.41*					
PCUN	2.30*				8.39**	
SOG	2.61*		-2.30*		9.59**	5.516*
MOG						

Note. T-statistics are reported for the same task source memory contrast and the different task source memory contrast. A positive t-statistic denotes hits+ judgements were associated with higher pattern similarity than hits- judgements, a negative t-statistic reflects the opposite direction. F-statistics are reported for the interaction (df = 1,16).
* statistically significant (*p* uncorrected)
** statistically significant (*p FDR*-corrected).

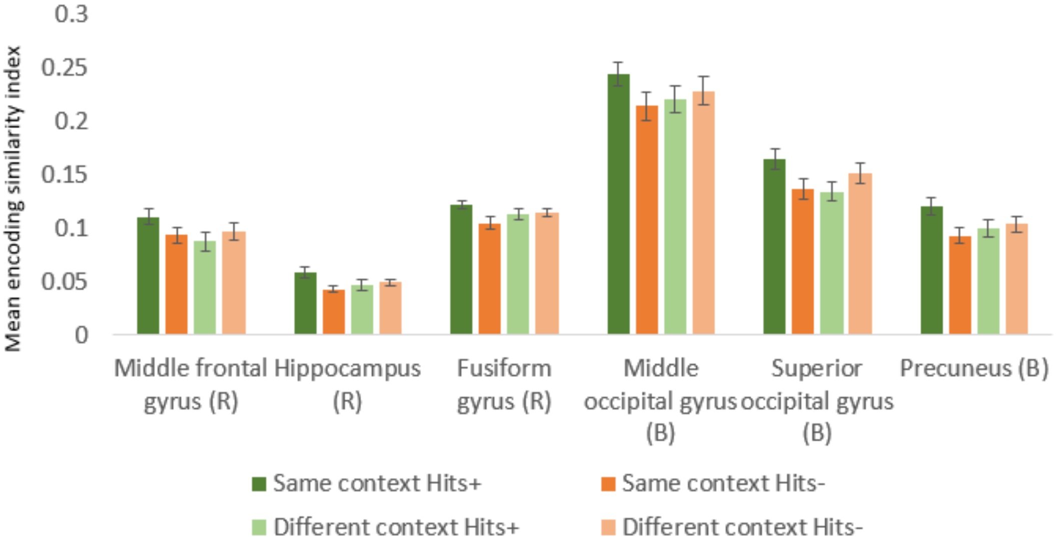


Figure 6.36. Experiment 4 (fMRI): Mean encoding-retrieval item-level similarity scores for hits+ and hits- judgements separately displayed for the two encoding conditions across the six ROIs. Error bars denote standard errors.

The same contrasts that were investigated in the ROI analyses were then also submitted to exploratory whole-brain searchlight analyses. The results are presented in Table 6.23. The searchlight analysis revealed trends indicating source memory effects in the same task condition, which did not survive *FWE*-corrections. Higher levels of item-level similarity in the right middle occipital gyrus and the cuneus were associated with hits+ judgements when compared to hits- judgements. A similar trend was observed for set-level similarity in the left middle temporal gyrus. In the different task condition, item- and set-level similarity in the ventromedial prefrontal cortex was found to be higher for hits- judgements than hits+ judgements. The interaction between source memory performance and encoding task condition was found to be significant at item- and set-level in the right inferior parietal gyrus, extending into the precentral gyrus. The item-level interaction in this right parietal region is illustrated in Figure 6.37, showing that ERS was higher for hits+ than hits- judgements in the same task condition but lower for hits+ than hits- judgements in the different task condition. A similar item-level trend was observed in the cuneus.

Table 6.23. *Summary of searchlight encoding-retrieval similarity analysis results (experiment 4, fMRI).*

Contrast	**Region**	**L/R**	**MNI coordinates (x,y,z)**	**BA**	***t*-statistic**	**Cluster size**
Same Task Source Memory (item-level)						
Hits+ > Hits-	Middle occipital gyrus	R	42, -76, 23	39	4.18†	51*
	Cuneus	B	-3, -79, 32	19	3.72†	44*
Different Task Source Memory (item-level)						
Hits- > Hits+	Ventromedial prefrontal cortex	B	6, 17, -4	25	5.06††	103**
Interaction (item-level)						
	Inferior parietal gyrus/ Precentral gyrus	R	45, -37, 53	4	4.11†	197**
	Cuneus/Precuneus	B	-3, -82, 35	19	3.67†	54*
Same Task Source Memory (set-level)						
Hits+ > Hits-	Middle temporal gyrus	L	-69, -34, -7	21	4.24†	57*
Different Task Source Memory (set-level)						
Hits- > Hits+	Ventromedial prefrontal cortex	L	-12, 32, -22	12/25	4.65†	50*
Interaction (set-level)						
	Inferior parietal lobe/Precentral gyrus	R	36, -13, 44	4/6	3.79†	101**

Note. L = left, R = right, B = bilateral, BA = approximate Brodmann Area. MNI coordinates refer to peak voxel coordinates.

* $p_{cluster} < 0.05$ (uncorrected)

** $p_{cluster} < 0.05$ (*FWE*-corrected)

† $p_{peak} < 0.001$ (uncorrected)

†† $p_{peak} < 0.05$ (*FWE*-corrected)

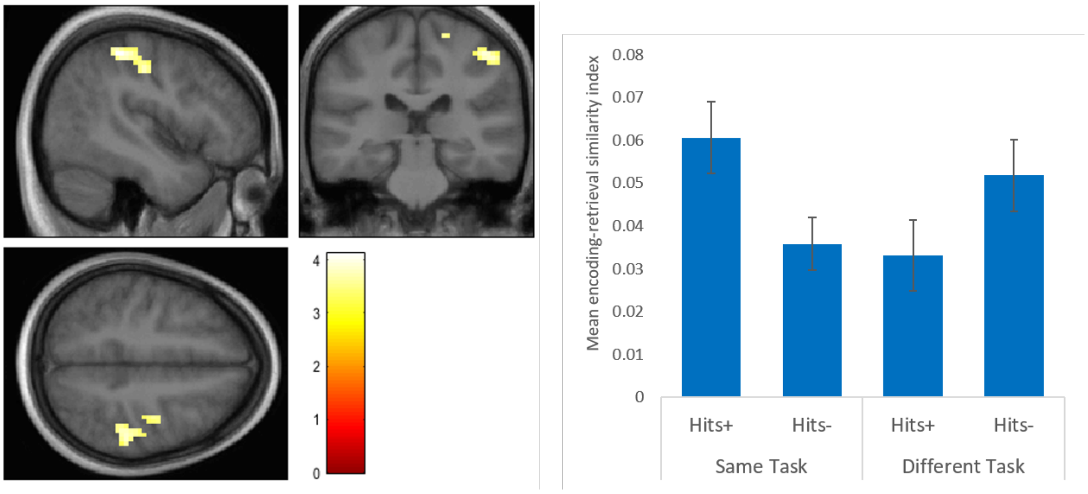


Figure 6.37. Experiment 4 (fMRI): item-level similarity indices in the right inferior parietal/precentral gyri.

6.4 Discussion

The present experiment investigated differences in neural similarity patterns relating source memory effects when stimuli are either repeated in the same context or repeatedly encoded in differing contexts. Behavioural results showed that different task encoding, when compared to same task encoding, was associated with better item memory but poorer source memory performance. Univariate analyses of the functional MRI data revealed repetition-related changes in mean activation that occurred in different regions and were differentially associated with subsequent source memory performance depending on the encoding task condition. Neural pattern similarity was assessed using RSA. The results supported the hypothesis that higher levels of pattern reactivation are associated with superior source memory performance when stimuli are repeatedly encoded in the same context. In the different encoding task condition, pattern reactivation in frontal and parietal regions was lower for subsequent hits+ than hits- judgements. These findings suggest that not reactivation but potentially the creation of multiple traces underlies the successful encoding and retrieval of context memory.

Behavioural results supported the hypothesis that the different encoding task condition was associated with fewer misses, i.e., superior item memory, but also with more hits- judgements, i.e., worse source memory, than the same encoding task condition. These results largely replicate the memory performance results observed in the EEG version of this experiment (Chapter 5). An interaction between memory performance and encoding task condition was reported in both experiments. These results add to existing body of research from retroactive interference paradigms (Anderson & Neely, 1996; Hupbach et al., 2007; G. Kim et al., 2017). This line of research has indicated that stimulus occurrence in multiple contexts may cause interference, resulting in higher levels of generalisation at the cost of contextual source information. In addition to weaker source memory performance, participants were also less likely to forget the stimulus itself, when it was encoded in differing contexts, suggesting that encoding variability is associated with better item memory (Bower, 1972; Hintzman, 1986; Nadel & Moscovitch, 1997). In addition to memory performance, RTs measured in the present experiment revealed an interesting pattern. Reaction times measured during the study phase suggested that repetition priming only occurred in the same context condition, as RTs to repeated stimuli did not gradually decrease in the different task condition. This is in line with previous research reporting no reliable repetition priming effects when words were repeated in different contexts (Ratcliff et al., 1985 Experiment 2), although contradictory results have been observed (Clarke & Morton, 1983; Jacoby, 1983; Jacoby & Dallas, 1981; Scarborough et al., 1979). Finally, in Chapter 5, RTs at test were found to be faster for stimuli encoded in the different task condition and for hits+ judgements. Similar trends were also reported in the present investigation, potentially indicating that items encoded in the different task condition and items corresponding to hits+ judgements could be more efficiently retrieved. Overall, the behavioural results provide additional support for the notion that encoding variability is associated with stronger item memory but worse performance in a source memory task requiring the retrieval of varying encoding contexts.

6.4.1 fMRI mass-univariate analysis results

Functional MRI data were examined to identify the neural correlates of same and different context encoding. BOLD signal change corresponding to same and different task encoding was observed in a number of frontal and parietal regions. Additionally, data were analysed with respect to repetition-related changes in either of the two encoding task conditions. Repetition enhancement and suppression effects were reported in the same encoding task condition, with enhancement in postcentral gyrus, middle temporal gyrus and precuneus, as well as, repetition suppression in inferior frontal gyrus predicting subsequent source memory performance. The different task condition was only associated with statistically significant repetition suppression effects, however, a trend was shown for repetition enhancement in the midcingulate cortex to predict subsequent source memory performance.

Because of the relative novelty of the present experimental design, a primary aim for univariate analyses was to contrast mean activation to same and different task encoding, when averaged over subsequent source memory performance and repetitions. In the same task condition, relative to the different task condition, mean activation was found to be higher in bilateral inferior parietal gyri and right precuneus. Additional trends of the same contrast were observed in right inferior frontal, middle frontal and middle temporal gyri. As those regions have been reported to exhibit general repetition enhancement effects (H. Kim, 2017), these effects may reflect repetition enhancement as observed in the same task condition of the present research. The reverse contrast showed higher mean activation to different compared to same task encoding in left middle and inferior frontal gyri, left medial orbito-frontal cortex, bilateral angular gyrus (though stronger in left hemisphere) and bilateral precuneus. Trends of the same contrast were reported in the left fusiform gyrus and hippocampus. Left lateral inferior frontal and parietal regions, including the angular gyrus and precuneus, have previously been associated with the integration of semantic features (Binder et al., 2009; Chou et al., 2009; Fairhall & Caramazza, 2013) and the generation of associative memories (Lundstrom et al., 2005). Moreover, the left inferior frontal gyrus has been associated with implicit semantic feature selection (Grindrod, Bilenko, Myers, & Blumstein, 2008) Therefore, increased mean activation in those regions during different task encoding may reflect processes of integration of semantic features and updating of contextual information. With regards to activation in the left medial orbito-frontal cortex, patients with lesions in limbic areas, including this medial frontal region, have previously been shown to have difficulty distinguishing currently relevant information from currently irrelevant information that was previously acquired (Schnider & Ptak, 1999). Therefore, it was suggested that the medial orbito-frontal cortex was important for suppressing irrelevant contextual information. Support for a role of the orbito-frontal cortex in temporal context encoding and retrieval was reported in an experiment involving healthy participants as well as patients with focal orbito-frontal lesions (Duarte, Henson, Knight, Emery, & Graham, 2010). However, this study emphasised that the orbito-frontal cortex was especially involved in temporal context encoding, while no such association was found for the encoding of spatial context. The present results suggest that this region may also be implicated when stimuli are encoded in varying contexts. Taken together, it appears that distinct brain regions are involved during the two encoding task conditions, adding to the hypothesis that the neural processes underlying same and different context encoding differ.

A second set of whole-brain analyses was concerned with repetition effects, measured separately for the two encoding conditions and whether repetition-related changes in mean activation predicted subsequent source memory performance. In the same encoding task condition, several brain regions were found to show repetition enhancement and suppression effects. Repetition enhancement was observed in left lateral parietal regions, including superior and inferior parietal gyri and the precuneus. Additional trends were observed in the left postcentral and middle temporal gyri. More interesting to the present investigation was that another contrast revealed repetition enhancement in some of those regions, namely the left postcentral and middle temporal gyri, to be higher for subsequent hits+ than hits- judgements. Repetition enhancement effects have previously been associated with subsequent memory performance (Segaert et al., 2013) and explicit retrieval during incidental encoding (Kim, 2017). Therefore, these results may suggest that explicit retrieval, as indexed by repetition enhancement in left postcentral and middle temporal gyri, may have facilitated subsequent retrieval of the associated encoding context. Repetition suppression effects were found in the inferior frontal gyrus, the left insula and the right cuneus, with additional trends of repetition suppression observed in bilateral fusiform and left cingulate gyri. Interestingly, the repetition suppression effect in left inferior frontal gyrus further predicted subsequent source memory performance. Decreases in mean activation across repetitions were stronger for subsequent hits+ than hits- judgements. Repetition suppression is not commonly associated with subsequent memory performance (Kim, 2017; Segaert et al., 2013). One study found that reduced repetition suppression was associated with superior memory performance (Xue et al., 2011), indicating that repetition suppression may be related to forgetting rather than remembering. In the present experiment, higher repetition suppression in left inferior frontal gyrus for subsequent correct source memory judgements may indicate that information relating to items repeated in the same context was easily integrated and, therefore, associated with repetition suppression. This is consistent with the left inferior frontal gyrus being implicated in the selection of competing features (Grindrod et al., 2008). In that same context, repetitions require lower levels of semantic feature integration and are associated with less competition, which may then be indexed by repetition suppression. While the association between repetition suppression and subsequent source memory performance is difficult to interpret within the fMRI literature, the results are consistent with the speculative hypothesis based on the EEG repetition effects presented in Chapter 5. Both, fMRI and EEG repetition effects, only occurred in the same task encoding condition and repetition effects were stronger for subsequent hits+ than hits- judgements. Interestingly, previous studies combining ERPs with PET or fMRI have linked the LPC to left inferior frontal regions (Düzel, Picton, et al., 2001; Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005). However, it is also important to point out that EEG repetition effects observed in single-trial analyses only occurred between the first and second stimulus presentation, while fMRI repetition suppression here was modelled across all four presentations. Moreover, from a statistical point of view, the fMRI mass-univariate results are more closely related to the ERP than the single-trial EEG analyses. Thus, while some exciting parallels were observed, adding to the tentative prediction that repetition-related EEG amplitude changes may reflect similar neural processes as repetition suppression observed in fMRI, these hypotheses will have to be further tested in hypothesis-driven experiments.

In the different encoding task condition, no repetition effects survived multiple comparison corrections. However, a few notable trends were observed. Repetition suppression was observed in the left insula, right thalamus, left postcentral and inferior occipital gyri and the left posterior hippocampus. More interesting to the present investigation, however, repetition enhancement was found to be higher for subsequent hits+ than hits- judgements in the left midcingulate cortex. To the authors knowledge, the midcingulate cortex is rarely considered in relation to memory. However, the finding that repetition enhancement effects are stronger for subsequent hits+ than hits- judgements adds to a growing body of research, including the present research, suggesting that neural repetition enhancement predicts subsequent (source) memory performance (e.g., Heusser et al., 2013; Kremers et al., 2014; van den Honert et al., 2016; Vannini et al., 2013). Fewer and smaller repetition effects were reported in the different task condition compared to the same encoding task condition. This may partly be explained by the different task repetitions occurring in different runs. As between-run signal-to-noise ratio is higher, associated statistical power would be expected to be lower. However, previous research has also shown that repetition suppression interacts with repetition lag in that repetitions occurring closer in time to each other produce larger repetition suppression effects (Barron, Garvert, & Behrens, 2016; Xue et al., 2011). In the present experiment, same task repetitions were always associated with fewer intervening trials than different task repetitions. Finally though, the RTs measured in this experiment, indicated that repetition priming only occurred in the same task condition. As repetition suppression is thought to be the neural correlate of repetition priming (Ballesteros et al., 2013; Ward et al., 2013), this may explain the absence of significant repetition suppression effects in the different task condition. Overall, it appears that repetition-related changes are easier to detect when stimuli are repeated in the same context. Moreover, the present results supported a relationship between repetition enhancement and subsequent source memory performance.

6.4.2 Representational Similarity Analysis

Neural similarity patterns relating to encoding similarity and encoding-retrieval similarity (ERS) were examined to test the hypothesis that similarity patterns to encoding task condition interact with source memory performance. Reactivation, as indexed in higher pattern similarity, is beneficial for source memory when items are repeatedly encoded in the same context. However, when items are repeatedly encoded in different contexts, reactivation was predicted to facilitate generalisation of contextual information, which would result in poorer source memory for the contexts the items were initially encoded in. ROI analyses were performed in the right middle frontal gyrus, right hippocampus, right fusiform gyrus, bilateral middle occipital gyrus, bilateral superior occipital gyrus and bilateral precuneus. Exploratory searchlight analyses were carried out and revealed complementary results. Two measures of similarity were in the focus of these analyses: item-level and set-level similarity. Item-level similarity is thought to reflect reactivations of stimulus properties, while set-level similarity indexes reactivations of more general processes and information that is shared between all stimuli within a particular category, e.g., different task, hits+ judgements. Results from RSA presented in this chapter supported this theoretical hypothesis. For encoding similarity, an interaction was reported in the left posterior cingulate cortex and the precuneus. For ERS, this interaction between encoding task condition and source memory performance was observed in the precuneus, superior occipital gyrus and the right inferior parietal gyrus. These results provide fundamental support for the differential role of reactivation in different encoding strategies, namely mere repetition and encoding variability.

Encoding similarity

Subsequent source memory effects for encoding similarity, i.e., similarity between repeated encoding presentations, were only found in the same encoding task condition. Higher levels of item-level similarity in the precuneus were associated with superior subsequent source memory performance. A similar trend was observed in the middle frontal gyrus. Searchlight analyses revealed an additional effect in the bilateral midcingulate cortex and a trend for higher levels of item-level reactivation for subsequent hits+ than hits- judgements in the right inferior temporal lobe. The results suggests that items, which are represented more similarly across same context repetitions, are associated with superior source memory performance. Such a results is consistent with a large body of research supporting the reactivation view (Benjamin & Tullis, 2010; Thios & D'Agostino, 1976), which posits that reactivation of the same patterns facilitates successful memory encoding (van den Honert et al., 2016; Ward et al., 2013; Xue et al., 2010). At the set-level, same task encoding subsequent hits+ trials, encoded in the same task condition, were found to be more similar to each other than subsequent hits- trials in the right hippocampus with a similar trend observed in the right fusiform gyrus. Searchlight analyses revealed additional effects of this contrast in bilateral ventromedial prefrontal cortex, left posterior cingulate cortex and trends in left lateral middle frontal gyrus and midcingulate cortex. The set-level results for the same encoding task condition, suggest that items, for which the source can subsequently be retrieved, are more similarly represented to each other than items, for which the source cannot be retrieved later on. This indicates that processes and features, which are shared between subsequent hits+ judgements, are reactivated during same context repetitions. Both, the hippocampus and the ventromedial prefrontal cortex, have consistently been implicated in memory encoding and consolidation (e.g., Blumenfeld & Ranganath, 2007; Bonnici et al., 2012; Fletcher et al., 2003; Kim, 2011; Persson & Söderlund, 2015; Spaniol et al., 2009). More recent investigations have also focused on posterior parietal regions, such as the precuneus and poster cingulate cortex (see Gilmore, Nelson, & McDermott, 2015; Rugg & King, 2017; Sestieri, Shulman, & Corbetta, 2017). In the present research, the precuneus was found to represent subsequent hits+ judgements more similarly at the item-level than subsequent hits- judgements. At the set-level, subsequent hits+ compared to hits- judgements were represented more similarly to each other, suggesting that the right hippocampus, bilateral ventromedial prefrontal cortex and left posterior cingulate cortex are implicated in certain operations that are important for subsequent source memory retrieval. This interpretation is consistent with the notion that the hippocampus and posterior parietal regions bind contextual features to form a coherent memory representation to be stored in neocortical regions (H. Eichenbaum et al., 2007; Josselyn et al., 2015; Moscovitch & Winocur, 1992; Shimamura, 2011).

Although no statistically significant effects of subsequent source memory were reported in the different encoding task condition, evidence was found for an interaction. This interaction reflected higher pattern similarity in the same task condition to be associated with subsequent hits+ trials with the opposite direction in the different encoding task condition. This interaction was found to be significant at the set-level, with additional trends observed for item-level similarity. At the set level, the interaction in the left posterior cingulate cortex indicated that items resulting in subsequent hits+ judgements in the same task condition were more similar to each other. Items resulting in subsequent hits+ judgements in the different task condition were less similar to each other, when compared to subsequent hits- judgements. This finding suggests that stimuli repeatedly encoded in the same task instructions were more similarly represented to each other when the source could subsequently be retrieved. However, for stimuli encoded in different contexts, higher similarity between stimuli was associated with subsequent hits- judgements. This finding supports the prediction that higher levels of generalisation were associated with worse subsequent source memory performance. It further indicates that the processes underlying successful encoding of different contexts were more different between items, potentially providing support for the encoding variability view and the multiple trace theory (Bower, 1972; Hintzman, 1986; Martin, 1968; Nadel & Moscovitch, 1997). At the item-level, this interaction was observed in ROI analyses in the precuneus but did not survive corrections for multiple comparisons. Additional support for this interaction was found in searchlight analyses in the left posterior cingulate cortex, although again, not surviving multiple comparison corrections. Previous research has shown that pattern similarity in the posterior cingulate cortex was related to the amount of details that could later on be recalled (Bird, Keidel, Ing, Horner, & Burgess, 2015). The authors suggested that reinstatement in those posterior midline structures facilitated consolidation of complex events, which are, however, becoming more generic and somewhat less episodic through this consolidation process. The present results extend this hypothesis by adding that different context encoding is associated with lower pattern similarity in order to preserve unique contextual details. However, as the contrast between subsequent hits+ and hits- judgements was not significant in the different task condition, the interpretation remains somewhat speculative and requires further testing. Nonetheless, these findings are consistent with previous research, showing that reactivation of shared item features, possibly indexing generalisation, was associated with worse source memory for the encoding task (Kim et al., 2017).

Encoding-retrieval similarity

Source memory effects for encoding-retrieval similarity were generally in a similar direction as those observed for similarity between encoding presentations. In the same task condition, differences in pattern similarity relating to source memory performance did not survive multiple comparison corrections. However, trends were observed for item-level ERS to be higher for hits+ than hits- judgements in the right hippocampus, bilateral precuneus and superior occipital gyrus. Additional trends were observed in bilateral cuneus and right middle occipital gyrus. This indicates that successful source memory retrieval for items repeatedly encoded in the same context is associated with higher levels of reactivation of stimulus properties during the test phase when compared to unsuccessful source memory retrieval. This is in line with previous ERS results, suggesting pattern reactivation or reinstatement at test to enhance memory performance (Liang & Preston, 2017; Ritchey et al., 2013; Wing et al., 2015). Trends were also observed in the same task condition for set-level similarity to be higher for hits+ than hits- judgements in the right fusiform gyrus and the left middle temporal gyrus. These results indicate that, in the same encoding task condition, the features and processes underlying encoding-retrieval operations are more similar for hits+ than hits- judgements. Together with the same task item-level results, this provides further support for theoretical accounts, which propose that successful retrieval relies on similar operations taking place during the study and test phase, i.e., the encoding specificity principle (Tulving, 1983; Tulving

& Thomson, 1973) and the transfer-appropriate processing account (Morris et al., 1977).

In the different task condition, the source memory effects indicated lower similarity for hits+ than hits- judgements. At the item-level, this effect was reported in bilateral ventromedial prefrontal cortex with a similar trend observed in bilateral superior occipital gyrus. Similarly, different task set-level similarity was lower for hits+ than hits- judgements in the ventromedial prefrontal cortex, although this effect did not survive corrections for multiple comparisons. The ventromedial prefrontal cortex was suggested to be implicated in memory-guided decision-making (see Hebscher & Gilboa, 2016). It may be suggested that lower levels of ERS for hits+ than hits- judgements reflect the multiple traces that are available for an item, which was encoded in different contexts. Additionally, interactions reflecting the hypothesised direction of results were found to be significant at item- and set-level. At the item-level, this interaction was reported in bilateral precuneus and superior occipital gyrus with an additional trend in right middle frontal gyrus. Furthermore, searchlight analyses found the interaction to be significant in the right inferior parietal gyrus, extending into the precentral gyrus and an additional trend in the bilateral cuneus, extending into precuneus. These interactions suggest that successful source retrieval in the same context encoding condition was associated with higher levels of reactivation of stimulus properties between encoding and retrieval. On the other hand, successful retrieval in the different context encoding condition was associated with lower levels of reactivation of those stimulus-related patterns. Finally, set-level interactions did not survive multiple comparison corrections, but trends were observed in the bilateral superior occipital gyrus. Searchlight analyses also revealed significant interactions in right lateral inferior parietal gyrus, extending into precentral gyrus. Taken together, these interaction results may give rise to extending existing theoretical accounts. The transfer-appropriate processing framework (Morris et al., 1977), for example, does not account for the possibility that encoding operations may differ if stimuli are repeated in different contexts. If several different encoding operations were performed, the operations at retrieval may be predicted to reflect a blend of those encoding operations, however, this will likely involve generalisation, which is associated with a decrement in episodic details.

In conclusion, the present results provide support for the notion that same and different context encoding are supported by distinct mechanisms. Mere repetition of an item in the same context strengthens item and source memory by reactivation. When items are repeatedly encoded in different contexts, reactivation appears to promote generalisation at the cost of contextual features. Another mechanism, possibly the creation of multiple unique memory traces, underlies the successful encoding of multiple contexts, i.e., the extract of unique contextual features. Similar results were found for pattern similarity between encoding and retrieval. When only one context was present at encoding, reactivation or reinstatement of the same patterns during the test phase was associated with successful retrieval of this context. However, when an item was initially encoded in different contexts, higher ERS was associated with worse source memory performance. It was speculated that the observed lower levels of ERS for correct context retrieval might index the multiple traces that were available for the item. These results will have to be replicated in a hypothesis-driven design with a particular emphasis on ventromedial prefrontal and posterior cingulate cortex. The behavioural results indicated that different context encoding was associated with better item, but worse source memory, than same context encoding. Previous research had largely focused on the mechanisms underlying the forgetting of episodic details, with less emphasis on the mechanisms underlying successful context encoding. It is noteworthy that, although generalisation in the context of different task encoding was associated with worse source memory, such processes of abstraction and generalisation can often be very useful, as it has been suggested to be the basis of semantic knowledge (e.g., Binder & Desai, 2011; Cermak, 1984). In other words, while contextual information is sometimes important to be remembered, the creation of a more coherent, semantic memory is critical for making memory-guided decisions and future inferences.

SECTION 3

-

General Discussion

Chapter 7 - General Discussion and Conclusion

7.1 Chapter overview

The present research examined the effects of repetition on subsequent source memory performance and reinstatement of item and source information during the test phase. Electrophysiological and haemodynamic response data were collected. The primary aim of this research was to investigate fMRI pattern similarity between repeated encoding episodes and between encoding and retrieval. The majority of previous research presented the same stimuli repeatedly with the same encoding task instructions. This thesis aimed to identify how pattern similarity was influenced by changes to perceptual stimulus features or by changes to encoding task instructions. An additional aim was to establish the neural correlates of repeated encoding and reinstatement of source memory information. The present chapter will summarise the main results from four neuroimaging experiments and discuss the methodological concerns as well as theoretical implications and directions for future research.

7.2 Summary of results

7.2.1 Chapters 3 & 4: Encoding Modality

The experiments presented in Chapters 3 and 4 employed a similar experimental paradigm to test the effects of encoding modality and repetition on subsequent memory performance. Furthermore, this first set of experiments investigated reinstatement of encoding modality during the test phase. During the study phase, participants repeatedly encoded stimuli in three different encoding modality conditions. Stimuli were either repeatedly presented as pictures, repeatedly presented as words or the same concept was alternately presented as a picture or a word. During the test phase, all previously presented stimuli, along with the same number of new stimuli were presented as written words. Participants performed an old/new judgement task, assessing item memory, followed by a source memory task, assessing source memory for the modality in which stimuli were encoded during the study phase. This design allowed investigations of perceptual and conceptual repetitions, i.e., uni-modal picture or word encoding and multi-modal picture&word encoding, respectively. Moreover, reinstatement of pictorial information relating to a stimulus encoded as a picture, but cued with a word at test, could be examined in the absence of pictorial information during the test phase.

Behavioural results were largely consistent across the EEG and fMRI versions of this experimental paradigm. Item and source memory performance were close to a ceiling effect, resulting in too few misses to be included in neuroimaging analyses. Source memory performance was lower in the multi-modal encoding condition compared to the two uni-modal encoding conditions. The most item misses occurred in the picture-only encoding condition, which was likely because picture stimuli were cued with the corresponding written word in the test phase. As behavioural data were not the focus of the present paradigm, these will not be further discussed in this section.

Data from the EEG experiment presented in Chapter 3 were analysed using the event-related potential (ERP) technique. Two ERP components, namely the late positive potential (LPC) and the FN400, were measured during the study and test phase. The LPC is commonly associated with episodic memory recollection (e.g., Friedman & Johnson, 2000; Rugg & Curran, 2007; Wilding & Ranganath, 2012), while the FN400 has been proposed to play a role in familiarity judgements or semantic priming (e.g., Curran, 2000; Groh-Bordin et al., 2006; Yovel & Paller, 2004). Planned analyses were performed to test for interactions between subsequent source memory performance, repetition and encoding modality. No such interactions were revealed during the study phase. However, the analyses revealed a repetition effect during encoding, which appeared to be largely independent of subsequent source memory performance and encoding modality. To further investigate this repetition effect single-trial analyses were carried out. These analyses suggested that only a novelty effect, measured over parietal electrode sites, between the first and second presentation of a stimulus, was related to item-specific stimulus repetition. Moreover, single-trial analyses revealed that mean amplitudes measured during the time window of the repetition effect (around 300 – 550 ms post stimulus onset) correlated with an implicit measure of memory, reaction times. In other words, the more the voltage amplitudes increased in positivity over parietal sites between presentation 1 and 2 at encoding, the greater was the reduction in reaction times. In addition to this earlier occurring repetition effect, exploratory ERP analyses including a wider range of time windows for the LPC and FN400, revealed a later occurring (700 – 900 ms) parietal subsequent source memory effect. The data from the study phase suggested that stimulus repetition may shift the peak of the LPC forward, consistent with previous research (Renoult et al., 2012), which, in turn, may confound subsequent source memory effects that occur slightly later during the downhill slope rather than at the time of the peak. More importantly, the finding of a repetition effect only reflecting item-specific repetition at parietal sites between presentations 1 and 2, gives rise to the question what previously reported ERP repetition effects reflect if not item-specific repetition (Henson et al., 2004; Rugg & Doyle, 1994; Schendan & Kutas, 2003; Swick & Knight, 1997). Finally, during the test phase, LPC amplitudes to hits+ judgements differed based on encoding modality. This effect was suggested to indicate reinstatement of encoding modality during the test phase.

The fMRI data collected for this experimental paradigm were analysed using univariate and multivariate approaches, with a focus on multivariate representation similarity analyses. Univariate whole-brain analyses were conducted to examine repetition-related linear changes in mean activation within each one of the encoding modalities. Repetition suppression effects were found in the uni-modal encoding modalities (picture only, word only), indicating enhanced processing efficiency across repetitions (Buckner et al., 1998; Grill-Spector et al., 2006; Henson & Rugg, 2003; Schacter et al., 2007; Wig et al., 2005). However, these effects did not predict subsequent source memory performance. In the alternated picture&word encoding modality, a trend was observed that indicated that repetition enhancement was stronger in subsequent hits+ (high confidence correct item and correct source memory) than hits- (correct item but incorrect source memory) judgements. These increases in mean activation across repetitions were observed in inferior parietal regions, suggesting that they may reflect retrieval operations taking place during incidental encoding (Kim, 2017; Segaert et al., 2013). Such explicit retrieval may have contributed towards subsequent source memory success.

The main objective for the fMRI experiment was to assess differences in neural similarity patterns relating to source memory outcome and encoding modality. Across repeated encoding episodes, item-specific pattern reactivation in occipital gyri predicted subsequent source memory performance for stimuli encoded uni-modally. These patterns are in line with a large body of research suggesting that reactivation aids memory formation (e.g., van den Honert et al., 2016; Ward et al., 2013; Xue et al., 2010). For the multi-modal encoding condition, a trend indicated that subsequent hits+ judgements were associated with higher pattern similarity in inferior frontal and middle and superior temporal gyri. These regions were suggested to integrate stimulus features into conceptual, amodal representations (see Binder et al., 2009; Fairhall & Caramazza, 2013). An interesting trend was observed in the left hippocampus, suggesting pattern similarity to be lower for subsequent hits+ than hits- judgements. It was speculated that such a trend might reflect pattern separation signals (Favila et al., 2016; Karlsson Wirebring et al., 2015) and the extraction of unique encoding features between repetitions (Nadel & Moscovitch, 1997; Norman, 2010; O'Reilly et al., 2014), however, this effect remains to be replicated. Between encoding and retrieval, pattern similarity in superior occipital and posterior parietal regions was reported to be higher for hits+ than hits- judgements. Those source memory effects were found to be largely modality-independent. The findings are consistent with previous research contrasting pattern similarity for hits and misses (Ritchey et al., 2013; Wing et al., 2015). In addition to pattern similarity related to source memory performance, effects of encoding modality were considered, only including stimuli associated with hits+ judgements. Across repeated encoding presentations, occipital similarity patterns were higher for the uni-modal picture encoding condition compared to the other two encoding modalities. This was suggested to index that those regions were sensitive to processing visuo-perceptual information of picture stimuli. In contrast, inferior parietal regions represented items, which were alternately encoded as pictures and words, more similarly than stimuli in the uni-modal encoding modalities. This pattern of results may reflect conceptual processing and the integration of perceptual features into a coherent semantic representation (Bonnici et al., 2016; Devereux et al., 2013; Shimamura, 2011; Yazar et al., 2017). Finally, occipito-temporal encoding-retrieval similarity patterns indicated that pictorial information was reinstated during the test phase when concepts were cued with the corresponding word. However, this reinstatement effect did not extend to the stimulus-specific level. Therefore, this result may reflect processes underlying retrieval of more general source information related to pictorial stimuli from the study phase.

Taken together, the results reported in Chapters 3 and 4 provided novel insights into the mechanisms underlying repeated encoding of stimuli and retrieval of source memory information. Most notably, pattern similarity results were shown to be affected by the modality stimuli were encoded in, indicating that in addition to modality-independent source memory effects, different regions were implicated in source memory encoding depending on the encoding modality. Apart from a trend in the hippocampus, the results generally support the reactivation view (Benjamin & Tullis, 2010; Thios & D'Agostino, 1976) and the cortical reinstatement hypothesis by showing that higher pattern similarity, indexing reactivation, was related to source memory success. The EEG measures appeared to be less influenced by encoding modalities, especially the observed repetition effects. However, data from the test phase indicated that reinstatement of information from the study phase is reflected in LPC mean amplitudes at test. When interpreting the fMRI repetition suppression results in the light of the repetition-related EEG amplitudes changes, it was suggested that EEG repetition effects were more likely to reflect fMRI repetition suppression than enhancement. Consistent with the fMRI repetition suppression results presented in Chapter 4 and existing fMRI research (van den Honert et al., 2016; Ward et al., 2013), the EEG effects also did not predict subsequent source memory performance, but were linked to RTs as a measure of implicit memory.

7.2.2 Chapters 5 & 6

Chapters 5 and 6 include an EEG and an fMRI experiment using a similar experimental paradigm. These two experiments set out to test theoretical hypotheses regarding the neural correlates of repeated stimulus encoding in either the same or different contexts. Additionally, reinstatement effects relating to the encoding task conditions were examined. During a study phase, participants repeatedly encoded famous people's names in two encoding task conditions. Stimuli were either repeatedly encoded in the same context, i.e., participants performed the same encoding task at each repetition, or stimuli were repeatedly encoded in differing contexts, i.e., participants performed a different encoding task at each of the four stimulus presentations. During the test phase, participants performed an old/new judgement task, assessing item memory, followed by a source memory task, assessing source memory for the context/encoding task instructions under which the name was previously encoded. This paradigm allowed the direct comparison of two different encoding strategies: mere repetition and encoding variability and could, therefore, provide valuable insights into theoretical frameworks of repeated encoding and memory enhancement. Based on previous research and existing theoretical accounts, it was hypothesised that distinct processes underlie successful source memory encoding, when stimuli are either repeatedly encoded in the same context or in different contexts. Same context encoding was predicted to be associated with higher levels of reactivation, when the source was subsequently retrieved. In the different context condition, reactivation was proposed to interfere with subsequent retrieval of multiple contexts. Therefore, subsequent hits+ judgements were hypothesised to be associated with lower levels of reactivation, especially in fronto-parietal regions implicated in semantic integration and generalisation processes.

The behavioural data from both, the EEG and the fMRI version, revealed that same compared to different context encoding was associated with superior source memory but lower frequencies of correct item memory, as reflected in more misses in the same task condition. These results were in line with previous research employing retroactivate interference paradigms (Anderson & Neely, 1996; Hupbach et al., 2007; Kim et al., 2017), which suggested that items repeated in different contexts were likely to be generalised by forming a more stable, coherent memory representation. Moreover, superior item memory in the different task condition generally provides support for the encoding variability view, which proposes that context variability promotes the creation of multiple traces, resulting in a larger variety of retrieval cues and, thereby, enhancing item memory performance (Bower, 1972; Hintzman, 1986; Martin, 1968; Nadel & Moscovitch, 1997). The EEG data provided insights into dissociable mechanisms underlying same and different context encoding as well as differences during the test phase relating to encoding context condition. Multivariate fMRI analyses then allowed us to test the hypotheses regarding differences in reactivation underlying successful source memory formation and retrieval in the same and different context encoding conditions.

EEG data presented in Chapter 5 were analysed using the ERP technique as well as a single-trial approach. Mean amplitudes were extracted for an early frontal FN400 component (300 – 500 ms), a later (700 – 900 ms) frontal component, which showed sensitivity to subsequent memory performance in Chapter 3 (3.3.1.2) as well as for two LPC time windows (500 – 700 ms, 700 – 900 ms). ERP analyses revealed interactions between encoding context condition and repetition, indicating that repetition effects differed for the two encoding task conditions. This supports the notion of distinct underlying mechanisms of same and different context encoding. Patterns corresponding to the frontal component were less clear and require further investigations. LPC amplitudes, on the other hand, were shown to discriminate same context repetitions between the first and second presentation, indicating a novelty effect, while different context repetitions were reflected in a more gradual increase in mean amplitudes. Replicating the single-trial analyses from Chapter 3, a reliable repetition effect could only be identified over parietal electrode sites between around 450 – 700 ms post stimulus onset. When comparing item-specific repetition to a control measure, item-specific repetition only occurred in the same encoding task condition between presentation 1 and 2, which is largely consistent with findings from Chapter 3. However, in the experiment reported in Chapter 5, item-specific repetition-related increases were also shown to predict subsequent source memory performance. The time window for the repetition effect in this experiment (450 – 700 ms) overlaps more with the typical LPC time window, i.e., repetition occured later here than in Chapter 3. Therefore, it appears that whether repetition and subsequent source memory performance interact could depend on the timing of the repetition effect. Finally, LPC ERP waveforms at test were shown to be modulated by the encoding context condition, potentially reflecting reinstatement effects. As LPC amplitudes at test were larger for items encoded in varying contexts compared to the same encoding task condition, this difference may reflect the increased amount of retrieval cues and associated information available for items repeatedly encoded in different contexts (Wilding, 2000).

The fMRI data presented in Chapter 6 was analysed with univariate and multivariate approaches, with an emphasis on the representational similarity analyses, which directly assessed reactivation to test the theoretical hypotheses outlined above. Univariate whole-brain contrasts examined the main effects of same and different task encoding and how repetition effects within the two encoding task conditions interacted with subsequent source memory performance. Differences in mean activation to same and different task encoding were found across frontal and parietal regions. Higher mean activation to same relative to different context encoding was observed in inferior parietal brain regions. These effects seemed to overlap with repetition enhancement effects observed in the same encoding task condition. The different task condition was associated with higher mean activation in frontal regions and the angular gyrus. These effects were suggested to reflect the selection and integration of semantic features (Binder et al., 2009; Fairhall & Caramazza, 2013; Grindrod et al., 2008). Moreover, the results provided support for distinct brain regions to be implicated when stimuli are either repeatedly encoded in the same context or across different contexts. A second set of whole-brain analyses was performed to investigate repetition effects in the two encoding conditions. In the same encoding task condition, repetition enhancement was found to be stronger for subsequent hits+ than hits- judgements in left lateral postcentral and middle temporal gyri. These effects may reflect that some form of explicit retrieval took place during the incidental encoding phase (Kim, 2017; Segaert et al., 2013). Moreover, repetition suppression in the left inferior frontal gyrus predicted subsequent source memory performance. Consistent with this regions role in the selection of competing features (Grindrod et al., 2008), this effect was suggested to reflect facilitated integration of contextual information when items were repeatedly studied in the same context. The repetition suppression effect in the left inferior frontal gyrus predicting subsequent source memory performance was reminiscent of the EEG repetition effect reported in Chapter 5, as both predicted subsequent source memory performance and previous research has drawn links between the left parietal ERP and the left inferior frontal gyrus (Düzel, Picton, et al., 2001; Matsumoto et al., 2005). In line with predictions made from the EEG and fMRI repetition effects reported in Chapters 3 and 4, this may suggest a link between fMRI repetition suppression and reported amplitude changes in scalp EEG. However, as this hypothesis was beyond the scope of the present thesis, the predictions remain purely speculative until replicated in hypothesis-driven future research. In the different task condition, only a trend was observed, which indicated that repetition enhancement was stronger for subsequent hits+ than hits- judgements in the midcingulate cortex. This provided further evidence for an association between repetition enhancement and subsequent memory performance.

The primary aim of the present experimental paradigm was to test the hypothesis that reactivation differentially predicted subsequent source memory for the two encoding task conditions. Successful compared to unsuccessful context/source encoding in the same task condition was predicted to be associated with higher levels of reactivation across repetitions. Conversely, in the different task condition, successful compared to unsuccessful context encoding was proposed to be associated with lower levels of reactivation. Similar results were expected for encoding-retrieval similarity. The representational similarity analysis results provided support for these predictions. Across encoding repetitions, higher pattern similarity, indexing higher levels of reactivation, was associated with superior source memory performance for items that were repeatedly encoded in the same context. In posterior cingulate cortex and precuneus, interactions between encoding task condition and subsequent source memory performance indicated that pattern similarity was higher for subsequent hits- than hits+ judgements. The interaction suggested that different mechanisms underlie successful context encoding in the same and different encoding task condition, namely pattern reactivation and the creation of multiple traces, respectively. Similar findings were reported for similarity patterns between encoding and retrieval. When items were repeatedly encoded in the same context, occipito-temporal pattern reactivation or reinstatement was reported to be higher for hits+ than hits- judgements (although these trends did not survive multiple comparison corrections). In the different task condition, higher encoding-retrieval similarity was found to be associated with worse source memory performance, especially in the ventromedial prefrontal cortex. Interactions also revealed similar patterns of results in right lateral parietal regions. This effect was suggested to reflect the multiple traces that were created during encoding and now available during the retrieval of any particular item. These results support various theoretical accounts that may initially appear to be somewhat opposing. For example, the results from the same task condition support the reactivation view (Benjamin & Tullis, 2010) as well as the transfer-appropriate processing account and cortical reinstatement hypothesis (Morris et al., 1977). Results from the different task condition, on the other hand, support predictions from the multiple trace theory (Nadel & Moscovitch, 1997).

Taken together, the findings reported in Chapters 5 and 6 provide support for distinct neural operations to facilitate context encoding when using different encoding strategies, namely mere repetition or repetition in different contexts. Furthermore, comparing the fMRI mass-univarite repetition effects with the EEG repetition effects provided further preliminary support for an association between fMRI repetition suppression and the observed repetition-related EEG amplitude changes. Although somewhat preliminary at this stage, if replicated, the here presented RSA results may lead to a novel theoretical framework, which integrates a number of existing theoretical accounts to further our understanding of the complexities of memory encoding and retrieval (as discussed in 7.4). Such a framework would extend the transfer-appropriate processing and cortical reinstatement hypothesis (Morris et al., 1977) by integrating that, when different encoding operations are performed across multiple encoding episodes, this will also affect retrieval processes, as reflected in lower encoding-retrieval pattern similarity.

7.3 Methodological limitations and concerns

For the present research, a recognition-source memory paradigm was employed. This type of paradigm allows the researcher to objectively assess recollection, i.e., the retrieval of a particular item along with associated, episodic details (Tulving, 2002). Source memory judgements require participants to retrieve specific, criterial information relating to the study phase (Johnson et al., 1993). Therefore, correct source memory judgements provide us with a measure of recollection. However, incorrect source memory judgements can sometimes be more difficult to interpret. Typically, declarative memory research makes a distinction between recollection and familiarity (e.g., Curran et al., 2006; Diana et al., 2007; H. Eichenbaum et al., 2007), as often assessed with a remember-know (R-K) paradigm (Tulving, 1985). However, incorrect source judgements do not necessarily reflect familiarity judgements, because participants may still be able to remember details from the encoding episode, which were not assessed by the source memory task (see Voss & Paller, 2017). Therefore, recollection of non-criterial episodic information may occur during incorrect source memory judgements (Mulligan & Hirshman, 1997; Yonelinas & Jacoby, 1996). This issue has been raised in the context of neuroimaging studies and may explain weak or non-significant source memory effects in some paradigms. For example, when contrasting hippocampal activation to source memory hits and source memory misses, trials, during which participants were able to recollect non-criterial details, may also be associated with higher activation leading to the absence of source memory effects (Parks, 2007; Vilberg & Rugg, 2008) or even reversed effects (see Astur & Constable, 2004; Duarte et al., 2011; Rekkas et al., 2005). However, it has also been suggested that incorrect source memory judgements rely more on familiarity processes than correct judgements (Squire et al., 2007). For the present research questions, a source memory paradigm was chosen over the alternative approach, namely, the R-K procedure, in order to assess recollection objectively and test for pattern reinstatement relating to criterial information.

Overall, memory performance, especially item memory performance, was very high across all experiments, most likely due to the use of multiple encoding presentations. While memory research generally aims for above chance memory performance to limit the number of guesses, in the present research, the number of misses was too low to be included in any of the neuroimaging analyses. As the main objective was to further our understanding of pattern similarity in relation to memory processes, being able to contrast hits and misses in addition to contrasting source memory outcome, would have allowed some replications of previous research (e.g., Ritchey et al., 2013; Ward et al., 2013; Wing et al., 2015; Xue et al., 2010). Such replications would increase the validity of the novel findings surrounding source memory and encoding modality or encoding context condition, presented in this thesis. Moreover, a number of the present findings were revealed in exploratory analyses. Therefore, those research findings will have to be replicated in order to reach more reliable interpretations and stronger conclusions. Exploratory, data-driven analyses have long been claimed to be important to discover trends in the data that may otherwise be ignored and can lead to the development of novel research questions (Hoaglin, Mosteller, & Tukey, 1983; Loftus, 1993; Tukey, 1980). Furthermore, in neuroimaging research, exploratory approaches, such as searchlight analyses have become widely integrated and, when performed and interpreted cautiously, provide a tool to understand complex neural patterns and relate those to cognition (Cohen et al., 2017; Etzel, Zacks, & Braver, 2013).

7.3.1 Chapters 3 & 4

The behavioural data presented in Chapters 3 and 4 showed that not only item memory but also source memory performance was very high. Therefore, not only misses had to be excluded, but also for the EEG experiment, hits- judgements could not be further divided into the three encoding modalities due to low trial counts. Therefore, it was not possible to analyse ERPs with respect to all three factors of interest during the study phase, i.e., subsequent source memory performance, repetition and encoding modality. Instead, several analyses were carried out, always averaging across one factor, testing for interactions between the remaining two factors. The results from these analyses revealed a main effect of subsequent source memory but only when averaging across the repetition factor and not when averaged over the modality factor. This result indicates that averaging over one of the factors affected the obtained results. Furthermore, generally low trial counts result in lower statistical power. Psychological and neuroscience research has often been criticised for underpowered research, mostly due to small sample sizes but also because of multiple statistical comparisons aiming to test several hypotheses (Button et al., 2013; Maxwell, 2004; Poldrack et al., 2017). The present research is no exception to this, however, limited time and funding resources often make it impossible to meet the gold standard.

Moreover, in the experimental design used for experiment 1 and 2, some items were presented as pictures during the study phase but then cued with words during the recognition task. It could be argued that this constitutes an unfair comparison between the encoding modalities. However, this set of experiments did not investigate whether picture or word stimuli were better remembered, instead one of the aims was to test the hypothesis that reinstatement of pictorial information could be observed during the test phase when the concept was cued with a word, i.e., without the picture. Additionally, when choosing the stimuli from the Bank of Standardized Stimuli (BOSS) Phase II (Brodeur et al., 2014), only concepts with more than 70% name agreement were included.

7.3.2 Chapters 5 & 6

The main limitation of the experimental design used in experiments 3 and 4 (presented in Chapters 5 and 6) was that stimuli repeated in the same task condition were always repeated in the same block/run. Stimuli repeated in different contexts were repeated once per block/run. This created a systematic difference in repetition lag between the two encoding task conditions, whereby same task encoding was associated with shorter repetition lags than different task encoding. Although a control analysis (reported in 5.3.2.3) indicated that LPC amplitudes were not related to repetition lag, this consistent bias between the two conditions cannot be entirely controlled for in statistical analyses. Therefore, any differences between the two encoding task conditions may have arisen because of a difference in repetition lag rather than encoding context. However, there are a number of reasons to assume that the effect of lag was minimal. Previous research has shown that the effect of repetition lag on ERPs and haemodynamic responses was mainly quantitative and not qualitative (Henson et al., 2004), therefore, repetition lag is unlikely to explain the findings, which suggest distinct mechanisms to be involved in same and different task encoding. Moreover, research has demonstrated that lag effects are much more prevalent and have greater magnitudes when comparing immediate and distant repetitions (e.g., Henson, 2003; Renoult, Brodeur, & Debruille, 2010). In the present experimental design, study repetitions were typically spaced by multiple trials (i.e., EEG repetition lags: $M_{SameTask} = 29 \pm 1$, $M_{DifferentTask} = 144 \pm 2$; fMRI repetition lags: $M_{SameTask} = 24 \pm 1$, $M_{DifferentTask} = 120 \pm 2$). A knock-on effect of the limitation concerning this experimental design was that pattern similarity was highly affected by stimuli being either repeated within a run or across runs. Within-run pattern similarity was obviously going to be higher than across-run pattern similarity. Therefore, the two conditions could not directly be compared. However, this should not have affected the source memory contrasts within encoding conditions, nor the interactions showing opposite patterns for the two encoding conditions in relation to source memory performance.

In the discussion of Chapter 5, another issue was raised relating to the pseudo-randomisation of task order used in this experiment. In the different task condition, over frontal electrode sites, a repetition effect emerged that suggested presentations 1 and 3 to be associated with more frontal negativity compared to presentations 2 and 4. As previous research (e.g., Renoult et al., 2012; Van Strien et al., 2005), including Chapter 3 of the present thesis, has typically reported gradual increases in frontal negativity, it was speculated that the frontal repetition pattern reported in Chapter 5 may have been related to the way that task order was pseudo-randomised. This pseudo-randomisation meant that tasks were either presented in the order of 1, 2, 3, 4 or 3, 4, 1, 2 (1 = gender task, 2 = show business task, 3 = British task, 4 = like task). It was suggested that this frontal repetition pattern might reflect that, although all tasks required some form of semantic elaboration, the level of difficulty or processing depth required by tasks 1 and 3 may have been different from tasks 2 and 4. Additional analyses of task accuracy and RTs are presented in Appendix A and indicated that accuracies were higher in task 1 (gender) and task 3 (British) compared to task 2 (show business) in both experiments. Furthermore, RTs for responses in task 2 were slower compared to task 1 and 3. Together, these behavioural results suggest that task 2 was more difficult. Therefore, it is likely that the FN400 is less sensitive to repetition than it is to task difficulty and the level of required semantic elaboration. However, no such patterns were observed for the LPC and different levels of processing depth should not have affected pattern reactivation of individual items in the RSA.

7.4 Theoretical implications

The present research provided novel insights into repeated encoding and retrieval of source memory information. The results support a range of prominent theories of memory formation and retrieval. Most notably, the findings also provide influential support for pattern reactivation to have differential effects on source memory performance depending on whether material is encoded in the same or different contexts. Therefore, this evidence potentially prompts an extension of existing theories.

7.4.1 EEG investigations

Taken together, the EEG data presented in Chapters 3 and 5, revealed repetition and reinstatement effects. In Chapter 3, the results indicated that an early occurring repetition effect was independent of subsequent source memory and encoding modality. In contrast, the repetition effect reported in Chapter 5 was observed in a slightly later time window, which largely overlapped with the timing of the LPC. This repetition effect was further shown to predict subsequent source memory performance, consistent with the role of the LPC in episodic memory recollection (e.g., Friedman & Johnson, 2000; Rugg & Curran, 2007; Wilding & Ranganath, 2012). It therefore appears that the timing of the repetition effect determines whether it is related to subsequent source memory performance. This finding may explain why some research failed to demonstrated a link between ERP repetition effects and subsequent memory performance (e.g., Friedman et al., 1996), i.e., the repetition effect may have occurred earlier and therefore independently of memory processes, perhaps due to lower encoding task demands.

In both EEG investigations, the repetition enhancement in parietal positivity was related to decreases in reaction times, i.e., repetition priming. This indicates that irrespective of the timing of a parietal repetition effect, it is associated with an implicit measure of memory. In other words, the link between repetition and implicit memory would be more stable over time than the link between repetition and expliciti memory. Future research could focus on the latency of repetition effects and test the hypothesis that early repetition is only associated with implicit memory and occurs independently of explicit memory processes. Repetition effects occurring during the LPC time window, on the other hand, reflect implicit and explicit memory processes. Furthermore, future investigations should aim to examine what influences the latencies of repetition effects. It may be that the degree of semantic elaboration and episodic associations required by the encoding task, shift the latency of repetition effects. In the present research, participants either performed an indoor/outdoor judgement task or made semantic or personal judgements about famous people; the experiment in which famous people were judged is likely associated with deeper semantic and episodic stimulus processing. Single-trial analyses during the study phase suggested that the observed parietal repetition effects were only related to item-specific repetition between the first and second stimulus presentation, which was consistent across both EEG experiments. This result led to an interesting new research question concerning ERP repetition effects that occur after the second presentation. It may be that these repetition effects do not index item-specific repetition but rather repeated task performance in an ongoing experiment. This hypothesis remains to be tested. However, the parietal effects observed in these two experiments provided support for the LPC to index novelty. With the aim to draw potential parallels between the EEG and fMRI repetition effects, it was suggested that repetition-related changes in parietal EEG amplitudes may reflect fMRI repetition suppression rather than enhancement. Generally, because of the robustness of neural repetition effects, a repetition paradigm may provide an appropriate way of assessing similarities between EEG and fMRI results in future research. As the comparisons between those neuroimaging techniques was not the primary aim of this research, the here proposed hypotheses will have to be taken as speculative. While performing the same statistical tests may facilitate comparison between the results, it is often not appropriate or even feasible to do so, because scalp EEG data are inherently different from fMRI data. In order not to undermine the relative contribution of each technique (i.e., temporal resolution for EEG and spatial resolution for fMRI), the two resulting measures have to be treated as different. However, it is also important to highlight the need for increased integration of EEG and fMRI results in order to obtain a more comprehensive understanding of the complex mechanisms underlying repeated episodic memory encoding.

The EEG results for a frontal FN400 component did not particularly inform ongoing debates regarding its functional interpretation. In Chapter 3, FN400 mean amplitudes at study were shown to be modulated by repetition, potentially supporting the FN400 being associated with semantic priming (Voss & Paller, 2009; Yovel & Paller, 2004). However, the single-trial analyses indicated that this priming effect was not item specific. In Chapter 5, when stimuli were encoded in different contexts, the FN400 ERP repetition effect showed an unexplained pattern and no reliable frontally distributed repetition-related changes could be identified with mass-univariate analyses. It was speculated that the observed patterns, which were initially attributed to repetition, might instead reflect differences in semantic processing depth during the different tasks. Previous research indicated that FN400 amplitudes were sensitive to conceptual priming, but only when stimuli were rated as meaningful by the participants (Voss et al., 2010). Considering the heterogeneity of FN400 results in subsequent memory paradigms, it appears that this component may be modulated by a cognitive process that is typically not accounted for. Future research may investigate the impact of different depths of semantic elaboration and/or subjective meaning of stimulus and context on FN400 amplitudes.

Finally, in both EEG experiments, LPC amplitudes at test were shown to be sensitive to information associated with the study phase. This may indicate the reinstatement of such study phase information, i.e., encoding modality or encoding context. However, differences in ERP amplitudes do not truly reflect pattern reinstatement as they are merely based on mean activations rather than distributed patterns. Nonetheless, because of the vast amount of evidence supporting the LPC's role in recollection-based memory judgements (Chen et al., 2014; Duarte et al., 2004; Friedman & Johnson, 2000; Rugg & Curran, 2007; Wilding & Ranganath, 2012; Woodruff et al., 2006; Yu & Rugg, 2010), it is plausible that LPC amplitudes could be modulated by the content that is recollected. In Chapter 5, LPC amplitudes were shown to be larger for stimuli that were previously associated with multiple contexts compared to stimuli that were repeatedly encoded in only a single context. This was interpreted as indexing a larger amount of retrieval cues or associated information, in line with previous suggestions that LPC amplitudes are sensitive to the amount of episodic detail that is recollected (see Wilding, 2000). With respect to reinstatement during the test phase, multivariate frequency-analyses of intracranial EEG recordings have successfully demonstrated reinstatement effects (Yaffe et al., 2014; Zhang et al., 2015). However, those investigations typically involve pre-surgical patients and, therefore, generalisability to healthy populations is unclear. Future research may expand these LPC findings of content-sensitivity to pattern reinstatement by measuring spatio-temporal pattern similarity between encoding and retrieval. To the author's knowledge, only one study so far, has examined spatio-temporal EEG patterns in the context of memory formation (Lu, Wang, Chen, & Xue, 2015). It was reported that higher pattern similarity across repetitions was associated with superior episodic memory outcome, in line with previous fMRI research results (e.g., Ward et al., 2013; Xue et al., 2010). However, due to the novelty of using RSA for EEG data (i.e., the absence of well-define preprocessing and analysis pipelines) and the low trial counts in the present EEG experiments, the present thesis does not report any EEG RSA findings.

7.4.2 fMRI investigations

The mass-univariate fMRI investigations presented in Chapter 4 and 6 were primarily concerned with the effects of subsequent source memory performance and encoding modality or encoding context condition on repetition-related changes in mean activation. Both fMRI experiments provided support for an association between repetition enhancement effects and explicit memory processes. More precisely, repetition enhancement was found to be stronger for subsequent hits+ than hits- judgements. These enhancement effects were primarily observed in regions that are typically associated with semantic feature integration and representing items amodally (Binder et al., 2009; Fairhall & Caramazza, 2013; Grindrod et al., 2008), as well as regions that are part of a wider memory network (Cabeza et al., 2012; Johnson & Rugg, 2007; Kim, 2011; Rugg & King, 2017). It was therefore suggested that repetition enhancement effects reflected explicit retrieval during incidental encoding (Kim, 2017; Segaert et al., 2013) and that these explicit retrieval processes during the study phase contributed to successful source retrieval during the test phase. While repetition suppression was reported to be independent of subsequent source memory judgements in Chapter 4, in Chapter 6, repetition suppression in the left inferior frontal gyrus was found to be stronger for subsequent hits+ than hits- judgements when items were repeatedly studied in the same context. It was suggested that this effect may index decreasing levels of feature selection (Grindrod et al., 2008), because the context in which the item was encoded remained stable across repetitions. Generally, a vast amount of research reporting repetition-related changes in mean activation exists in the literature, however, the interpretation of such repetition effects is still debated (see Davis & Poldrack, 2013; Segaert et al., 2013). Because repetition is associated with increases in memory performance, it can be difficult to contrast hits and misses. Future research should aim to further our understanding of repetition-related changes in brain activity, which went beyond the scope of the present research. However, in order to understand how the brain processes repeated items in relation to subsequent memory performance, more conclusive interpretations of repetition suppression and enhancement effects need to be reached.

The primary aim of the present research was to investigate how the relationship between pattern similarity and source memory performance is influenced by encoding modality or encoding context. Using RSA, the first fMRI investigation (Chapter 4) focused on contrasting pattern similarity for hits+ and hits- judgements in a modality-independent context as well as within three different encoding modalities. Across repeated encoding presentations, the results supported the reactivation view (Benjamin & Tullis, 2010; Thios & D'Agostino, 1976), by showing that higher pattern similarity was generally associated with superior subsequent source memory. Interestingly, pattern similarity in occipital gyri predicted subsequent source memory in the uni-modal conditions, while pattern similarity in frontal and temporal gyri predicted source memory performance in the multi-modal encoding condition. Similarity patterns in occipital gyri were thought to reflect reactivation of stimulus-specific perceptual features, while similarity in frontal and temporal gyri was suggested to index feature integration through reactivation of conceptual features (Binder et al., 2009; Fairhall & Caramazza, 2013). This indicates that reactivation of different stimulus properties may have contributed to successful source memory formation. Moreover, when successful source memory encoding, i.e., subsequent hits+ judgements, was compared across the different encoding modalities, occipital-temporal pattern similarity was found to reflect processing of visuo-perceptual information of stimuli repeatedly encoded as pictures. Inferior parietal regions, on the other hand, represented items alternately encoded as pictures and words more similarly, which was interpreted as indexing conceptual processing and feature integration in regions corresponding to semantic processing (Bonnici et al., 2016; Devereux et al., 2013; Shimamura, 2011; Yazar et al., 2017). Finally, ERS patterns relating to source memory performance were found to be largely independent of encoding modality. Higher ERS for hits+ than hits- judgements was reported in superior occipital and posterior parietal regions, which is consistent with previous research (e.g., Ritchey et al., 2013; Wing et al., 2015). Moreover, evidence was provided for the reinstatement of pictorial information during the test phase when items encoded as pictures were cued with the corresponding word. Those results support not only the reactivation view, but also theories proposing similar processes to take place during encoding and retrieval, such as the encoding specificity principle (Tulving, 1983; Tulving & Thomson, 1973), the transfer-appropriate processing account (Morris et al., 1977) and the cortical reinstatement hypothesis (Nyberg et al., 2000; Rugg et al., 2008; Wheeler et al., 2000).

A second fMRI investigation (Chapter 6) was concerned with the effects of encoding context condition on similarity patterns. Theoretical accounts, initially based on behavioural data, suggested that repetition-related improvements in memory performance underlie either reactivation (Thios & D'Agostino, 1976) or encoding variability (Hintzman, 1986; Hintzman & Block, 1971). Research employing retroactive interference paradigms showed that context memory is impaired when the same item is repeated in multiple contexts. The behavioural results reported in Chapters 5 and 6 largely support this notion, as different task encoding was associated with worse source memory (Anderson & Neely, 1996; Hupbach et al., 2007; G. Kim et al., 2017; McGovern, 1964). However, different as compared to same task encoding was also associated with superior item memory, providing some support for the encoding variability view (Hintzman, 1986; Hintzman & Block, 1971). It was suggested that stimulus repetition in a different context, reactivates the memory associated with the first context (McClelland et al., 1995; Norman & O'Reilly, 2003) in order to integrate the novel context by generalising across the two (Richter et al., 2016; Schlichting & Preston, 2015; Schlichting et al., 2014; Shohamy & Wagner, 2008; Zeithamova & Preston, 2010). This interpretation could explain superior item memory as well as worse source memory to be associated with different context encoding. However, no explanation has been put forward for the successful encoding of contextual information during different context encoding. In the present research, reactivation was predicted to enhance source memory in the same task condition, but hinder successful source encoding in the different task condition. The RSA results generally supported these predictions. Interactions between source memory performance and encoding task condition indicated that pattern similarity in the same task condition was higher for hits+ than hits- judgements, consistent with previous research (e.g., van den Honert et al., 2016) and supporting the reactivation view (Benjamin & Tullis, 2010; Thios & D'Agostino, 1976). However, in the different task condition, similarity was lower for hits+ than hits- judgements. Across encoding presentations, this interaction was reported in the posterior cingulate cortex and the precuneus. It was suggested that reactivation was associated with worse context memory, indicating that another mechanism, potentially the creation of multiple traces (Nadel & Moscovitch, 1997), is associated with successful context encoding. Similar patterns of results were observed for encoding-retrieval similarity. Interactions in lateral parietal regions, superior occipital gyri and precuneus revealed higher levels of reactivation to be associated with superior source memory in the same task condition but worse source memory in the different task condition. Additionally, encoding-retrieval pattern similarity to items encoded in multiple contexts was lower for hits+ than hits- judgements in the ventromedial prefrontal cortex. These findings partly supported a variety of theoretical accounts, but also indicate that those existing frameworks should be further developed to incorporate the present findings in one comprehensive theory. For example, the results relating to different task encoding largely support the multiple trace theory, but similar to the CLS account (McClelland et al., 1995; Norman & O'Reilly, 2003; O'Reilly & Norman, 2002), this framework suggests that it is mainly the hippocampus that is involved extracting unique episodic and contextual features by assigning distinct representations to each event (Nadel & Moscovitch, 1997; Norman, 2010; O'Reilly et al., 2014). Here, evidence was provided for posterior parietal regions to be engaged in similar processes, by representing items associated with multiple contexts less similarly when the context is successfully encoded. Furthermore, the results from Chapters 4 and 6 consistently supported an important role for reactivation in memory formation and retrieval.

Because same and different task encoding was shown to be associated with differential item and source memory outcomes as well as different levels of pattern reactivation, future theoretical accounts should aim to incorporate the relative benefits of item and context encoding and how these processes are supported or hindered by reactivation. Moreover, because of the relative novelty of the experimental design employed in experiments 3 and 4, the results will have to be replicated to reach stronger conclusions. The key findings from the present research also have potentially far-reaching real world implications, as they provide insights into two different encoding strategies, i.e., mere repetition and encoding variability. Future research may investigate how behavioural strategies can enhance or hinder neural reactivation in order to optimise memory performance. Moreover, a paradigm with more balanced frequencies of hits+ and hits- judgements as well as misses, will likely provide additional insights into the role of reactivation in item memory encoding and retrieval. The present results have led to exciting new research questions, showing that generalisation and neural reactivation inhibit multiple context encoding. However, it is important to remember that generalisation across contexts is also often useful for memory formation (e.g., Binder & Desai, 2011; Cermak, 1984).

7.4.3 Lay summary of theoretical implications

We have known for a long time now that repeated learning typically leads to better memory performance. Despite numerous theoretical frameworks, it remains largely unclear how repetition boosts memory performance. Two different explanations of how repetitions improves our memory have been put forward: 1) repetitions cause the initial memory to be reactivated, which makes it more stable, 2) each repetition is encoded as a unique event, therefore, we have more ways of accessing a memory compared to when it is only encoded once. These theories have developed over time to integrate relevant behavioural, cognitive and neural results. The present research was designed to test the predictions from those theoretical accounts during different forms of repeated learning, for example, when presented with an object either repeatedly as a picture, repeatedly as a word or as both alternatively, or if we repeated a to-be-learnt stimulus in the same context or in different contexts. Objective measures of memory performance and brain activation were obtained during experiments in which participants repeatedly learned different stimuli followed by a memory test. We probed different types of memories: 1) participants' memory for the stimulus they had previously learned, termed *item memory*, and 2) their memory for additional details relating to the learning event, such as whether a stimulus was a picture or a word or whether they had learnt in one or multiple contexts, termed *source memory*. Generally, our results indicated that memory performance was improved when brain activation patterns were reactivated across repetitions, including during the test phase when memories were retrieved. We did find that those pattern reactivations occurred in different brain regions depending on whether a stimulus was presented as a picture or word or both. This indicates that different brain regions are involved during the learning of different kinds of stimuli, but they appear to perform a similar mechanism – reactivation – in order to boost memory performance. Additionally, when participants remembered that they previously encountered the picture of an object, despite being probed with the correspding word during the memory test, the brain reactivated the patterns relating to the pictures presented during the learning phase. One exception to this general finding of reactivation supporting memory was observed when participants learnt stimuli in different contexts. Here, higher brain pattern reactivation was associated with poorer source memory, i.e., memory for the contexts a stimulus was studied in. This may be explained, because reactivation leads to higher levels of generalisation across repeated events, which typically makes us remember the gist better but at the cost of additional information specific to either one of the times we encountered the event. Finally, if the time it takes for the brain to process and display repetition-related changes overlaps with the time at which memory-related processes occur, it may be easier for us to predict subsequent memory performance from brain measures. Overall, our results suggested that mere repetition was associated with better source memory performance but repeatedly learning something in different contexts improves our memory of the actual stimulus and these two outcomes are supported by different underlying brainc mechanisms.

7.5 General conclusion

To summarise, the research presented in this thesis examined the neural correlates of different repeated encoding conditions in relation to subsequent source memory performance as well as reinstatement effects observed during the test phase. A particular emphasise was placed in the role of pattern reactivation in source memory formation and retrieval.

The results generally supported theories of reactivation and reinstatement, as it was shown that higher pattern similarity, indexing higher levels of reactivation, was associated with superior source memory performance. Pattern reactivation was found to predict source memory in different regions, depending on the modality stimuli were encoded in. Reactivation of different stimulus features was suggested to predict source memory performance when stimuli were repeated perceptually or conceptually. However, when items were encoded in different contexts, lower levels of reactivation across repeated encoding and between encoding and retrieval were associated with superior source memory performance. These results were mostly obtained in posterior midline and lateral parietal regions but also in the ventromedial prefrontal cortex. The findings indicated that two different mechanism underlie successful context encoding when stimuli are either repeatedly encoded in the same context or associated with multiple contexts, namely pattern reactivation and the creation of multiple traces, respectively. Moreover, the EEG results suggested that the timing of a repetition effect indicates whether it predicts subsequent source memory performance. The present findings have furthered our understanding of repeated encoding of item and source memory information and developed novel questions and directions for future research.

References

Addante, R. J., Ranganath, C., Olichney, J., & Yonelinas, A. P. (2012). Neurophysiological evidence for a recollection impairment in amnesia patients that leaves familiarity intact. *Neuropsychologia*, *50*(13), 3004–3014. https://doi.org/10.1016/j.neuropsychologia.2012.07.038

Addante, R. J., Ranganath, C., & Yonelinas, A. P. (2012). Examining ERP correlates of recognition memory: Evidence of accurate source recognition without recollection. *NeuroImage*, *62*(1), 439–450. https://doi.org/10.1016/j.neuroimage.2012.04.031

Allan, K., Robb, W. G. K., & Rugg, M. D. (2000). The effect of encoding manipulations on neural correlates of episodic retrieval. *Neuropsychologia*, *38*(8), 1188–1205. https://doi.org/10.1016/S0028-3932(00)00013-0

Anderson, M. C., & Neely, J. H. (1996). Interference and Inhibition in Memory Retrieval. In E. L. Bjork & R. A. Bjork (Eds.), *Memory. Handbook of Perception and Cognition* (2nd ed., pp. 237–313). San Diego, CA: Academic Press. https://doi.org/10.1016/B978-012102570-0/50010-0

Angel, L., Isingrini, M., Bouazzaoui, B., & Fay, S. (2013). Neural correlates of encoding processes predicting subsequent cued recall and source memory. *Neuroreport*, *24*(4), 176–180. https://doi.org/10.1097/WNR.0b013e32835d8452

Ashburner, J., Barnes, G., Chen, C.-C., Daunizeau, J., Flandin, G., Friston, K. J., … Phillips, C. (2016). SPM12 Manual. Retrieved August 17, 2016, from http://www.fil.ion.ucl.ac.uk/spm/doc/manual.pdf

Astur, R. S., & Constable, R. T. (2004). Hippocampal dampening during a relational memory task. *Behavioural Neuroscience*, *118*(4), 667–675.

Baddeley, A. D. (1978). The trouble with levels: A reexamination of Craik and Lockhardt's framework for memory research. *Psychological Reviews*, *85*(3), 139–152. https://doi.org/10.1037/h0021465

Bakker, A., Kirwan, C. B., Miller, M., & Stark, C. E. L. (2009). Pattern separation in the human hippocampal CA3 and dentate gyrus, *1640*(2008), 1640–1643. https://doi.org/10.1126/science.1152882

Ballesteros, S., Bischof, G. N., Goh, J. O., & Park, D. C. (2013). Neural correlates of conceptual object priming in young and older adults: An event-related functional magnetic resonance imaging study. *Neurobiology of Aging*, *34*(4), 1254–1264. https://doi.org/10.1016/j.neurobiolaging.2012.09.019

Ballesteros, S., González, M., Mayas, J., García-Rodríguez, B., & Reales, J. M. (2009). Cross-modal repetition priming in young and old adults. *European Journal of Cognitive Psychology*, *21*(April 2014), 366–387. https://doi.org/10.1080/09541440802311956

Ballesteros, S., & Reales, J. M. (2004). Intact haptic priming in normal aging and Alzheimer's disease: Evidence for dissociable memory systems. *Neuropsychologia*, *42*(8), 1063–1070. https://doi.org/10.1016/j.neuropsychologia.2003.12.008

Banks, W. P. (1970). Signal detection theory and human memory. *Psychological Bulletin*, *74*(2), 81–99.

Barron, H. C., Garvert, M. M., & Behrens, T. E. J. (2016). Repetition suppression: A means to index neural representations using BOLD? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150355. https://doi.org/10.1098/rstb.2015.0355

Benjamin, A. S., & Tullis, J. (2010). What makes distributed practice effective?

Cognitive Psychology, *61*(3), 228–247. https://doi.org/10.1016/j.cogpsych.2010.05.004

Berman, S., Friedman, D., & Cramer, M. (1991). ERPs during continuous recognition memory for words and pictures. *Bulletin of the Psychonomic Society*, *29*(2), 113–116.

Biederman, I., & Cooper, E. E. (1991). Evidence for complete translational and reflectional invariance in visual object priming. *Perception*, *20*, 585–593.

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, *15*(11), 527–536. https://doi.org/10.1016/j.tics.2011.10.001

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*(12), 2767–2796. https://doi.org/10.1093/cercor/bhp055

Binder, J. R., Medler, D. A., Desai, R. H., Conant, L. L., & Liebenthal, E. (2005). Some neurophysiological constraints on models of word naming. *NeuroImage*, *27*(3), 677–693. https://doi.org/10.1016/j.neuroimage.2005.04.029

Bird, C. M., Keidel, J. L., Ing, L. P., Horner, A. J., & Burgess, N. (2015). Consolidation of complex events via reinstatement in posterior cingulate cortex. *Journal of Neuroscience*, *35*(43), 14426–14434. https://doi.org/10.1523/JNEUROSCI.1774-15.2015

Blondin, F., & Lepage, M. (2005). Decrease and increase in brain activity during visual perceptual priming: An fMRI study on similar but perceptually different complex visual scenes. *Neuropsychologia*, *43*(13), 1887–1900. https://doi.org/10.1016/j.neuropsychologia.2005.03.021

Blumenfeld, R. S., & Ranganath, C. (2007). Prefrontal cortex and long-term memory encoding: An integrative review of findings from neuropsychology and neuroimaging. *The Neuroscientist*, *13*(3), 280–291. https://doi.org/10.1177/1073858407299290

Bonnici, H. M., Chadwick, M. J., Lutti, A., Hassabis, D., Weiskopf, N., & Maguire, E. A. (2012). Detecting representations of recent and remote autobiographical memories in vmPFC and hippocampus. *The Journal of Neuroscience*, *32*(47), 16982–16991. https://doi.org/10.1523/JNEUROSCI.2475-12.2012

Bonnici, H. M., Richter, F. R., Yazar, Y., & Simons, J. S. (2016). Multimodal feature integration in the angular gyrus during episodic and semantic retrieval. *Journal of Neuroscience*, *36*(20), 5462–5471. https://doi.org/10.1523/JNEUROSCI.4310-15.2016

Bosch, S. E., Jehee, J. F. M., Fernández, G., & Doeller, C. F. (2014). Reinstatement of associative memories in early visual cortex is signaled by the hippocampus. *The Journal of Neuroscience*, *34*(22), 7493–7500. https://doi.org/10.1523/JNEUROSCI.0805-14.2014

Bower, G. H. (1972). Stimulus-sampling theory of encoding variability. In A. W. Melton & E. Martin (Eds.), *Coding processes in human memory* (pp. 85–123). Washington, DC: V. H. Winston.

Bray, J. F., Robbins, D., & Witcher, W. B. (1976). Encoding variability theory and the spacing effect in associate learning. *Memory & Cognition*, *4*(5), 548–552. https://doi.org/10.3758/BF03213217

Brewer, J. B., Zhao, Z., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). Making memories: Brain activity that predicts how well visual experience will be remembered. *Science*, *281*, 1185–1187.

Bröder, A., & Meiser, T. (2007). Measuring Source Memory. *Journal of Psychology*, *215*(1), 52–60. https://doi.org/10.1027/0044-3409.215.1.52

Brodeur, M. B., Guérard, K., & Bouras, M. (2014). Bank of Standardized Stimuli (BOSS) phase II: 930 new normative photos. *PLoS ONE*, *9*(9). https://doi.org/10.1371/journal.pone.0106953

Brown, T. I., Staresina, B. P., & Wagner, A. D. (2015). Noninvasive functional and anatomical imaging of the human medial temporal lobe. *Cold Spring Harbor Perspectives in Biology*, *7*(4), a021840.

Buckner, R. L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D. L., … Dale, A. M. (1998). Correlates of object priming revealed by event-related fMRI. *NeuroImage*, *7*(4 PART II), S49.

Bullmore, E. T., Suckling, J., Overmeyer, S., Rabe-Hesketh, S., Taylor, E., & Brammer, M. J. (1999). Global, voxel, and cluster tests, by theory and permutation, for a difference between two groups of structural MR images of the brain. *IEEE Transactions on Medical Imaging*, *18*(1), 32–42. https://doi.org/10.1109/42.750253

Bunzeck, N., Schütze, H., & Düzel, E. (2006). Category-specific organization of prefrontal response-facilitation during priming. *Neuropsychologia*, *44*(10), 1765–1776. https://doi.org/10.1016/j.neuropsychologia.2006.03.019

Button, K. S., Ioannidis, J. P. A., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S. J., & Munafò, M. R. (2013). Power failure: Why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, *14*(5), 365–376. https://doi.org/10.1038/nrn3475

Cabeza, R., Ciaramelli, E., & Moscovitch, M. (2012). Cognitive contributions of the ventral parietal cortex: An integrative theoretical account. *Trends in Cognitive Sciences*, *16*(6), 338–352. https://doi.org/10.1016/j.tics.2012.04.008

Cabeza, R., & Moscovitch, M. (2013). Memory systems, processing modes, and components: functional neuroimaging evidence. *Perspectives on Psychological Science*, *8*(1), 49–55. https://doi.org/10.1177/1745691612469033

Caggiano, D. M., Jiang, Y., & Parasuraman, R. (2006). Aging and repetition priming for targets and distracters in a working memory task. *Neuropsychology, Development, and Cognition. Section B, Aging, Neuropsychology and Cognition*, *13*(859), 552–573. https://doi.org/10.1080/138255890969555

Cansino, S., & Trejo-Morales, P. (2008). Neurophysiology of successful encoding and retrieval of source memory. *Cognitive, Affective & Behavioral Neuroscience*, *8*(1), 85–98. https://doi.org/10.3758/CABN.8.1.85

Cansino, S., Trejo-Morales, P., & Hernandez-Ramos, E. (2010). Age-related changes in neural activity during source memory encoding in young, middle-aged and elderly adults. *Neuropsychologia*, *48*(9), 2537–2549. https://doi.org/10.1016/j.neuropsychologia.2010.04.032

Caramazza, A. (1996). Pictures, words and the brain. *Nature*, *383*(6597), 216–217. https://doi.org/10.1038/383216a0

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, *129*(3), 564–583. https://doi.org/10.1093/brain/awl004

Cave, C. B., Bost, P. R., & Cobb, R. E. (1996). Effects of color and pattern on implicit picture memory. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *22*(3), 639–653.

Cepeda, N. J., Pashler, H., Vul, E., Wixted, J. T., & Rohrer, D. (2006). Distributed practice in verbal recall tasks: A review and quantitative synthesis.

Psychological Bulletin, *132*(3), 354–380. https://doi.org/10.1037/0033-2909.132.3.354

Cermak, L. S. (1984). The episodic semantic distinction in amnesia. In L. R. Squire & N. Butters (Eds.), *The neuropsychology of memory* (pp. 52–62). New York: Guilford Press.

Chanales, A. J. H., Oza, A., Favila, S. E., & Kuhl, B. A. (2017). Overlap among spatial memories triggers repulsion of hippocampal representations. *Current Biology*, *27*(15), 2307–2317.e5. https://doi.org/10.1016/j.cub.2017.06.057

Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*(10), 913–919. https://doi.org/10.1038/13217

Chen, Y. Y., Lithgow, K., Hemmerich, J. A., & Caplan, J. B. (2014). Is what goes in what comes out? Encoding and retrieval event-related potentials together determine memory outcome. *Experimental Brain Research*, *232*(10), 3175–3190. https://doi.org/10.1007/s00221-014-4002-1

Chou, T.-L., Chen, C.-W., Wu, M.-Y., & Booth, J. R. (2009). The role of inferior frontal gyrus and inferior parietal lobule in semantic processing of Chinese characters. *Experimental Brain Research*, *198*(4), 465–475. https://doi.org/10.1007/s00221-009-1942-y.The

Cichy, R. M., Chen, Y., & Haynes, J. D. (2011). Encoding the identity and location of objects in human LOC. *NeuroImage*, *54*(3), 2297–2307. https://doi.org/10.1016/j.neuroimage.2010.09.044

Clarke, R., & Morton, J. (1983). Cross modality facilitation in tachistoscopic word recognition. *The Quarterly Journal of Experimental Psychology Section A*, *35*(1), 79–96. https://doi.org/10.1080/14640748308402118

Cohen, J. D., Daw, N., Engelhardt, B., Hasson, U., Li, K., Niv, Y., … Willke, T. L. (2017). Computational approaches to fMRI analysis. *Nature Neuroscience*, *20*(3), 304–313. https://doi.org/10.1038/nn.4499

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.-A., & Michel, F. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain*, *123*(2), 291–307. https://doi.org/10.1093/brain/123.2.291

Corkin, S. (2013). *Permanent present tense: The unforgettable life of the amnesic patient, H.M.* New York: Basic Books.

Craik, F. I. M., & Lockhart, R. S. (1972). Levels of processing: A framework for memory research. *Journal of Verbal Learning and Verbal Behavior*, *11*(6), 671–684. https://doi.org/10.1016/S0022-5371(72)80001-X

Crowder, R. G. (1976). *Principles of learning and memory*. Hillsdale, NJ: Erlbaum.

Curran, T. (2000). Brain potentials of recollection and familiarity. *Memory & Cognition*, *28*(6), 923–938. https://doi.org/10.3758/BF03209340

Curran, T., Tepe, K. L., & Piatt, C. (2006). Event-related potential explorations of dual processes in recognition memory. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Binding in human memory: A neurocognitive approach* (pp. 467–492). Oxford: Oxford University Press.

Cycowicz, Y. M., & Friedman, D. (2003). Source memory for the color of pictures: Event-related brain potentials (ERPs) reveal sensory-specific retrieval-related activity. *Psychophysiology*, *40*(3), 455–464. https://doi.org/10.1111/1469-8986.00047

Cycowicz, Y. M., Friedman, D., & Snodgrass, J. G. (2001). Remembering the color of objects: An ERP investigation of source memory. *Cerebral Cortex*, *11*(4), 322–334. https://doi.org/10.1093/cercor/11.4.322

Danker, J. F., & Anderson, J. R. (2010). The ghosts of brain states past: Remembering reactivates the brain regions engaged during encoding. *Psychological Bulletin*, *136*(1), 87–102. https://doi.org/10.1037/a0017937

Daselaar, S. M., Prince, S. E., & Cabeza, R. (2004). When less means more: Deactivations during encoding that predict subsequent memory. *NeuroImage*, *23*(3), 921–927. https://doi.org/10.1016/j.neuroimage.2004.07.031

Daselaar, S. M., Veltman, D. J., Rombouts, S. A. R. B., Raaijmakers, Jeroen, G. W., & Jonker, C. (2005). Aging affects both perceptual and lexical/semantic components of word stem priming: An event-related fMRI study. *Neurobiology of Learning and Memory*, *83*(3), 251–262. https://doi.org/10.1016/j.nlm.2005.01.005

Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology*, *16*(6), 693–700. https://doi.org/10.1016/j.conb.2006.10.012

Davachi, L., Maril, A., & Wagner, A. D. (2001). When keeping in mind supports later bringing to mind: Neural markers of phonological rehearsal predict subsequent remembering. *Journal of Cognitive Neuroscience*, *13*(8), 1059–1070. https://doi.org/10.1162/089892901753294356

Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(4), 2157–2162. https://doi.org/10.1073/pnas.0337195100

Davis, T., & Poldrack, R. A. (2013). Measuring neural representations with fMRI: Practices and pitfalls. *Annals of the New York Academy of Sciences*, *1296*(1), 108–134. https://doi.org/10.1111/nyas.12156

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Desai, R., Conant, L. L., Waldron, E., & Binder, J. R. (2006). fMRI of past tense processing: The effects of phonological complexity and task difficulty. *Journal of Cognitive Neuroscience*, *18*(2), 278–297. https://doi.org/10.1162/089892906775783633

Devereux, B. J., Clarke, A., Marouchos, A., & Tyler, L. K. (2013). Representational similarity analysis reveals commonalities and differences in the semantic processing of words and objects. *The Journal of Neuroscience*, *33*(48), 18906–18916. https://doi.org/10.1523/JNEUROSCI.3809-13.2013

Diana, R. A., Van Den Boom, W., Yonelinas, A. P., & Ranganath, C. (2011). ERP correlates of source memory: Unitized source information increases familiarity-based retrieval. *Brain Research*, *1367*, 278–286. https://doi.org/10.1016/j.brainres.2010.10.030

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, *11*(9), 379–386. https://doi.org/10.1016/j.tics.2007.08.001

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2013). Parahippocampal cortex activation during context reinstatement predicts item recollection. *Journal of Experimental Psychology. General*, *142*(4), 1287–1297. https://doi.org/10.1037/a0034029

Do, J., Park, S., Lee, Y., Tark, K., Jeon, M., & Yi, D.-J. (2016). Multivoxel pattern similarity predicts subsequent recollection for scenes repeated across different encoding contexts. In *Cognitive Neuroscience Society* (Vol. April). New York.

Duarte, A., Henson, R. N. A., Knight, R. T., Emery, T., & Graham, K. S. (2010). The orbitofrontal cortex is necessary for temporal context memory. *Journal of Cognitive Neuroscience*, *22*(8), 1819–1831. https://doi.org/10.1162/jocn.2009.21316.The

Duarte, A., Henson, R. N., & Graham, K. S. (2011). Stimulus content and the neural correlates of source memory. *Brain Research*, *1373*, 110–123. https://doi.org/10.1016/j.brainres.2010.11.086

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*(3), 255–272. https://doi.org/10.1016/j.cogbrainres.2003.10.010

Dudai, Y. (2012). The restless engram: Consolidations never end. *Annual Review of Neuroscience*, *35*(1), 227–247. https://doi.org/10.1146/annurev-neuro-062111-150500

Durso, F. T., & Johnson, M. K. (1979). Facilitation in naming and categorizing repeated pictures and words. *Journal of Experimental Psychology: Human Learning and Memory*, *5*(5), 449–459. Retrieved from http://dx.doi.org/10.1037/0278-7393.5.5.449

Düzel, E., Picton, T. W., Cabeza, R., Yonelinas, A. P., Scheich, H., Heinze, H. J., & Tulving, E. (2001). Comparative electrophysiological and hemodynamic measures of neural activation during memory-retrieval. *Human Brain Mapping*, *13*(2), 104–123. https://doi.org/10.1002/hbm.1028

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 Sciences of the United States of America*, *98*(14), 8101–8106. https://doi.org/10.1073/pnas.131205798

Ebbinghaus, H. (1964). *Memory: A contribution to experimental psychology*. (Transl., H. A. Ruger, & C. E. Bussenius, Eds.). New York: Dover Publications. (Original work published in 1885 by Teachers College, Columbia University). Retrieved from http://psychclassics.yorku.ca/Ebbinghaus/index.htm

Eger, E., Ashburner, J., Haynes, J.-D., Dolan, R. J., & Rees, G. (2008). fMRI activity patterns in human LOC carry information about object exemplars within category. *Journal of Cognitive Neuroscience*, *20*(2), 356–370. https://doi.org/10.1162/jocn.2008.20019

Eichenbaum, H. (2000). A cortical–hippocampal system for declarative memory. *Nature Reviews Neuroscience*, *1*(1), 41–50. https://doi.org/10.1038/35036213

Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, *30*(February), 123–152. https://doi.org/10.1146/annurev.neuro.30.051606.094328

Eldridge, L. L., Sarfatti, S., & Knowlton, B. J. (2002). The effect of testing procedure on remember-know judgments. *Psychonomic Bulletin & Review*, *9*(1), 139–145.

Elman, J. A., Rosner, Z. A., Cohn-Sheehy, B. I., Cerreta, A. G., & Shimamura, A. P. (2013). Dynamic changes in parietal activation during encoding: Implications for human learning and memory. *NeuroImage*, *82*, 44–52. https://doi.org/10.1016/j.neuroimage.2013.05.113

Epstein, R. A., Parker, W. E., & Feiler, A. M. (2008). Two kinds of fMRI repetition suppression? Evidence for dissociable neural mechanisms. *Journal of Neurophysiology*, *99*(6), 2877–2886. https://doi.org/10.1152/jn.90376.2008

Estrada-Manilla, C., & Cansino, S. (2012). Event-related potential variations in the encoding and retrieval of different amounts of contextual information. *Behavioural Brain Research*, *232*(1), 190–201. https://doi.org/10.1016/j.bbr.2012.04.012

Etzel, J. A., Zacks, J. M., & Braver, T. S. (2013). Searchlight analysis: Promise, pitfalls, and potential. *NeuroImage*, *78*, 261–269. https://doi.org/10.1016/j.neuroimage.2013.03.041

Fairhall, S. L., & Caramazza, A. (2013). Brain regions that represent amodal conceptual knowledge. *The Journal of Neuroscience*, *33*(25), 10552–10558. https://doi.org/10.1523/JNEUROSCI.0051-13.2013

Favila, S. E., Chanales, A. J. H., & Kuhl, B. A. (2016). Experience-dependent hippocampal pattern differentiation prevents interference during subsequent learning. *Nature Communications*, *6*, 1–10. https://doi.org/10.1038/ncomms11066

Fernández, G., Weyerts, H., Tendolkar, I., Smid, H. G. O. M., Scholz, M., & Heinze, H.-J. (1998). Event-related potentials of verbal encoding into episodic memory: Dissociation between the effects of subsequent memory performance and distinctiveness. *Psychophysiology*, *35*(6), 709–720. https://doi.org/10.1111/1469-8986.3560709

Fleischman, D. A. (2007). Repetition priming in aging and Alzheimer’s disease: An integrative review and future directions. *Cortex*, *43*(7), 889–897. https://doi.org/10.1016/S0010-9452(08)70688-9

Fletcher, P. C., Frith, C. D., Baker, S. C., Shallice, T., Frackowiak, R. S. J., & Dolan, R. J. (1995). The Mind’s Eye—Precuneus activation in memory-related imagery. *NeuroImage*. https://doi.org/10.1006/nimg.1995.1025

Fletcher, P. C., Stephenson, C. M. E., Carpenter, T. A., Donovan, T., & Bullmore, E. T. (2003). Regional brain activations predicting subsequent memory success: An event-related fMRI study of the influence of encoding tasks. *Cortex*, *39*(4–5), 1009–1026. https://doi.org/10.1016/S0010-9452(08)70875-X

Friedman, D., & Johnson, R. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: a selective review. *Microscopy Research and Technique*, *51*(1), 6–28. https://doi.org/10.1002/1097-0029(20001001)51:1<6::AID-JEMT2>3.0.CO;2-R

Friedman, D., Ritter, W., & Snodgrass, J. G. (1996). ERPs during study as a function of subsequent direct and indirect memory testing in young and old adults. *Cognitive Brain Research*, *4*(1), 1–13. https://doi.org/10.1016/0926-6410(95)00041-0

Friedman, D., & Trott, C. (2000). An event-related potential study of encoding in young and older adults. *Neuropsychologia*, *38*(5), 542–557. https://doi.org/10.1016/S0028-3932(99)00122-0

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *360*(1456), 815–836. https://doi.org/10.1098/rstb.2005.1622

Gabrielili, J. D. E., Fleischman, D. A., Margaret Keane, I. M., Reminger, S. L., & Morrell, F. (1995). Double dissociation between memory systems underlying explicit and implicit memory in the human brain. *Psychological Science*, *6*(2), 76–82. https://doi.org/10.1111/j.1467-9280.1995.tb00310.x

Gilmore, A. W., Nelson, S. M., & McDermott, K. B. (2015). A parietal memory network revealed by multiple MRI methods. *Trends in Cognitive Sciences*, *19*(9), 534–543. https://doi.org/10.1016/j.tics.2015.07.004

Glenberg, A., Smith, S. M., & Green, C. (1977). Type I rehearsal: Maintenance and more. *Journal of Verbal Learning and Verbal Behavior*, *16*(3), 339–352. https://doi.org/10.1016/S0022-5371(77)80055-8

Gordon, A. M., Rissman, J., Kiani, R., & Wagner, A. D. (2014). Cortical reinstatement mediates the relationship between content-specific encoding activity and subsequent recollection decisions. *Cerebral Cortex*, *24*(12), 3350–3364. https://doi.org/10.1093/cercor/bht194

Grady, C. L., Mcintosh, A. R., Rajah, M. N., & Craik, F. I. M. (1998). Neural correlates of the episodic encoding of pictures and words. *Proceedings of the National Academy of Sciences*, *95*(5), 2703–2708. https://doi.org/10.1073/pnas.95.5.2703

Graf, P., Squire, L. R., & Mandler, G. (1984). The information that amnesic patients do not forget. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *10*(1), 164–178.

Greene, R. L. (1987). Effects of maintenance rehearsal on human memory. *Psychological Bulletin*, *102*(3), 403–413.

Griffin, M., DeWolf, M., Keinath, A., Liu, X., & Reder, L. (2013). Identical versus conceptual repetition FN400 and parietal old/new ERP components occur during encoding and predict subsequent memory. *Brain Research*, *1512*, 68–77. https://doi.org/10.1016/j.brainres.2013.03.014

Grill-Spector, K., Henson, R. N. A., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*(1), 14–23. https://doi.org/10.1016/j.tics.2005.11.006

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under different viewing conditions in the human lateral occipital complex. *Neuron*, *24*(1), 187–203. https://doi.org/10.1016/S0896-6273(00)80832-6

Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, *107*(1–3), 293–321. https://doi.org/10.1016/S0001-6918(01)00019-1

Grindrod, C. M., Bilenko, N. Y., Myers, E. B., & Blumstein, S. E. (2008). The role of the left inferior frontal gyrus in implicit semantic competition and selection: An event-related fMRI study. *Brain Research*, *1229*, 167–178. https://doi.org/10.1016/j.brainres.2008.07.017

Groh-Bordin, C., Busch, N. A., Herrmann, C. S., & Zimmer, H. D. (2007). Event-related potential repetition effects at encoding predict memory performance at test. *Neuroreport*, *18*(18), 1905–1909. https://doi.org/10.1097/WNR.0b013e3282f2a61d

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*(4), 1879–1890. https://doi.org/10.1016/j.neuroimage.2006.04.215

Groppe, D. M., Urbach, T. P., & Kutas, M. (2011a). Mass univariate analysis of event-related brain potentials/fields I: A critical tutorial review. *Psychophysiology*, *48*(12), 1711–1725. https://doi.org/10.1111/j.1469-8986.2011.01273.x.Mass

Groppe, D. M., Urbach, T. P., & Kutas, M. (2011b). Mass univariate analysis of event-related brain potentials/fields II: Simulation studies. *Psychophysiology*, *48*(12), 1726–1737. https://doi.org/10.1111/j.1469-8986.2011.01272.x

Guillem, F., Rougier, A., & Claverie, B. (1999). Short- and long-delay intracranial ERP repetition effects dissociate memory systems in the human brain. *Journal of Cognitive Neuroscience*, *11*(4), 437–458.

Guo, C., Duan, L., Li, W., & Paller, K. A. (2006). Distinguishing source memory and item memory: Brain potentials at encoding and retrieval. *Brain Research*, *1118*(1), 142–154. https://doi.org/10.1016/j.brainres.2006.08.034

Halgren, E., Baudena, P., Heit, G., Clarke, J. M., Marinkovic, K., & Clarke, M. (1994). Spatio-temporal stages in face and word processing. 1. Depth-recorded potentials in the human occipital, temporal and parietal lobes. *Journal of Physiology - Paris*, *88*(1), 1–50.

Handy, T. C. (2005). *Event-related potentials: A methods handbook*. Cambridge, MA: MIT Press.

Haxby, J. V. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, *293*(5539), 2425–2430. https://doi.org/10.1126/science.1063736

Hebscher, M., & Gilboa, A. (2016). A boost of confidence: The role of the ventromedial prefrontal cortex in memory, decision-making, and schemas. *Neuropsychologia*, *90*, 46–58. https://doi.org/10.1016/j.neuropsychologia.2016.05.003

Henderson, L. (1982). *Orthography and word recognition in reading*. San Diego, CA: Academic Press.

Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, *70*(1), 53–81. https://doi.org/10.1016/S0301-0082(03)00086-8

Henson, R. N. A. (2005). A mini-review of fMRI studies of human medial temporal lobe activity associated with recognition memory. *The Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology*, *58*(3–4), 340–360. https://doi.org/10.1080/02724990444000113

Henson, R. N. A., Cansino, S., Herron, J. E., Robb, W. G. K., & Rugg, M. D. (2003). A familiarity signal in human anterior medial temporal cortex? *Hippocampus*, *13*(2), 301–304. https://doi.org/10.1002/hipo.10117

Henson, R. N. A., & Rugg, M. D. (2003). Neural response supression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia*, *41*(3), 263–270.

Henson, R. N. A., Rylands, A., Ross, E., Vuilleumeir, P., & Rugg, M. D. (2004). The effect of repetition lag on electrophysiological and haemodynamic correlates of visual object priming. *NeuroImage*, *21*(4), 1674–1689. https://doi.org/10.1016/j.neuroimage.2003.12.020

Henson, R. N. A., Shallice, T., & Dolan, R. J. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, *287*(5456), 1269–1272. https://doi.org/10.1126/science.287.5456.1269

Herron, J. E., Henson, R. N. A., & Rugg, M. D. (2004). Probability effects on the neural correlates of retrieval success: An fMRI study. *NeuroImage*, *21*(1), 302–310. https://doi.org/10.1016/j.neuroimage.2003.09.039

Heusser, A. C., Awipi, T., & Davachi, L. (2013). The ups and downs of repetition: Modulation of the perirhinal cortex by conceptual repetition predicts priming and long-term memory. *Neuropsychologia*, *51*(12), 2333–2343. https://doi.org/10.1016/j.neuropsychologia.2013.04.018

Hintzman, D. L. (1986). Schema abstraction in a multiple-trace memory model. *Psychological Review*, *93*(4), 411–428. https://doi.org/10.1037/0033-

295X.93.4.411

Hintzman, D. L., & Block, R. A. (1971). Repetition and memory: Evidence for a multiple-trace hypothesis. *Journal of Experimental Psychology*, *88*(3), 297–306. https://doi.org/10.1037/h0030907

Hoaglin, D. C., Mosteller, F., & Tukey, J. W. (1983). *Understanding Robust and Exploratory Data Analysis*. New York: Wiley Series in probability and mathematical statistics.

Holm, A., Ranta-aho, P. O., Sallinen, M., Karjalainen, P. A., & Muller, K. (2006). Relationship of P300 single-trial responses with reaction time and preceding stimulus sequence. *International Journal of Psychophysiology*, *61*(2), 244–252. https://doi.org/10.1016/j.ijpsycho.2005.10.015

Hoppstädter, M., Baeuchl, C., Diener, C., Flor, H., & Meyer, P. (2015). Simultaneous EEG-fMRI reveals brain networks underlying recognition memory ERP old/new effects. *NeuroImage*, *116*, 112–122. https://doi.org/10.1016/j.neuroimage.2015.05.026

Horner, A. J., & Henson, R. N. A. (2008). Priming, response learning and repetition suppression. *Neuropsychologia*, *46*(7), 1979–1991. https://doi.org/10.1016/j.neuropsychologia.2008.01.018

Huettel, S. A., Song, A. W., & McCarthy, G. (2014). *Functional Magnetic Resonance Imaging* (Third Edit). Sunderland, MA, US: Sinaur Associates, Inc.

Hupbach, A., Gomez, R., Hardt, O., & Nadel, L. (2007). Reconsolidation of episodic memories: A subtle reminder triggers integration of new information. *Learning & Memory*, *14*(1–2), 47–53. https://doi.org/10.1101/lm.365707

Jacoby, L. L. (1983). Perceptual enhancement: Persistent effects of an experience. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *9*(1), 21–38. https://doi.org/10.1037/0278-7393.9.1.21

Jacoby, L. L., & Dallas, M. (1981). On the relationship between autobiographical memory and perceptual learning. *Journal of Experimental Psychology*, *110*(3), 306–340. https://doi.org/10.1037/0096-3445.110.3.306

Jimura, K., & Poldrack, R. A. (2012). Analyses of regional-average activation and multivoxel pattern information tell complementary stories. *Neuropsychologia*, *50*(4), 544–552. https://doi.org/10.1016/j.neuropsychologia.2011.11.007

Johansson, M., & Mecklinger, A. (2003). The late posterior negativity in ERP studies of episodic memory: Action monitoring and retrieval of attribute conjunctions. *Biological Psychology*, *64*(1–2), 91–117. https://doi.org/10.1016/S0301-0511(03)00104-2

Johnson, J. D., McDuff, S. G. R., Rugg, M. D., & Norman, K. A. (2009). Recollection, familiarity, and cortical reinstatement: A multivoxel pattern analysis. *Neuron*, *63*(5), 697–708. https://doi.org/10.1016/j.neuron.2009.08.011

Johnson, J. D., Minton, B. R., & Rugg, M. D. (2008). Content dependence of the electrophysiological correlates of recollection. *NeuroImage*, *39*(1), 406–416. https://doi.org/10.1016/j.neuroimage.2007.08.050

Johnson, J. D., Price, M. H., & Leiker, E. K. (2015). Episodic retrieval involves early and sustained effects of reactivating information from encoding. *NeuroImage*, *106*, 300–310. https://doi.org/10.1016/j.neuroimage.2014.11.013

Johnson, J. D., & Rugg, M. D. (2007). Recollection and the reinstatement of encoding-related cortical activity. *Cerebral Cortex*, *17*(11), 2507–2515. https://doi.org/10.1093/cercor/bhl156

Johnson, J. D., Suzuki, M., & Rugg, M. D. (2013). Recollection, familiarity, and content-sensitivity in lateral parietal cortex: A high-resolution fMRI study.

Frontiers in Human Neuroscience, *7*(May), 219. https://doi.org/10.3389/fnhum.2013.00219

Johnson, M. K., Hashtroudi, S., & Lindsay, D. S. (1993). Source monitoring. *Psychological Bulletin*. https://doi.org/10.1037/0033-2909.114.1.3

Johnson, M. K., Kounios, J., & Nolde, S. F. (1997). Electrophysiological brain activity and memory source monitoring. *Neuroreport*, *8*(5), 1317–1320. https://doi.org/10.1097/00001756-199703240-00051

Johnson, R. J. (1992). Event-related brain potentials. In I. Litvan & Y. Agid (Eds.), *Progressive supranuclear palsy: Clinical and research approaches.* (pp. 122–154). New York: Oxford University Press.

Johnson, R. J. (1995). Event-related potential insights into the neurobiology of memory systems. In F. Boller & J. Grafman (Eds.), *Handbook of Neuropsychology* (Vol. 10, pp. 135–164). Amsterdam, The Netherlands: Elsevier B.V. Retrieved from d:/pdf/Johnson 1995 Chapter.pdf%5Cnhttp://brainlab.psych.qc.cuny.edu/pdfs/ERP Insights into the Neurobiology of Memory Systems.pdf

Josselyn, S. A., Köhler, S., & Frankland, P. W. (2015). Finding the engram. *Nature Reviews Neuroscience*, *16*(9), 521–534. https://doi.org/10.1038/nrn4000

Karlsson Wirebring, L., Wiklund-Hornqvist, C., Eriksson, J., Andersson, M., Jonsson, B., & Nyberg, L. (2015). Lesser neural pattern similarity across repeated tests is associated with better long-term memory retention. *Journal of Neuroscience*, *35*(26), 9595–9602. https://doi.org/10.1523/JNEUROSCI.3550-14.2015

Kazmerski, V. A., & Friedman, D. (1997). Old/new differences in direct and indirect memory tests using pictures and words in within- and cross-form conditions: Event-related potential and behavioral measures. *Cognitive Brain Research*, *5*(4), 255–272. https://doi.org/10.1016/S0926-6410(97)00004-9

Kensinger, E. A., & Schacter, D. L. (2006). Amygdala activityis associated with the successful encoding of item, but not source, information for positive and negative stimuli. *Journal of Neuroscience*, *26*(9), 2564–2570. https://doi.org/10.1523/JNEUROSCI.5241-05.2006

Kensinger, E. A., & Schacter, D. L. (2007). Remembering the specific visual details of presented objects: Neuroimaging evidence for effects of emotion. *Neuropsychologia*, *45*(13), 2951–2962. https://doi.org/10.1016/j.neuropsychologia.2007.05.024

Khader, P., Burke, M., Bien, S., Ranganath, C., & Rösler, F. (2005). Content-specific activation during associative long-term memory retrieval. *NeuroImage*, *27*(4), 805–816. https://doi.org/10.1016/j.neuroimage.2005.05.006

Khader, P., Heil, M., & Rösler, F. (2005). Material-specific long-term memory representations of faces and spatial positions: Evidence from slow event-related brain potentials. *Neuropsychologia*, *43*(14), 2109–2124. https://doi.org/10.1016/j.neuropsychologia.2005.03.012

Khateb, A., Pegna, A. J., Michel, C. M., Landis, T., & Annoni, J. M. (2002). Dynamics of brain activation during an explicit word and image recognition task: An electrophysiological study. *Brain Topography*, *14*(3), 197–213. https://doi.org/10.1023/A:1014502925003

Kim, G., Norman, K. A., & Turk-Browne, N. B. (2017). Neural overlap in item representations across episodes impairs context memory. *BioRxiv*, *preprint*. Retrieved from http://www.biorxiv.org/content/early/2017/04/10/125971

Kim, H. (2011). Neural activity that predicts subsequent memory and forgetting: A meta-analysis of 74 fMRI studies. *NeuroImage*, *54*(3), 2446–2461. https://doi.org/10.1016/j.neuroimage.2010.09.045

Kim, H. (2016). Default network activation during episodic and semantic memory retrieval: A selective meta-analytic comparison. *Neuropsychologia*, *80*, 35–46. https://doi.org/10.1016/j.neuropsychologia.2015.11.006

Kim, H. (2017). Brain regions that show repetition suppression and enhancement: A meta-analysis of 137 neuroimaging experiments. *Human Brain Mapping*, *38*(4), 1894–1913. https://doi.org/10.1002/hbm.23492

King, D. R., de Chastelaine, M., Elward, R. L., Wang, T. H., & Rugg, M. D. (2015). Recollection-related increases in functional connectivity predict individual differences in memory accuracy. *Journal of Neuroscience*, *35*(4), 1763–1772. https://doi.org/10.1523/JNEUROSCI.3219-14.2015

Kirsnert, K., & Smith, M. C. (1974). Modality effects in word identification. *Memory and Cognition*, *2*(4), 637–640.

Koen, J. D., & Rugg, M. D. (2016). Memory reactivation predicts resistance to retroactive interference : Evidence from multivariate classification and pattern similarity analyses. *The Journal of Neuroscience*, *36*(15), 4389–4399. https://doi.org/10.1523/JNEUROSCI.4099-15.2016

Kolers, P. A. (1973). Remembering operations. *Memory & Cognition*, *1*(3), 347–355.

Kolers, P. A. (1976). Reading a year later. *Journal of Experimental Psychology: Human Learning and Memory*, *2*(5), 554–565. Retrieved from http://dx.doi.org/10.1037/0278-7393.2.5.554

Korsnes, M. S., & Magnussen, S. J. (2014). fMRI evidence for dissociation between priming and conscious recognition. *Journal of Integrative Neuroscience*, *13*(3), 1–9.

Koutstaal, W., Wagner, A. D., Rotte, M., Maril, A., Buckner, R. L., & Schacter, D. L. (2001). Perceptual specificity in visual object priming: Functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia*, *39*(2), 184–199. https://doi.org/10.1016/S0028-3932(00)00087-7

Kremers, N. A. W., Deuker, L., Kranz, T. A., Oehrn, C., Fell, J., & Axmacher, N. (2014). Hippocampal control of repetition effects for associative stimuli. *Hippocampus*, *24*(7), 892–902. https://doi.org/10.1002/hipo.22278

Kriegeskorte, N., & Bandettini, P. (2007). Analyzing for information, not activation, to exploit high-resolution fMRI. *NeuroImage*, *38*(4), 649–662. https://doi.org/10.1016/j.neuroimage.2007.02.022

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis - connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, *2*(November), 1–28. https://doi.org/10.3389/neuro.06.004.2008

Kuhl, B. A., & Chun, M. M. (2014). Successful remembering elicits event-specific activity patterns in lateral parietal cortex. *The Journal of Neuroscience*, *34*(23), 8051–8060. https://doi.org/10.1523/JNEUROSCI.4328-13.2014

Kuhl, B. A., Rissman, J., Chun, M. M., & Wagner, A. D. (2011). Fidelity of neural reactivation reveals competition between memories. *Proceedings of the National Academy of Sciences*, *108*(14), 5903–5908. https://doi.org/10.1073/pnas.1016939108

Kuhl, B. A., Rissman, J., & Wagner, A. D. (2012). Multi-voxel patterns of visual category representation during episodic encoding are predictive of subsequent memory. *Neuropsychologia*, *50*(4), 458–469. https://doi.org/10.1016/j.neuropsychologia.2011.09.002

Kuperberg, G. R. (2004). Electroencephalography, event-related potentials, and magnetoencephalography. In S. Rauch & D. Doughtery (Eds.), *Psychiatric Neuroimaging: A Primer for Clinicians* (1st ed., pp. 117–128). Arlington, VA: American Psychiatric Publishing.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, *62*(14), 1–27. https://doi.org/10.1146/annurev.psych.093008.131123

Lacy, J. W., Yassa, M. A., Stark, S. M., Muftuler, L. T., & Stark, C. E. L. (2011). Distinct pattern separation related transfer functions in human CA3/dentate and CA1 revealed using high-resolution fMRI and variable mnemonic similarity. *Learning & Memory (Cold Spring Harbor, N.Y.)*, *18*(1), 15–18. https://doi.org/10.1101/lm.1971111

LaRocque, K. F., Smith, M. E., Carr, V. A., Witthoft, N., Grill-Spector, K., & Wagner, A. D. (2013). Global similarity and pattern separation in the human medial temporal lobe predict subsequent memory. *The Journal of Neuroscience*, *33*(13), 5466–5474. https://doi.org/10.1523/JNEUROSCI.4293-12.2013

Leutgeb, J. K., Leutgeb, S., Moser, M.-B., & Moser, E. I. (2007). Pattern separation in the dentate gyrus and CA3 of the hippocampus. *Science*, *315*(5814), 961–966. https://doi.org/10.1126/science.1135801

Levy, B. J., & Wagner, A. D. (2013). Measuring memory reactivation with functional MRI: Implications for psychological theory. *Perspectives on Psychological Science*, *8*(1), 72–78. https://doi.org/10.1177/1745691612469031

Li, Q., Guo, C., & Jiang, Y. (2008). Brain potentials and repetition effects during encoding and retrieval of words. *Neuroreport*, *19*(14), 1365–1368. https://doi.org/10.1097/WNR.0b013e32830c8dda

Liang, J. C., & Preston, A. R. (2017). Medial temporal lobe reinstatement of content-specific details predicts source memory. *Cortex*, *91*, 67–78. https://doi.org/10.1016/j.cortex.2016.09.011

Lockhart, R. S., & Murdock, B. B. (1970). Memory and the theory of signal detection. *Psychological Bulletin*, *74*(2), 100–109.

Loftus, G. R. (1993). A picture is worth a thousandp values: On the irrelevance of hypothesis testing in the microcomputer age. *Behavior Research Methods, Instruments, & Computers*, *25*(2), 250–256. https://doi.org/10.3758/BF03204506

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature Reviews Neuroscience*, *453*(June), 869–878. https://doi.org/10.1038/nature06976

Logothetis, N. K., & Wandell, B. A. (2004). Interpreting the BOLD signal. *Annual Review of Physiology*, *66*(1), 735–769. https://doi.org/10.1146/annurev.physiol.66.082602.092845

Lohnas, L. J., & Davachi, L. (2017). Disentangling interactions between context switches and the spacing effect. In *Cognitive Neuroscience Society*. San Francisco.

Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, *8*(April), 1–14. https://doi.org/10.3389/fnhum.2014.00213

Lu, Y., Wang, C., Chen, C., & Xue, G. (2015). Spatiotemporal neural pattern similarity supports episodic memory. *Current Biology*, *25*, 780–785. https://doi.org/10.1016/j.cub.2015.01.055

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

Luck, S. J. (2014). *An introduction to the Event-Related Potential Technique* (2nd ed.). London, England: MIT Press.

Luck, S. J., & Kappenman, E. S. (2011). *The Oxford handbook of event-related potential components*. New York: Oxford University Press.

Lundstrom, B. N., Ingvar, M., & Petersson, K. M. (2005). The role of precuneus and left inferior frontal cortex during source memory episodic retrieval. *NeuroImage*, *27*(4), 824–834. https://doi.org/10.1016/j.neuroimage.2005.05.008

Lundstrom, B. N., Petersson, K. M., Andersson, J., Johansson, M., Fransson, P., & Ingvar, M. (2003). Isolating the retrieval of imagined pictures during episodic memory: Activation of the left precuneus and left prefrontal cortex. *NeuroImage*, *20*(4), 1934–1943. https://doi.org/10.1016/j.neuroimage.2003.07.017

Maccotta, L., & Buckner, R. L. (2004). Evidence for neural effects of repetition that directly correlate with behavioral priming. *Journal of Cognitive Neuroscience*, *16*(9), 1625–1632. https://doi.org/10.1162/0898929042568451

MacEvoy, S. P., & Epstein, R. A. (2009). Decoding the representation of multiple simultaneous objects in human occipitotemporal cortex. *Current Biology*, *19*(11), 943–947. https://doi.org/10.1016/j.cub.2009.04.020

MacEvoy, S. P., & Epstein, R. A. (2011). Constructing scenes from objects in human occipitotemporal cortex. *Nature Neuroscience*, *14*(10), 1323–1329. https://doi.org/10.1038/nn.2903

Mack, M. L., Love, B. C., & Preston, A. R. (2016). Dynamic updating of hippocampal object representations reflects new conceptual knowledge. *Proceedings of the National Academy of Sciences*, *113*(46), 13203–13208. https://doi.org/10.1073/pnas.1614048113

Maldjian, J. A., Laurienti, P. J., Kraft, R. A., & Burdette, J. H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *NeuroImage*, *19*(3), 1233–1239. https://doi.org/10.1016/S1053-8119(03)00169-1

Mangels, J. A., Manzi, A., & Summerfield, C. (2010). The first does the work, but the third time's the charm: The effects of massed repetition on episodic encoding of multimodal face-name associations. *Journal of Cognitive Neuroscience*, *22*(3), 457–473. https://doi.org/10.1162/jocn.2009.21201

Mangels, J. A., Picton, T. W., & Craik, F. I. M. (2001). Attention and successful episodic encoding: An event-related potential study. *Cognitive Brain Research*, *11*(1), 77–95. https://doi.org/10.1016/S0926-6410(00)00066-5

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Martin, E. (1968). Stimulus meaningfulness and paired-associate transfer: An encoding variability hypothesis. *Psychological Review*, *75*(5), 421–441. https://doi.org/10.1037/h0026301

Matsumoto, A., Iidaka, T., Haneda, K., Okada, T., & Sadato, N. (2005). Linking semantic priming effect in functional MRI and event-related potentials. *NeuroImage*, *24*(3), 624–634. https://doi.org/10.1016/j.neuroimage.2004.09.008

Maxwell, S. E. (2004). The Persistence of Underpowered Studies in Psychological

Research: Causes, Consequences, and Remedies. *Psychological Methods*, *9*(2), 147–163. https://doi.org/10.1037/1082-989X.9.2.147

Mayes, A. R., Montaldi, D., & Migo, E. (2007). Associative memory and the medial temporal lobes. *Trends in Cognitive Sciences*, *11*(3), 126–135. https://doi.org/10.1016/j.tics.2006.12.003

McBride, D. M., & Dosher, B. A. (2002). A comparison of conscious and automatic memory processes for picture and word stimuli: A process dissociation analysis. *Consciousness and Cognition*, *11*(3), 423–460. https://doi.org/10.1016/S1053-8100(02)00007-7

McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, *7*(7), 293–299. https://doi.org/10.1016/S1364-6613(03)00134-7

McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, *102*(3), 419–457.

McGovern, J. B. (1964). Extinction of associations in four transfer paradigms. *Psychological Monographs: General and Applied*, *78*(16), 1–21. https://doi.org/http://dx.doi.org/10.1037/h0093873

Mechanic, A. (1964). The responses involved in the rote learning of verbal materials. *Journal of Verbal Learning and Verbal Behavior*, *3*(1), 30–36. https://doi.org/10.1016/S0022-5371(64)80056-6

Mechelli, A., Sartori, G., Orlandi, P., & Price, C. J. (2006). Semantic relevance explains category effects in medial fusiform gyri. *NeuroImage*, *30*(3), 992–1002. https://doi.org/10.1016/j.neuroimage.2005.10.017

Mecklinger, A., Johansson, M., Parra, M., & Hanslmayr, S. (2007). Source-retrieval requirements influence late ERP and EEG memory effects. *Brain Research*, *1172*(1), 110–123. https://doi.org/10.1016/j.brainres.2007.07.070

Mecklinger, A., Rosburg, T., & Johansson, M. (2016). Reconstructing the past: The late posterior negativity (LPN) in episodic memory studies. *Neuroscience & Biobehavioral Reviews*, *68*, 621–638. https://doi.org/10.1016/j.neubiorev.2016.06.024

Menard, M. T., Kosslyn, S. M., Thompson, W. L., Alpert, N. M., & Rauch, S. L. (1996). Encoding words and pictures: A positron emission tomography study. *Neuropsychologia*, *34*(3), 185–194. https://doi.org/10.1016/0028-3932(95)00099-2

Michel, C. M., Murray, M. M., Lantz, G., Gonzalez, S., Spinelli, L., & Grave de Peralta, R. (2004). EEG source imaging. *Clinical Neurophysiology*, *115*(10), 2195–2222. https://doi.org/10.1016/j.clinph.2004.06.001

Milner, B., Squire, L. R., & Kandel, E. R. (1998). Cognitive neuroscience and the study of memory. *Neuron*, *20*(3), 445–468. https://doi.org/10.1016/S0896-6273(00)80987-3

Mion, M., Patterson, K., Acosta-Cabronero, J., Pengas, G., Izquierdo-Garcia, D., Hong, Y. T., … Nestor, P. J. (2010). What the left and right anterior fusiform gyri tell us about semantic memory. *Brain*, *133*(11), 3256–3268. https://doi.org/10.1093/brain/awq272

Mitchell, D. B. (2006). Nonconscious priming after 17 years: Invulnerable implicit memory? *Psychological Science*, *17*(11), 925–929. https://doi.org/10.1111/j.1467-9280.2006.01805.x

Mitchell, D. B., & Bruss, P. J. (2003). Age differences in implicit memory:

Conceptual, perceptual or methodological? *Psychology and Aging*, *18*(4), 807–822.

Mitchell, K. J., & Johnson, M. K. (2009). Source monitoring 15 years later: What have we learned from fMRI about the neural mechanisms of source memory? *Psychological Bulletin*, *135*(4), 638–677. https://doi.org/10.1037/a0015849

Mitchell, R. L. C. (2005). The BOLD response during Stroop task-like inhibition paradigms: Effects of task difficulty and task-relevant modality. *Brain and Cognition*, *59*(1), 23–37. https://doi.org/10.1016/j.bandc.2005.04.001

Mollison, M. V., & Curran, T. (2012). Familiarity in source memory. *Neuropsychologia*, *50*(11), 2546–2565. https://doi.org/10.1016/j.neuropsychologia.2012.06.027

Monsell, S. (1985). Repetition and the lexicon. In A. W. Ellis (Ed.), *Progresses in the psychology of language Vol. 2* (pp. 147–195). London, England: Erlbaum.

Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning and Verbal Behavior*, *16*(5), 519–533. https://doi.org/10.1016/S0022-5371(77)80016-9

Moscovitch, M. (1992). Memory and working-with-memory: A component process model based on modules and central systems. *Journal of Cognitive Neuroscience*, *4*(3), 257–267. https://doi.org/10.1162/jocn.1992.4.3.257

Moscovitch, M., & Winocur, G. (1992). Frontal lobes and memory. In L. R. Squire (Ed.), *The Encyclopedia of Learning and Memory: A Volumes in Neuropsychology* (pp. 182–187). New York: Macmillan.

Mulligan, N. W., & Hirshman, E. (1997). Measuring the bases of recognition memory: An investigation of the process-dissociation framework. *Journal of Experimental Psychology: Learning Memory and Cognition*, *23*(2), 280–304.

Mumford, J. A., Turner, B. O., Ashby, F. G., & Poldrack, R. A. (2012). Deconvolving BOLD activation in event-related designs for multivoxel pattern classification analyses. *NeuroImage*, *59*(3), 2636–2643. https://doi.org/10.1016/j.neuroimage.2011.08.076

Naccache, L., & Dehaene, S. (2001). The priming method : Imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cerebral Cortex*, *11*(October), 966–974. https://doi.org/10.1093/cercor/11.10.966

Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion in Neurobiology*, *7*(2), 217–227. https://doi.org/10.1016/S0959-4388(97)80010-4

Neville, H. J., Kutas, M., Chesney, G., & Schmidt, A. L. (1986). Event-related brain potentials during initial encoding and recognition memory of congruous and incongruous words. *Journal of Memory and Language*, *25*(1), 75–92. https://doi.org/10.1016/0749-596X(86)90022-7

Nieuwenhuis, S., & De Rover, M. (2014). Event-related potentials. In *Encyclopedia of Psychopharmacology* (pp. 1–6). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-27772-6_289-2

Norman, K. A. (2010). How hippocampus and cortex contribute to recognition memory: Revisiting the complementary learning systems model. *Hippocampus*, *20*(11), 1217–1227. https://doi.org/10.1002/hipo.20855

Norman, K. A., & O’Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review*, *110*(4), 611–646. https://doi.org/10.1037/0033-295X.110.4.611

Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, *10*(9), 424–430. https://doi.org/10.1016/j.tics.2006.07.005

Nyberg, L., Habib, R., Mcintosh, A. R., & Tulving, E. (2000). Reactivation of encoding-related brain activity during memory retrieval. *Proceedings of the National Academy of Sciences*, *97*, 11120–11124. https://doi.org/10.1073/pnas.97.20.11120

Nyberg, L., McIntosh, A. R., Cabeza, R., Habib, R., Houle, S., & Tulving, E. (1996). General and specific brain regions involved in encoding and retrieval of events: What, where, and when. *Proceedings of the National Academy of Sciences*, *93*(20), 11280–11285. https://doi.org/10.1073/pnas.93.20.11280

O'Reilly, R. C., Bhattacharyya, R., Howard, M. D., & Ketz, N. (2014). Complementary learning systems. *Cognitive Science*, *38*(6), 1229–1248. https://doi.org/10.1111/j.1551-6709.2011.01214.x

O'Reilly, R. C., & McClelland, J. L. (1994). Hippocampal conjunctive encoding , storage , and recall: Avoiding a trade-off. *Hippocampus*, *4*(6), 661–682. https://doi.org/10.1002/hipo.450040605

O'Reilly, R. C., & Norman, K. A. (2002). Hippocampal and neocortical contributions to memory: Advances in the complementary learning systems framework. *Trends in Cognitive Sciences*, *6*(12), 505–510.

Olichney, J. M., Iragui, V. J., Salmon, D. P., Riggins, B. R., Morris, S. K., & Kutas, M. (2006). Absent event-related potential (ERP) word repetition effects in mild Alzheimer's disease. *Clinical Neurophysiology*, *117*(6), 1319–1330. https://doi.org/10.1016/j.clinph.2006.02.022

Olichney, J. M., Van Petten, C., Paller, K. A., Salmon, D. P., Iragui, V. J., & Kutas, M. (2000). Word repetition in amnesia. Electrophysiological measures of impaired and spared memory. *Brain: A Journal of Neurology*, *123*(Pt 9), 1948–1963. https://doi.org/10.1093/brain/123.9.1948

Opitz, B. (2010). Context-dependent repetition effects on recognition memory. *Brain and Cognition*, *73*(2), 110–118. https://doi.org/10.1016/j.bandc.2010.04.003

Otten, L. J. (2007). Fragments of a larger whole: Retrieval cues constrain observed neural correlates of memory encoding. *Cerebral Cortex*, *17*(9), 2030–2038. https://doi.org/10.1093/cercor/bhl111

Otten, L. J., & Rugg, M. D. (2001a). Electrophysiological correlates of memory encoding are task-dependent. *Cognitive Brain Research*, *12*(1), 11–18. https://doi.org/10.1016/S0926-6410(01)00015-5

Otten, L. J., & Rugg, M. D. (2001b). Task-dependency of the neural correlates of episodic encoding as measured by fMRI. *Cerebral Cortex*, *11*(12), 1150–1160. https://doi.org/10.1093/cercor/11.12.1150

Otten, L. J., & Rugg, M. D. (2001c). When more means less: Neural activity related to unsuccessful memory encoding. *Current Biology*, *11*(19), 1528–1530. https://doi.org/10.1016/S0960-9822(01)00454-7

Paller, K. A., & Gross, M. (1998). Brain potentials associated with perceptual priming vs explicit remembering during the repetition of visual word-form. *Neuropsychologia*, *36*(6), 559–571. https://doi.org/10.1016/S0028-3932(97)00132-2

Paller, K. A., Hutson, C. A., Miller, B. B., & Boehm, S. G. (2003). Neural manifestations of memory with and without awareness. *Neuron*, *38*(3), 507–516. https://doi.org/10.1016/S0896-6273(03)00198-3

Paller, K. A., & Kutas, M. (1992). Brain potentials during memory retrieval provide neurophysiological support for the distinction between conscious recollection and priming. *Journal of Cognitive Neuroscience*, *4*(4), 375–392. https://doi.org/10.1162/jocn.1992.4.4.375

Paller, K. A., Kutas, M., & Mayes, A. R. (1987). Neural correlates of encoding in an incidental learning paradigm. *Electroencephalography and Clinical Neurophysiology*, *67*(4), 360–371. https://doi.org/10.1016/0013-4694(87)90124-6

Paller, K. A., McCarthy, G., & Wood, C. C. (1988). ERPs predictive of subsequent recall and recognition performance. *Biological Psychology*, *26*, 269–276.

Paller, K. A., & Wagner, A. D. (2002). Observing the transformation of experience into memory. *Trends in Cognitive Sciences*, *6*(2), 93–102. https://doi.org/10.1016/S1364-6613(00)01845-3

Paré, D., & Quirk, G. J. (2017). When scientific paradigms lead to tunnel vision:Lessons from the study of fear. *Npj Science of Learning*, *2*(1), 6. https://doi.org/10.1038/s41539-017-0007-4

Park, H., Uncapher, M. R., & Rugg, M. D. (2008). Effects of study task on the neural correlates of source encoding. *Learning & Memory*, *15*, 417–425. https://doi.org/10.1101/lm.878908

Parks, C. M. (2007). The role of noncriterial recollection in estimating recollection and familiarity. *Journal of Memory and Language*, *57*(1), 81–100. https://doi.org/10.1016/j.jml.2007.03.003

Pereira, F., Mitchell, T., & Botvinick, M. (2009). Machine learning classifiers and fMRI: a tutorial overview. *NeuroImage*, *45*(1 Suppl), S199–S209. https://doi.org/10.1016/j.neuroimage.2008.11.007

Persson, J., & Nyberg, L. (2000). Conjunction analysis of cortical activations common to encoding and retrieval. *Microscopy Research and Technique*, *51*(1), 39–44. https://doi.org/10.1002/1097-0029(20001001)51:1<39::AID-JEMT4>3.0.CO;2-Q

Persson, J., & Söderlund, H. (2015). Hippocampal hemispheric and long-axis differentiation of stimulus content during episodic memory encoding and retrieval: An activation likelihood estimation meta-analysis. *Hippocampus*, *25*(12), 1614–1631. https://doi.org/10.1002/hipo.22482

Poldrack, R. A., Baker, C. I., Durnez, J., Gorgolewski, K. J., Matthews, P. M., Munafò, M. R., … Yarkoni, T. (2017). Scanning the horizon:Towards transparent and reproducible neuroimaging research. *Nature Reviews Neuroscience*, *18*(2), 115–126. https://doi.org/10.1038/nrn.2016.167

Poldrack, R. A., Mumford, J. A., & Nichols, T. E. (2011). *Handbook of functional MRI data analysis*. Cambridge University Press.

Postman, L., & Knecht, K. (1983). Encoding variability and retention. *Journal of Verbal Learning and Verbal Behavior*, *22*(2), 133–152. https://doi.org/10.1016/S0022-5371(83)90101-9

Postman, L., & Underwood, B. J. (1973). Critical issues in interference theory. *Memory & Cognition*, *1*(1), 19–40. https://doi.org/10.3758/BF03198064

Ranganath, C., Cohen, M. X., & Brozinsky, C. J. (2005). Working memory maintenance contributes to long-term memory formation: Neural and behavioral evidence. *Journal of Cognitive Neuroscience*, *17*(7), 994–1010. https://doi.org/10.1162/0898929054475118

Ranganath, C., Yonelinas, A. P., Cohen, M. X., Dy, C. J., Tom, S. M., & D’Esposito, M. (2004). Dissociable correlates of recollection and familiarity within the medial temporal lobes. *Neuropsychologia*, *42*(1), 2–13.

https://doi.org/10.1016/j.neuropsychologia.2003.07.006

Ratcliff, R., Hockley, W., & McKoon, G. (1985). Components of activation: Repetition and priming effects in lexical decision and recognition. *Journal of Experimental Psychology: General*, *114*(4), 435–450. https://doi.org/10.1037//0096-3445.114.4.435

Reagh, Z. M., & Yassa, M. A. (2014). Repetition strengthens target recognition but impairs similar lure discrimination: Evidence for trace competition. *Learning & Memory*, *21*(7), 342–346. https://doi.org/10.1101/lm.034546.114

Rekkas, P. V., Westerveld, M., Skudlarski, P., Zumer, J., Pugh, K., Spencer, D. D., & Constable, R. T. (2005). Neural correlates of temporal-order judgments versus those of spatial-location: Deactivation of hippocampus may facilitate spatial performance. *Brain and Cognition*, *59*(2), 103–113. https://doi.org/10.1016/j.bandc.2005.05.013

Renoult, L., Brodeur, M. B., & Debruille, J. B. (2010). Semantic processing of highly repeated concepts presented in single-word trials: Electrophysiological and behavioral correlates. *Biological Psychology*, *84*(2), 206–220. https://doi.org/10.1016/j.biopsycho.2010.01.014

Renoult, L., Wang, X., Calcagno, V., Prévost, M., & Debruille, J. B. (2012). From N400 to N300: Variations in the timing of semantic processing with repetition. *NeuroImage*, *61*(1), 206–215. https://doi.org/10.1016/j.neuroimage.2012.02.069

Ress, D., & Heeger, D. J. (2003). Neural correlates of perception in early visual cortex. *Nature Neuroscience*, *6*(4), 414–420. https://doi.org/10.1002/ana.22528.Toll-like

Richter, F. R., Chanales, A. J. H., & Kuhl, B. A. (2016). Predicting the integration of overlapping memories by decoding mnemonic processing states during learning. *NeuroImage*, *124*, 323–335. https://doi.org/10.1016/j.neuroimage.2015.08.051

Rissman, J., & Wagner, A. D. (2012). Distributed representations in memory: Insights from functional brain imaging. *Annual Review of Psychology*, *63*(1), 101–128. https://doi.org/10.1146/annurev-psych-120710-100344

Ritchey, M., Wing, E. A., LaBar, K. S., & Cabeza, R. (2013). Neural similarity between encoding and retrieval is related to memory via hippocampal interactions. *Cerebral Cortex*, *23*(12), 2818–2828. https://doi.org/10.1093/cercor/bhs258

Roediger, H. L., & McDermott, K. B. (1993). Implicit memory in normal human subjects. In H. Spinnler & J. Boller (Eds.), *The Handbook of Neuropsychology* (Vol. 9, pp. 63–131). Amsterdam, The Netherlands: Elsevier.

Rosenbaum, R. S., Köhler, S., Schacter, D. L., Moscovitch, M., Westmacott, R., Black, S. E., … Tulving, E. (2005). The case of K.C.: Contributions of a memory-impaired person to memory theory. *Neuropsychologia*, *43*(7), 989–1021. https://doi.org/10.1016/j.neuropsychologia.2004.10.007

Rösler, F., Heil, M., & Hennighausen, E. (1995). Distinct cortical activation patterns during long-term memory retrieval of verbal, spatial, and color information. *Journal of Cognitive Neuroscience*, *7*, 51–65. https://doi.org/10.1162/jocn.1995.7.1.51

Rossell, S. L., Price, C. J., & Nobre, A. C. (2003). The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia*, *41*(5), 550–564. https://doi.org/10.1016/S0028-3932(02)00181-1

Rugg, M. D., & Allan, K. (1999). Memory retrieval: An electrophysiological perspective. In M. S. Gazzaniga (Ed.), *The New Cognitive Neurosciences* (2nd ed., pp. 805–816). MIT Press. Retrieved from https://www.scopus.com/record/display.uri?eid=2-s2.0-84872110393&origin=inward&txGid=0

Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences*, *11*(6), 251–257. https://doi.org/10.1016/j.tics.2007.04.004

Rugg, M. D., & Doyle, M. C. (1994). Event-related potentials and stimulus repetition in direct and indirect tests of memory. In H.-J. Heinze, T. F. Munte, & G. R. Mangun (Eds.), *Cognitive Electrophysiology* (pp. 124–148). Boston: Birkhauser.

Rugg, M. D., Johnson, J. D., Park, H., & Uncapher, M. R. (2008). Encoding-retrieval overlap in human episodic memory: A functional neuroimaging perspective. *Progress in Brain Research*, *169*(May), 339–352. https://doi.org/10.1016/S0079-6123(07)00021-0

Rugg, M. D., & King, D. R. (2017). Ventral lateral parietal cortex and episodic memory retrieval. *Cortex*, 1–13. https://doi.org/10.1016/j.cortex.2017.07.012

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*(6676), 595–598. https://doi.org/10.1038/33396

Rugg, M. D., Schloerscheidt, A. M., & Mark, R. E. (1998). An electrophysiological comparison of two indices of recollection. *Journal of Memory and Language*, *39*(1), 47–69. https://doi.org/10.1006/jmla.1997.2555

Rugg, M. D., & Vilberg, K. L. (2013). Brain networks underlying episodic memory retrieval. *Current Opinion in Neurobiology*, *23*(2), 255–260. https://doi.org/10.1016/j.conb.2012.11.005

Rugg, M. D., Vilberg, K. L., Mattson, J. T., Yu, S. S., Johnson, J. D., & Suzuki, M. (2012). Item memory, context memory and the hippocampus: FMRI evidence. *Neuropsychologia*, *50*(13), 3070–3079. https://doi.org/10.1016/j.neuropsychologia.2012.06.004

Rugg, M. D., & Yonelinas, A. P. (2003). Human recognition memory: A cognitive neuroscience perspective. *Trends in Cognitive Sciences*, *7*(7), 313–319. https://doi.org/10.1016/S1364-6613(03)00131-1

Sanquist, T. F., Rohrbaugh, J. W., Syndulko, K., & Lindsley, D. B. (1980). Electrocortical signs of levels of processing: Perceptual analysis and recognition memory. *Psychophysiology*. https://doi.org/10.1111/j.1469-8986.1980.tb02299.x

Sayres, R., & Grill-Spector, K. (2006). Object-selective cortex exhibits performance-independent repetition suppression. *Journal of Neurophysiology*, *95*(October), 995–1007. https://doi.org/10.1152/jn.00500.2005

Scarborough, D. L., Cortese, C., & Scarborough, H. S. (1977). Frequency and repetition effects in lexical memory. *Journal of Experimental Psychology: Human Perception and Performance*, *3*, 1–17.

Scarborough, D. L., Gerard, L., & Cortese, C. (1979). Accessing lexical memory: The transfer of word repetition effects across task and modality. *Memory & Cognition*, *7*(1), 3–12. https://doi.org/10.3758/BF03196928

Schacter, D. L., & Buckner, R. L. (1998). Priming and the brain. *Neuron*, *20*, 185–195. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=pubmed&cmd=Retrieve&dopt=AbstractPlus&list_uids=959311384869848337related:EcUnNJ8oUA0J

Schacter, D. L., Wagner, A. D., & Buckner, R. L. (2000). Memory Systems of 1999.

In E. Tulving & F. I. M. Craik (Eds.), *Oxford Handbook of Memory* (pp. 627–643). Oxford, UK: Oxford University Press.

Schacter, D. L., Wig, G. S., & Stevens, W. D. (2007). Reductions in cortical activity during priming. *Current Opinion in Neurobiology*, *17*(2), 171–176. https://doi.org/10.1016/j.conb.2007.02.001

Schendan, H. E., & Kutas, M. (2003). Time course of processes and representations supporting visual object identification and memory. *Journal of Cognitive Neuroscience*, *15*(1), 111–135. https://doi.org/10.1162/089892903321107864

Schlichting, M. L., & Preston, A. R. (2015). Memory integration: Neural mechanisms and implications for behavior. *Current Opinion in Behavioral Sciences*, *1*, 1–8. https://doi.org/10.1016/j.cobeha.2014.07.005

Schlichting, M. L., Zeithamova, D., & Preston, A. R. (2014). CA1 subfield contributions to memory integration and inference. *Hippocampus*, *24*(10), 1248–1260. https://doi.org/10.1002/hipo.22310

Schnider, A., & Ptak, R. (1999). Spontaneous confabulators fail to suppress currently irrelevant memory traces. *Nature Neuroscience1*, *2*(7), 677–681. https://doi.org/10.1038/10236

Schott, B. H., Henson, R. N. A., Richardson-Klavehn, A., Becker, C., Thoma, V., Heinze, H.-J., & Düzel, E. (2005). Redefining implicit and explicit memory: The functional neuroanatomy of priming, remembering, and control of retrieval. *Proceedings of the National Academy of Sciences*, *102*(4), 1257–1262. https://doi.org/10.1073/pnas.0409070102

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery & Psychiatry*, *20*(1), 11–21. https://doi.org/10.1136/jnnp.20.1.11

Segaert, K., Weber, K., de Lange, F. P., Petersson, K. M., & Hagoort, P. (2013). The suppression of repetition enhancement: A review of fMRI studies. *Neuropsychologia*, *51*(1), 59–66. https://doi.org/10.1016/j.neuropsychologia.2012.11.006

Segalowitz, S., Van Roon, P. M., & Dywan, J. (1997). The ERP late positivity: A graduated response to stimulus repetition. *Neuroreport*, *8*(3), 757–760. https://doi.org/10.1097/00001756-199702100-00035

Seghier, M. L. (2013). The angular gyrus: Multiple functions and multiple subdivisions. *The Neuroscientist*, *19*(1), 43–61. https://doi.org/10.1177/1073858412440596

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, and Cognition*, *24*(4), 1005–1025. https://doi.org/10.1037/0278-7393.24.4.1005

Sestieri, C., Shulman, G. L., & Corbetta, M. (2017). The contribution of the human posterior parietal cortex to episodic memory. *Nature Reviews. Neuroscience*, *18*(3), 183–192. https://doi.org/10.1038/nrn.2017.6

Shepard, R. N. (1967). Recognition memory for words, sentences, and pictures. *Journal of Verbal Learning and Verbal Behavior*, *6*(1), 156–163. https://doi.org/10.1016/S0022-5371(67)80067-7

Shimamura, A. P. (2011). Episodic retrieval and the cortical binding of relational activity. *Cognitive, Affective, & Behavioral Neuroscience*, *11*(3), 277–291. https://doi.org/10.3758/s13415-011-0031-4

Shohamy, D., & Wagner, A. D. (2008). Integrating Memories in the Human Brain: Hippocampal-Midbrain Encoding of Overlapping Events. *Neuron*, *60*(2), 378–

389. https://doi.org/10.1016/j.neuron.2008.09.023

Simons, J. S., Garrison, J. R., & Johnson, M. K. (2017). Brain Mechanisms of Reality Monitoring. *Trends in Cognitive Sciences*, *21*(6), 462–473. https://doi.org/10.1016/j.tics.2017.03.012

Simons, J. S., Owen, A. M., Fletcher, P. C., & Burgess, P. W. (2005). Anterior prefrontal cortex and the recollection of contextual information. *Neuropsychologia*, *43*(12), 1774–1783. https://doi.org/10.1016/j.neuropsychologia.2005.02.004

Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. *Nature Reviews Neuroscience*, *4*(8), 637–648. https://doi.org/10.1038/nrn1178

Smith, M. E. (1993). Neurophysiological manifestations of recollective experience during recognition memory judgments. *Journal of Cognitive Neuroscience*, *5*(1), 1–13. https://doi.org/10.1162/jocn.1993.5.1.1

Spaniol, J., Davidson, P. S. R., Kim, A. S. N., Han, H., Moscovitch, M., & Grady, C. L. (2009). Event-related fMRI studies of episodic encoding and retrieval: Meta-analyses using activation likelihood estimation. *Neuropsychologia*, *47*(8–9), 1765–1779. https://doi.org/10.1016/j.neuropsychologia.2009.02.028

Squire, L. R. (2004). Memory systems of the brain: A brief history and current perspective. *Neurobiology of Learning and Memory*, *82*(3), 171–177. https://doi.org/10.1016/j.nlm.2004.06.005

Squire, L. R., Wixted, J. T., & Clark, R. E. (2007). Recognition memory and the medial temporal lobe: A new perspective. *Nature Reviews Neuroscience*, *8*(11), 872–883.

Standing, L., Conezio, J., & Haber, R. N. (1970). Perception and memory for pictures: Single-trial learning of 2500 visual stimuli. *Psychonomic Science*, *19*(2), 73–74. https://doi.org/10.3758/BF03337426

Staresina, B. P., Alink, A., Kriegeskorte, N., & Henson, R. N. A. (2013). Awake reactivation predicts memory in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(52), 21159–21164. https://doi.org/10.1073/pnas.1311989110

Staresina, B. P., Henson, R. N. A., Kriegeskorte, N., & Alink, A. (2012). Episodic reinstatement in the medial temporal lobe. *Journal of Neuroscience*, *32*(50), 18150–18156. https://doi.org/10.1523/JNEUROSCI.4156-12.2012.Episodic

Stark, C. E. L., & Okado, Y. (2003). Making memories without trying: Medial temporal lobe activity associated with incidental memory formation during recognition. *Journal of Neuroscience*, *23*(17), 6748–6753. https://doi.org/23/17/6748 [pii]

Starrfelt, R., & Gerlach, C. (2007). The visual what for area: Words and pictures in the left fusiform gyrus. *NeuroImage*, *35*(1), 334–342. https://doi.org/10.1016/j.neuroimage.2006.12.003

Stern, C. E., Corkin, S., González, R. G., Guimaraes, A. R., Baker, J. R., Jennings, P. J., … Rosen, B. R. (1996). The hippocampal formation participates in novel picture encoding: evidence from functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences, USA*, *93*(16), 8660–8665. https://doi.org/10.1073/pnas.93.16.8660

Suzuki, M., Johnson, J. D., & Rugg, M. D. (2011). Decrements in hippocampal activity with item repetition during continuous recognition: An fMRI study. *Journal of Cognitive Neuroscience*, *23*(6), 1522–1532. https://doi.org/10.1162/jocn.2010.21535

Swick, D., & Knight, R. T. (1997). Event-related potentials differentiate the effects of aging on word and nonword repetition in explicit and implicit memory tasks. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *23*(1), 123–142. https://doi.org/10.1037/0278-7393.23.1.123

Tendolkar, I., Doyle, M. C., & Rugg, M. D. (1997). An event-related potential study of retroactive interference in memory. *NeuroReport*, *8*(2), 501–506.

Thakral, P. P., Wang, T. H., & Rugg, M. D. (2015). Cortical reinstatement and the confidence and accuracy of source memory. *NeuroImage*, *109*, 118–129. https://doi.org/10.1016/j.neuroimage.2015.01.003

Thakral, P. P., Wang, T. H., & Rugg, M. D. (2017). Decoding the content of recollection within the core recollection network and beyond. *Cortex*, *91*, 101–113. https://doi.org/10.1016/j.cortex.2016.12.011

Thios, S. J., & D'Agostino, P. R. (1976). Effects of repetition as a function of study-phase retrieval. *Journal of Verbal Learning and Verbal Behavior*, *15*(5), 529–536. https://doi.org/10.1016/0022-5371(76)90047-5

Tompary, A., & Davachi, L. (2017). Consolidation Promotes the Emergence of Representational Overlap in the Hippocampus and Medial Prefrontal Cortex. *Neuron*, *96*(1), 228–241.e5. https://doi.org/10.1016/j.neuron.2017.09.005

Tonegawa, S., Pignatelli, M., Roy, D. S., & Ryan, T. J. (2015). Memory engram storage and retrieval. *Current Opinion in Neurobiology*, *35*, 101–109. https://doi.org/10.1016/j.conb.2015.07.009

Tukey, J. W. (1980). We need both exploratory and confirmatory. *American Statistician*, *34*(1), 23–25. https://doi.org/10.1080/00031305.1980.10482706

Tulving, E. (1972). Episodic and semantic memory. In E. Tulving & D. W. (Eds.), *Organization of memory* (pp. 381–403). New York: Academic Press.

Tulving, E. (1983). *Elements of episodic memory*. New York: Oxford University Press.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology-Psychologie Canadienne*, *26*(1), 1–12. https://doi.org/10.1093/bja/aev337

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, *53*, 1–25. https://doi.org/10.1146/annurev.psych.53.100901.135114

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science*, *247*(4940), 302–306. https://doi.org/10.1126/science.2296719

Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, *80*(5), 352–373. https://doi.org/10.1037/h0020071

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., … Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, *15*(1), 273–289. https://doi.org/10.1006/nimg.2001.0978

Uncapher, M. R., & Rugg, M. D. (2005). Encoding and the durability of episodic memory: A functional magnetic resonanceimaging study. *Journal of Neuroscience*, *25*(31), 7260–7267. https://doi.org/10.1523/JNEUROSCI.1641-05.2005

van den Honert, R. N., McCarthy, G., & Johnson, M. K. (2016). Reactivation during encoding supports the later discrimination of similar episodic memories. *Hippocampus*, *26*(9), 1168–1178. https://doi.org/10.1002/hipo.22598

Van Strien, J. W., Hagenbeek, R. E., Stam, C. J., Rombouts, S. A. R. B., & Barkhof, F. (2005). Changes in brain electrical activity during extended continuous word recognition. *NeuroImage*, *26*(3), 952–959. https://doi.org/10.1016/j.neuroimage.2005.03.003

Van Turennout, M., Bielamowicz, L., & Martin, A. (2003). Modulation of neural activity during object naming: Effects of time and practice. *Cerebral Cortex*, *13*(4), 381–391. https://doi.org/10.1093/cercor/13.4.381

Vandenberghe, R., Price, C. J., Wise, R., Josephs, O., & Frackowiak, R. S. J. (1996). Functional anatomy of a common semantic system for words and pictures. *Nature*. https://doi.org/10.1038/383254a0

Vannini, P., Hedden, T., Sullivan, C., & Sperling, R. A. (2013). Differential functional response in the posteromedial cortices and hippocampus to stimulus repetition during successful memory encoding. *Human Brain Mapping*, *34*(7), 1568–1578. https://doi.org/10.1002/hbm.22011

Vilberg, K. L., & Rugg, M. D. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*, *46*(7), 1787–1799. https://doi.org/10.1016/j.neuropsychologia.2008.01.004

Voss, J. L., & Federmeier, K. D. (2011). FN400 potentials are functionally identical to N400 potentials and reflect semantic processing during recognition testing. *Psychophysiology*, *48*(4), 532–546. https://doi.org/10.1111/j.1469-8986.2010.01085.x.FN400

Voss, J. L., & Paller, K. A. (2008a). Brain substrates of implicit and explicit memory: The importance of concurrently acquired neural signals of both memory types. *Neuropsychologia*, *46*(13), 3021–3029. https://doi.org/10.1016/j.neuropsychologia.2008.07.010.Brain

Voss, J. L., & Paller, K. A. (2008b). Neural substrates of remembering: Electroencephalographic studies. *Memory Systems. Vol. 3 of Learning and Memory: A Comprehensive Reference*, *1*, 79–98. https://doi.org/10.1016/B978-012370509-9.00106-6

Voss, J. L., & Paller, K. A. (2009). Remembering and knowing: Electrophysiological distinctions at encoding but not retrieval. *NeuroImage*, *46*(1), 280–289. https://doi.org/10.1016/j.neuroimage.2009.01.048

Voss, J. L., & Paller, K. A. (2017). *Neural substrates of remembering : Event-related potential studies*. *Learning and Memory: A Comprehensive Reference* (Third Edit). Elsevier. https://doi.org/10.1016/B978-0-12-805159-7.03031-X

Voss, J. L., Schendan, H. E., & Paller, K. A. (2010). Finding meaning in novel geometric shapes influences electrophysiological correlates of repetition and dissociates perceptual and conceptual priming. *NeuroImage*, *49*(3), 2879–2889. https://doi.org/10.1016/j.neuroimage.2009.09.012

Vuilleumier, P., Henson, R. N. A., Driver, J., & Dolan, R. J. (2002). Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. *Nature Neuroscience*, *5*(5), 491–499. https://doi.org/10.1038/nn839

Wagner, A. D., Koutstaal, W., & Schacter, D. L. (1999). When encoding yields remembering: Insights from event-related neuroimaging. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *354*(1387), 1307–1324. https://doi.org/10.1098/rstb.1999.0481

Wagner, A. D., Schacter, D. L., Rotte, M., Koutstaal, W., Maril, A., Dale, A. M., … Buckner, R. L. (1998). Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science*, *281*(5380), 1188–1191. https://doi.org/10.1126/science.281.5380.1188

Ward, E. J., Chun, M. M., & Kuhl, B. A. (2013). Repetition suppression and multi-voxel pattern similarity differentially track implicit and explicit visual memory.

The Journal of Neuroscience, *33*(37), 14749–14757. https://doi.org/10.1523/JNEUROSCI.4889-12.2013

Warrington, E. K., & Weiskrantz, L. (1974). The effect of prior learning on subsequent retention in amnesic patients. *Neuropsychologia*, *12*(4), 419–428.

Watson, T. D., Azizian, A., Berry, S., & Squires, N. K. (2005). Event-related potentials as an index of similarity between words and pictures. *Psychophysiology*, *42*(4), 361–368. https://doi.org/10.1111/j.1469-8986.2005.00295.x

Weldon, M. S., & Roediger, H. L. (1987). Altering retrieval demands reverses the picture superiority effect. *Memory & Cognition*, *15*(4), 269–280. https://doi.org/10.3758/BF03197030

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, USA*, *97*(20), 11125–11129.

Wig, G. S., Grafton, S. T., Demos, K. E., & Kelley, W. M. (2005). Reductions in neural activity underlie behavioral components of repetition priming. *Nature Neuroscience*, *8*(9), 1228–1233. https://doi.org/10.1038/nn1515

Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology*, *8*(2), 227–233. https://doi.org/10.1016/S0959-4388(98)80144-X

Wiggs, C. L., Weisberg, J., & Martin, A. (2006). Repetition priming across the adult lifespan - The long and short of it. *Aging, Neuropsychology, and Cognition*, *13*(3–4), 308–325. https://doi.org/10.1080/138255890968718

Wilding, E. L. (1999). Separating retrieval strategies from retrieval success: An event- related potential study of source memory. *Neuropsychologia*, *37*(4), 441–454. https://doi.org/10.1016/S0028-3932(98)00100-6

Wilding, E. L. (2000). In what way does the parietal ERP old/new effect index recollection? *International Journal of Psychophysiology*, *35*(1), 81–87. https://doi.org/10.1016/S0167-8760(99)00095-1

Wilding, E. L., & Ranganath, C. (2012). Electrophysiological Correlates of Episodic Memory Processes. In *The Oxford Handbook of Event-Related Potential Components*. Oxford University Press. https://doi.org/10.1093/oxfordhb/9780195374148.013.0187

Wilding, E. L., & Rugg, M. D. (1996). An event-related potential study of recognition memory with and without retrieval of source. *Brain*, *119*(3), 889–905. https://doi.org/10.1093/brain/119.3.889

Wilding, E. L., & Rugg, M. D. (1997). An event related potential study of memory for words spoken aloud or heard. *Neuropsychologia*, *35*(9), 1185–1195. https://doi.org/10.1016/S0028-3932(97)00048-1

Wing, E. A., Ritchey, M., & Cabeza, R. (2015). Reinstatement of individual past events revealed by the similarity of distributed activation patterns during encoding and retrieval. *Journal of Cognitive Neuroscience*, *27*(4), 1–13. https://doi.org/10.1162/jocn_a_00740

Winkler, I., Debener, S., Muller, K.-R., & Tangermann, M. (2015). On the influence of high-pass filtering on ICA-based artifact reduction in EEG-ERP. *Proceedings of the Annual International Conference of the IEEE Engineering in Medicine and Biology Society, EMBS*, *2015–Novem*, 4101–4105. https://doi.org/10.1109/EMBC.2015.7319296

Wixted, J. T. (2009). Remember/Know judgments in cognitive neuroscience: An illustration of the underrepresented point of view. *Learning & Memory*, *16*, 406–412. https://doi.org/10.1101/lm.1312809.familiarity

Woodruff, C. C., Hayama, H. R., & Rugg, M. D. (2006). Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Brain Research*, *1100*(1), 125–135. https://doi.org/10.1016/j.brainres.2006.05.019

Woroch, B., & Gonsalves, B. D. (2010). Event-related potential correlates of item and source memory strength. *Brain Research*, *1317*, 180–191. https://doi.org/10.1016/j.brainres.2009.12.074

Xiang, J. Z., & Brown, M. W. (2004). Neuronal responses related to long-term recognition memory processes in prefrontal cortex. *Neuron*, *42*(5), 817–829. https://doi.org/10.1016/j.neuron.2004.05.013

Xiao, X., Dong, Q., Gao, J., Men, W., Poldrack, R. A., & Xue, G. (2017). Transformed neural pattern reinstatement during episodic memory retrieval. *The Journal of Neuroscience*, *37*(11), 2986–2998. https://doi.org/10.1523/JNEUROSCI.2324-16.2017

Xue, G., Dong, Q., Chen, C., Lu, Z.-L., Mumford, J. A., & Poldrack, R. A. (2013). Complementary role of frontoparietal activity and cortical pattern similarity in successful episodic memory encoding. *Cerebral Cortex*, *23*(7), 1562–1571. https://doi.org/10.1093/cercor/bhs143

Xue, G., Dong, Q., Chen, C., Lu, Z., Mumford, J. A., & Poldrack, R. A. (2010). Greater neural pattern similarity across repetitions is associated with better memory. *Science*, *330*(6000), 97–101. https://doi.org/10.1126/science.1193125

Xue, G., Mei, L., Chen, C., Lu, Z., Poldrack, R. A., & Dong, Q. (2011). Spaced learning enhances subsequent recognition memory by reducing neural repetition suppression. *Journal of Cognitive Neuroscience*, *23*(7), 1624–1633.

Yaffe, R. B., Kerr, M. S. D., Damera, S., Sarma, S. V., Inati, S. K., & Zaghloul, K. A. (2014). Reinstatement of distributed cortical oscillations occurs with precise spatiotemporal dynamics during successful memory retrieval. *Proceedings of the National Academy of Sciences*, *111*(52), 18727–18732. https://doi.org/10.1073/pnas.1417017112

Yassa, M. A., & Reagh, Z. M. (2013). Competitive Trace Theory: A Role for the hippocampus in contextual interference during retrieval. *Frontiers in Behavioral Neuroscience*, *7*(August), 1–13. https://doi.org/10.3389/fnbeh.2013.00107

Yazar, Y., Bergström, Z. M., & Simons, J. S. (2017). Reduced multimodal integration of memory features following continuous theta burst stimulation of angular gyrus. *Brain Stimulation*, *10*(3), 624–629. https://doi.org/10.1016/j.brs.2017.02.011

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*(3), 441–517. https://doi.org/10.1006/jmla.2002.2864

Yonelinas, A. P., & Jacoby, L. L. (1996). Noncriterial recollection: familiarity as automatic, irrelevant recollection. *Consciousness and Cognition*, *5*(5), 131–141. https://doi.org/10.1006/ccog.1996.0008

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*(11), 3002–3008. https://doi.org/10.1523/JNEUROSCI.5295-04.2005

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*(2), 789–800. https://doi.org/10.1016/j.neuroimage.2003.09.034

Yu, S. S., & Rugg, M. D. (2010). Dissociation of the electrophysiological correlates of familiarity strength and item repetition. *Brain Research*, *1320*, 74–84. https://doi.org/10.1016/j.brainres.2009.12.071

Zago, L., Fenske, M. J., Aminoff, E., & Bar, M. (2005). The rise and fall of priming: How visual exposure shapes cortical representations of objects. *Cerebral Cortex*, *15*(11), 1655–1665. https://doi.org/10.1093/cercor/bhi060

Zeithamova, D., Manthuruthil, C., & Preston, A. R. (2016). Repetition suppression in the medial temporal lobe and midbrain is altered by event overlap. *Hippocampus*, *26*(11), 1464–1477. https://doi.org/10.1002/hipo.22622

Zeithamova, D., & Preston, A. R. (2010). Flexible Memories: Differential Roles for Medial Temporal Lobe and Prefrontal Cortex in Cross-Episode Binding. *Journal of Neuroscience*, *30*(44), 14676–14684. https://doi.org/10.1523/JNEUROSCI.3250-10.2010

Zhang, H., Fell, J., Staresina, B. P., Weber, B., Elger, C. E., & Axmacher, N. (2015). Gamma power reductions accompany stimulus-specific representations of dynamic events. *Current Biology*, *25*(5), 635–640. https://doi.org/10.1016/j.cub.2015.01.011

Appendices

Appendix A – Encoding task accuracy and reaction times (experiments 3 and 4)

Chapter 5: Encoding task accuracy and reaction times

While the remainder of the manuscript is primarily concerned with the effects of encoding conditions (same vs. different encoding context), in this section, differences in behavioural performance across the four encoding tasks (gender, show business, British, like) are analysed. First, frequencies of correct answers to the gender, show business and British task were compared in a repeated-measures ANOVA with the factor task. The main effect of task was significant, $F_{1,27} = 24.984$, $p < .001$, with most of the correct responses made in the gender task ($M = 91\% \pm 15$), followed by the British task ($M = 80\% \pm 9$) and the least correct responses were given to the show business question ($M = 69\% \pm 10$). Although participants responded to the question whether they liked the famous person more often with ‘yes’ ($M = 58\% \pm 17$) than with ‘no’ ($M = 42\% \pm 17$), this difference was not statistically significant, $t_{20} = 2.039$, $p = .055$.

RTs to the three tasks (gender, show business, British) were analysed in terms of correct and incorrect responses. A 3 x 2 repeated-measures ANOVA revealed a main effect of task, $F_{2,38} = 6.821$, $p = .003$, and a main effect of task accuracy, $F_{1,19} = 11.500$, $p = .003$. Follow-up analyses revealed that RTs to the show business task were slower than RTs to both, the gender task, $p = .021$, and the British task, $p = .037$. Correct responses were also given faster than incorrect responses. A paired samples t-test revealed that ‘yes’ responses were made faster than ‘no’ responses in the like task, $t_{20} = 2.449$, $p = .024$.

Chapter 6: Encoding task accuracy and reaction times

As in the EEG version of this experiment, this section is only concerned with effects across behavioural performance in the four encoding tasks (gender, show business, British, like). First, frequencies of correct responses were compared across tasks in a one-way repeated-measures ANOVA with three levels (gender, show business, British). This ANOVA revealed a main effect of task, $F_{2,32} = 52.513$, $p < .001$, with all three tasks differing in terms of correct responses, all $p < .001$. The most correct responses were given in the gender task, followed by the British task and the least correct responses were made in the show business task. A paired-samples t-test was carried out on the frequencies of like and dislike responses made in the like task. No statistically significant differences were found, $t_{16} = 1.766$, $p = .096$, with a tendency for more like ($M = 58 \pm 19$) than dislike responses ($M = 42 \pm 19$).

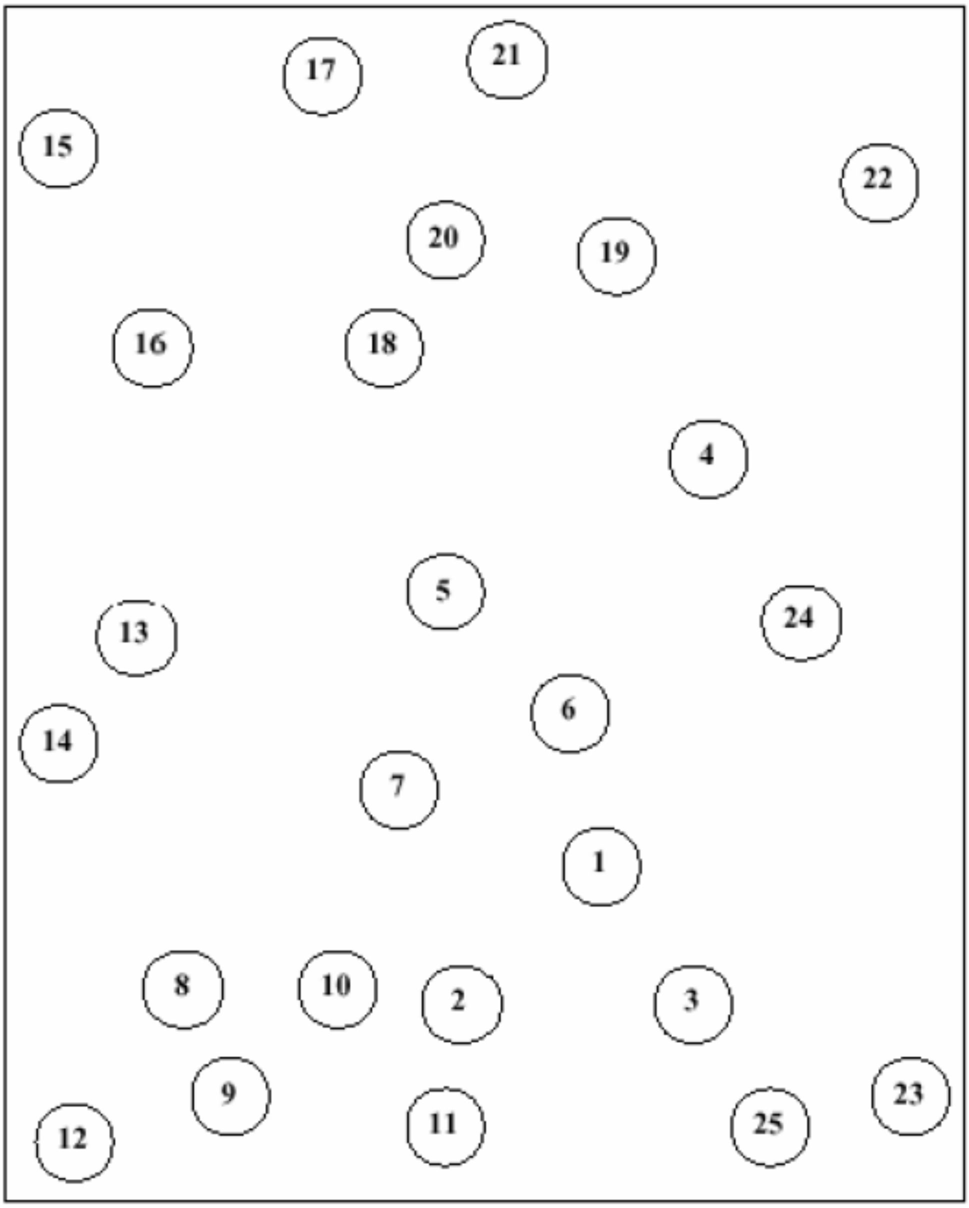
RTs to the three tasks were analysed in terms of correct and incorrect responses. A 3 x 2 repeated-measures ANOVA revealed a main effects of task, $F_{2,32} = 7.186$, $p = .003$, and task performance, $F_{1,16} = 6.666$, $p = .020$. Follow-up analyses revealed that RTs to the gender task were faster than RTs to both, the show business task, $p = .026$, and the British task, $p = .027$. Correct responses were also given faster than incorrect responses. No statistically significant differences were found in RTs for ‘yes’ and ‘no’ responses in the like task, $t_{16} = 0.736$, $p = .472$.

Appendix B – Trail-making task

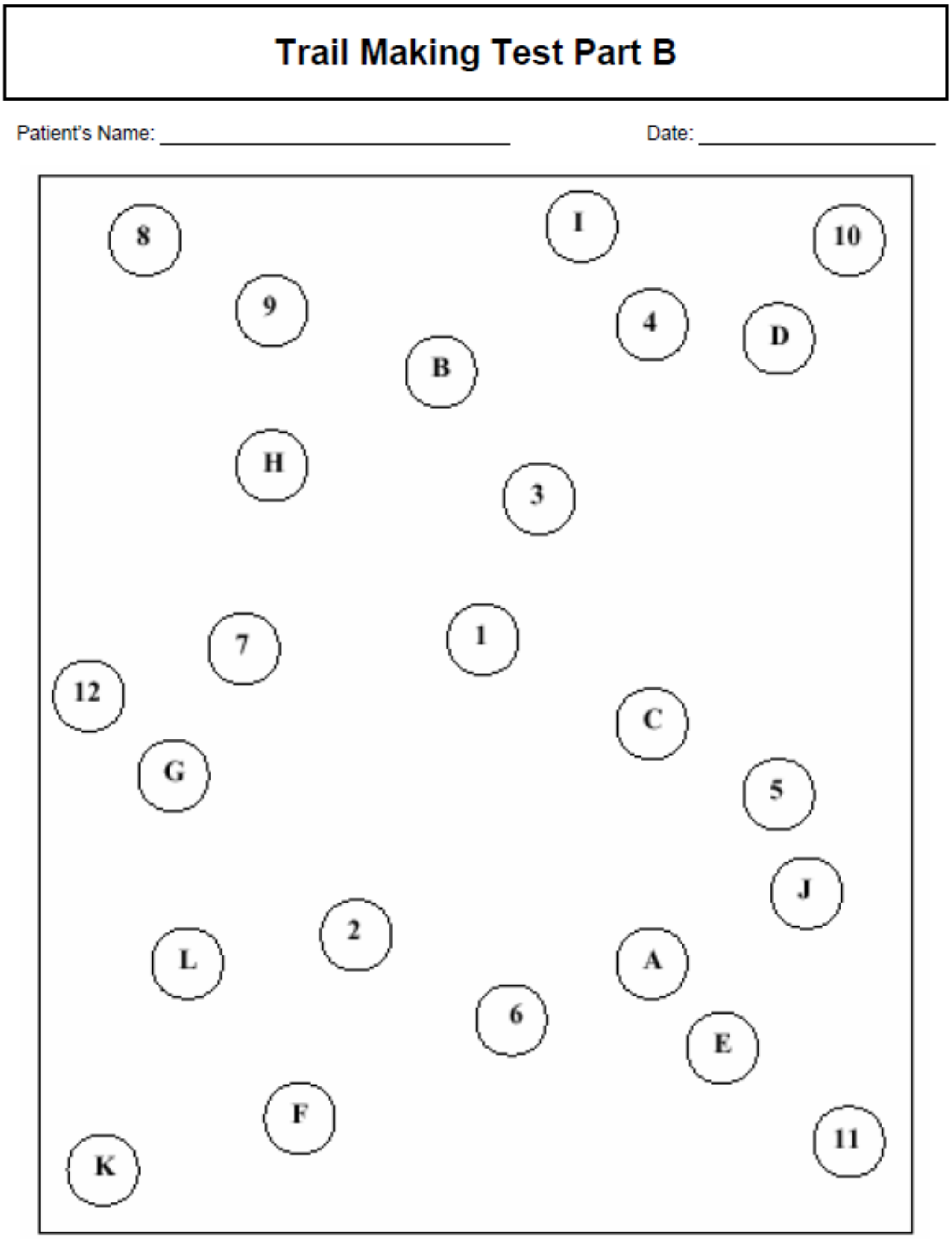
The researcher instructed participants to draw a lines to connect the numbers in ascending order. This task was merely a distractor task.

Trail Making Test Part A

Patient's Name: ______________________________ Date: ____________________



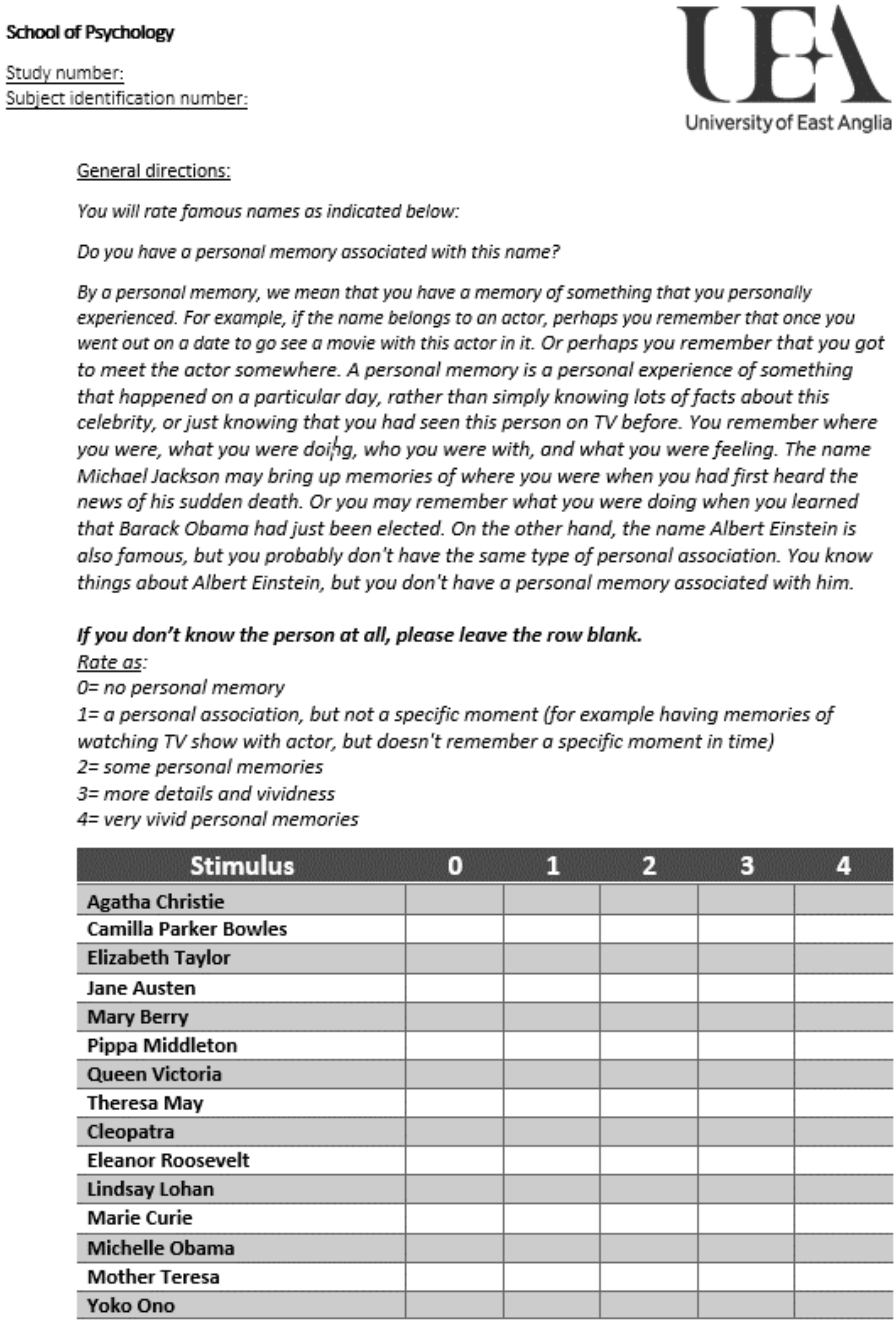
The researcher instructed participants to draw lines to connect the circles in an ascending patterns, but with the added task of alternating between the numbers and letters (i.e., 1-A-2-B-3-C, etc.).



Trail Making Test Part B

Patient's Name: ______________________________ Date: ____________________

Appendix C – Personal memories questionnaire



School of Psychology

University of East Anglia

Study number:
Subject identification number:

General directions:

You will rate famous names as indicated below:

Do you have a personal memory associated with this name?

By a personal memory, we mean that you have a memory of something that you personally experienced. For example, if the name belongs to an actor, perhaps you remember that once you went out on a date to go see a movie with this actor in it. Or perhaps you remember that you got to meet the actor somewhere. A personal memory is a personal experience of something that happened on a particular day, rather than simply knowing lots of facts about this celebrity, or just knowing that you had seen this person on TV before. You remember where you were, what you were doing, who you were with, and what you were feeling. The name Michael Jackson may bring up memories of where you were when you had first heard the news of his sudden death. Or you may remember what you were doing when you learned that Barack Obama had just been elected. On the other hand, the name Albert Einstein is also famous, but you probably don't have the same type of personal association. You know things about Albert Einstein, but you don't have a personal memory associated with him.

If you don't know the person at all, please leave the row blank.

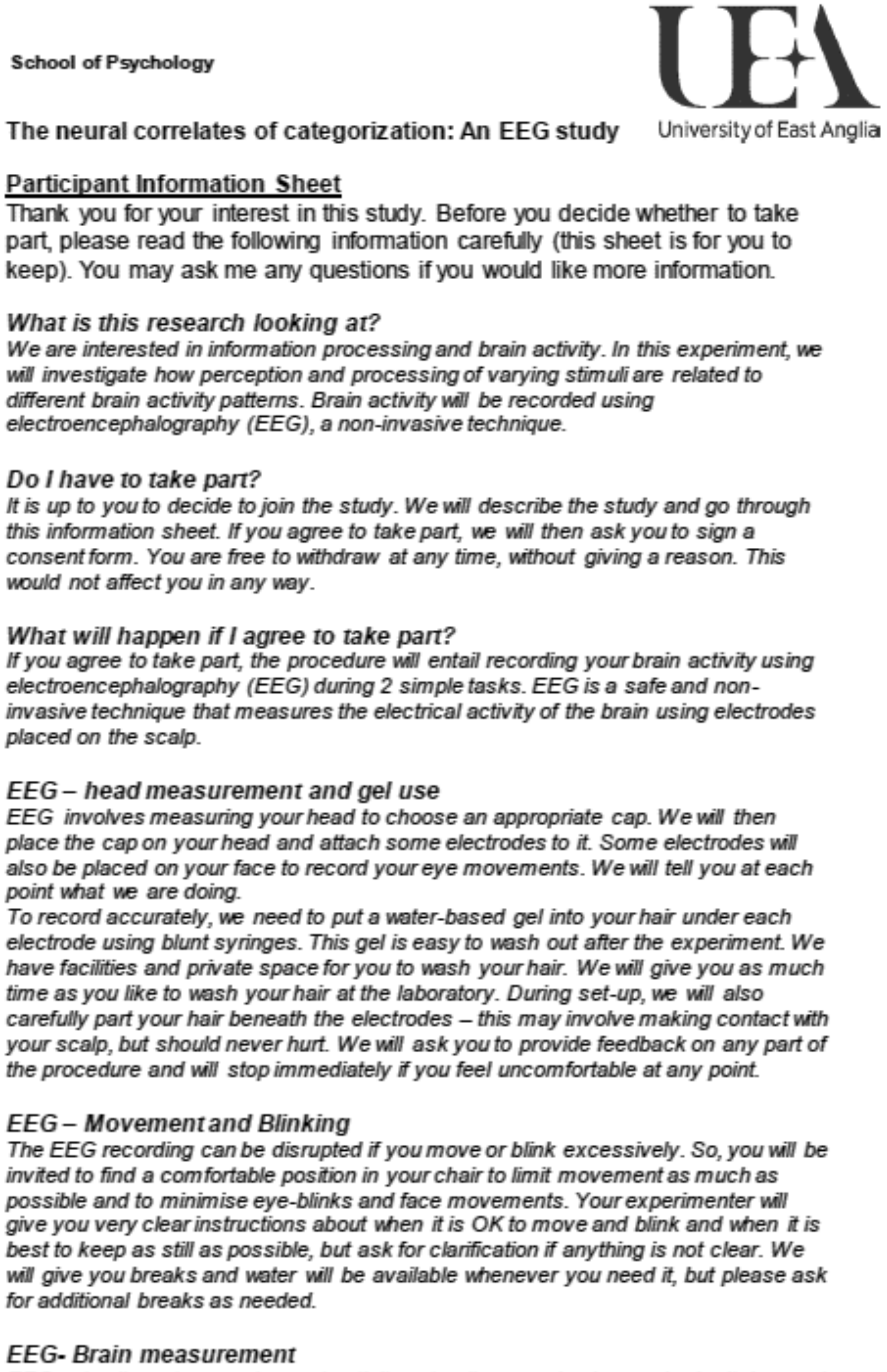
Rate as:
0= no personal memory
1= a personal association, but not a specific moment (for example having memories of watching TV show with actor, but doesn't remember a specific moment in time)
2= some personal memories
3= more details and vividness
4= very vivid personal memories

Stimulus	0	1	2	3	4
Agatha Christie					
Camilla Parker Bowles					
Elizabeth Taylor					
Jane Austen					
Mary Berry					
Pippa Middleton					
Queen Victoria					
Theresa May					
Cleopatra					
Eleanor Roosevelt					
Lindsay Lohan					
Marie Curie					
Michelle Obama					
Mother Teresa					
Yoko Ono					

Emma Bunton					
Helen Mirren					
Jessie J					
Kate Beckinsale					
Keira Knightly					
Maggie Smith					
Victoria Beckham					
Anne Hathway					
Celine Dion					
Halle Berry					
Julia Roberts					
Lady Gaga					
Meryl Streep					
Oprah Winfrey					
Tina Turner					
Andy Murray					
Cat Stevens					
Ed Miliband					
Jamie Oliver					
Lewis Carroll					
Prince Harry					
William Shakespeare					
Albert Einstein					
Elvis Presley					
Jimi Hendrix					
Michael Jackson					
Osama Bin Laden					
Roger Federer					
Steve Jobs					
Vincent Van Gogh					
Daniel Craig					
Ed Sheeran					
Harry Styles					
Keith Richards					
Michael McIntyre					
Noel Gallagher					
Robert Pattinson					
Simon Cowell					
David Guetta					
Eminem					
Hugh Jackman					
Leonardo DiCaprio					
Morgan Freeman					

Tom Hanks					
Zac Efron					
Amy Winehouse					
Vivienne Westwood					
Miuccia Prada					
Sarah Palin					
Emma Watson					
Lilly Allen					
Britney Spears					
Sarah Jessica Parker					
Peter Kay					
Tony Blair					
Pablo Picasso					
David Attenborough					
Mick Jagger					
Bruce Willis					
Justin Timberlake					
Delia Smith					
Rebecca Adlington					
Angela Merkel					
Maria Sharapova					
Jennifer Saunders					
Sharon Osbourne					
Nicole Kidman					
Alfred Hitchcock					
Jonny Wilkinson					
Kurt Cobain					
Michael Jordan					
Chris Moyles					
Robbie Williams					
David Hasselhoff					
Lionel Richie					
Heather Mills					
Princess Diana					
Avril Lavigne					
Marilyn Monroe					
Annie Mac					
Julianne Moore					
Jennifer Aniston					
Mariah Carey					
Charles Darwin					
Mo Farah					
Barack Obama					

Appendix D – Information sheet, consent form, debrief (EEG)



School of Psychology

University of East Anglia

The neural correlates of categorization: An EEG study

Participant Information Sheet

Thank you for your interest in this study. Before you decide whether to take part, please read the following information carefully (this sheet is for you to keep). You may ask me any questions if you would like more information.

What is this research looking at?

We are interested in information processing and brain activity. In this experiment, we will investigate how perception and processing of varying stimuli are related to different brain activity patterns. Brain activity will be recorded using electroencephalography (EEG), a non-invasive technique.

Do I have to take part?

It is up to you to decide to join the study. We will describe the study and go through this information sheet. If you agree to take part, we will then ask you to sign a consent form. You are free to withdraw at any time, without giving a reason. This would not affect you in any way.

What will happen if I agree to take part?

If you agree to take part, the procedure will entail recording your brain activity using electroencephalography (EEG) during 2 simple tasks. EEG is a safe and non-invasive technique that measures the electrical activity of the brain using electrodes placed on the scalp.

EEG – head measurement and gel use

EEG involves measuring your head to choose an appropriate cap. We will then place the cap on your head and attach some electrodes to it. Some electrodes will also be placed on your face to record your eye movements. We will tell you at each point what we are doing.

To record accurately, we need to put a water-based gel into your hair under each electrode using blunt syringes. This gel is easy to wash out after the experiment. We have facilities and private space for you to wash your hair. We will give you as much time as you like to wash your hair at the laboratory. During set-up, we will also carefully part your hair beneath the electrodes – this may involve making contact with your scalp, but should never hurt. We will ask you to provide feedback on any part of the procedure and will stop immediately if you feel uncomfortable at any point.

EEG – Movement and Blinking

The EEG recording can be disrupted if you move or blink excessively. So, you will be invited to find a comfortable position in your chair to limit movement as much as possible and to minimise eye-blinks and face movements. Your experimenter will give you very clear instructions about when it is OK to move and blink and when it is best to keep as still as possible, but ask for clarification if anything is not clear. We will give you breaks and water will be available whenever you need it, but please ask for additional breaks as needed.

EEG- Brain measurement

EEG only allows to record neural activity naturally occurring in your brain. It does not stimulate any part of your brain, nor allow to "read your mind". It will not be used to diagnose any condition.

If you wish to receive more information about EEG before you decide to take part, please feel free to ask us. The experiment will take between 2 and 3 hours.

Are there any problems with taking part?

The placement of the EEG cap is not painful, although there may be minor discomfort. Some people find that their skin may be slightly reddened after the electrodes are removed. This reddening will disappear within a few hours. If you experience any irritation or inconvenience during the study, you can choose to stop at any time.

Will it help me if I take part?

If you are interested in how the EEG works, this is a great opportunity to learn something about it. Furthermore, your participation will benefit the programme of research

How will you store the information that I give you?

All information which you provide during the study will be stored in accordance with the 1998 Data Protection Act and kept strictly confidential. The chief investigator will be the custodian of the anonymous research data. If you have electronic data make sure participants know it will be on a password protected computer. Where are you going to store paper information – it should be stored in a locked storage area – preferably in an academic's filing cabinet in a locked office. Make it clear that data won't be linked to anyone's name. You could also let participants know that only you and the research team will have access to the data. You must adhere to the ethics committee's protocols on data storage.

How will the data be used?

The data collected within this study will be used in my doctoral thesis. It may also be presented in journals and at conferences. However, only group data will be presented and you will never be identified.

What happens if I agree to take part, but change my mind later?

You have the right to withdraw from the study at any time but once you have completed the study you will not be able to because of the anonymous nature of the data.

How do I know that this research is safe for me to take part in?

Participants need to know that the research has been approved by an ethics committee and when e.g. All research in the University is looked at by an independent group of people, called a Research Ethics Committee, to protect your safety, rights, wellbeing and dignity. This research was approved by the Psychology Research Ethics Committee at the University of East Anglia on 11/03/2015.

You are under no obligation to agree to take part in this research.

If you do agree you can **withdraw at any time without giving a reason.**

Contact details:

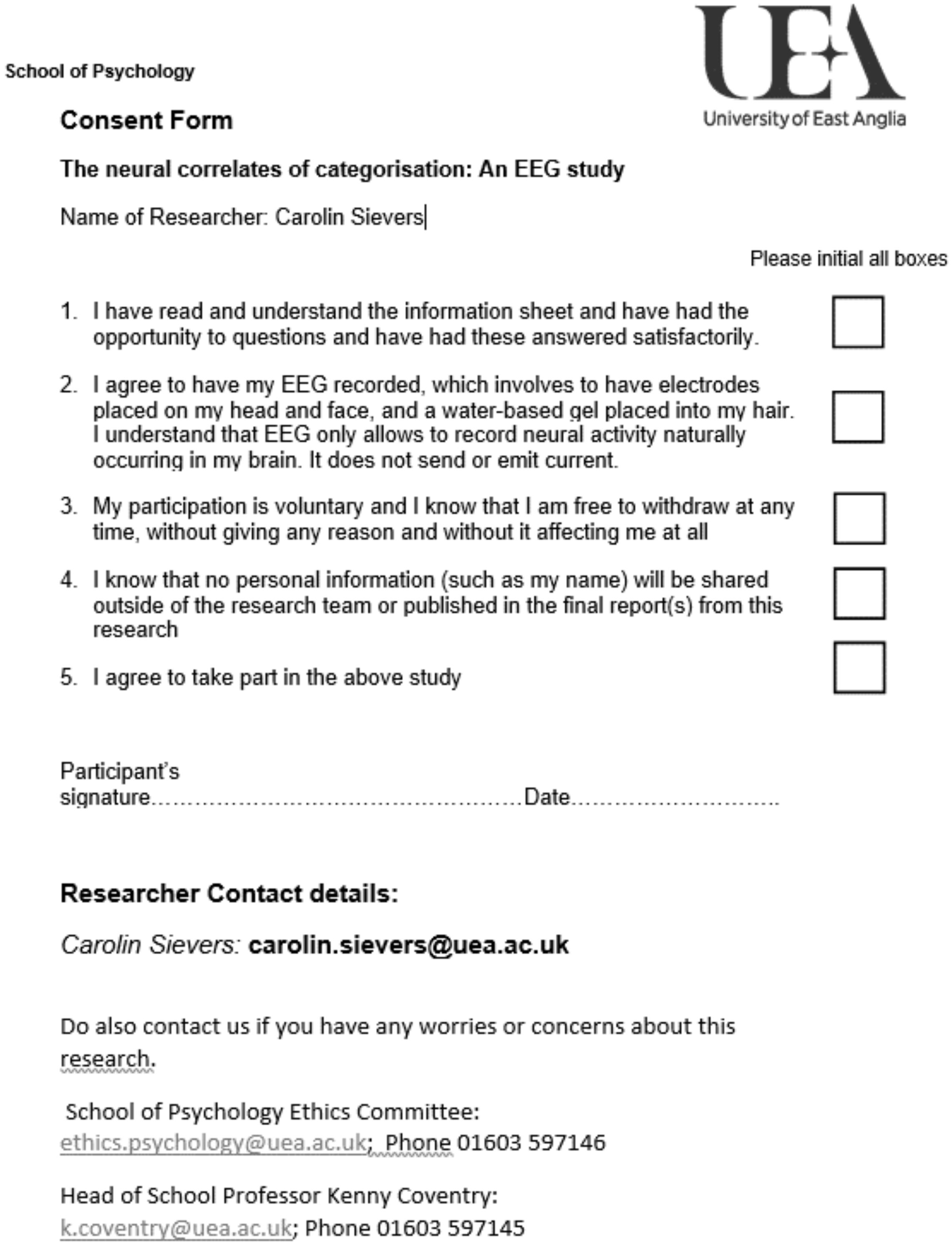
- Researcher: Carolin Sievers (carolin.sievers@uea.ac.uk)
- Supervisor: Dr. Louis Renoult (l.renoult@uea.ac.uk)

Do also contact us if you have any worries or concerns about this research.

School of Psychology Ethics Committee: ethics.psychology@uea.ac.uk; Phone 01603 597146

Head of School Professor Kenny Coventry: k.coventry@uea.ac.uk; Phone 01603 597145

ii



School of Psychology

University of East Anglia

Consent Form

The neural correlates of categorisation: An EEG study

Name of Researcher: Carolin Sievers

Please initial all boxes

1. I have read and understand the information sheet and have had the opportunity to questions and have had these answered satisfactorily. ☐
2. I agree to have my EEG recorded, which involves to have electrodes placed on my head and face, and a water-based gel placed into my hair. I understand that EEG only allows to record neural activity naturally occurring in my brain. It does not send or emit current. ☐
3. My participation is voluntary and I know that I am free to withdraw at any time, without giving any reason and without it affecting me at all ☐
4. I know that no personal information (such as my name) will be shared outside of the research team or published in the final report(s) from this research ☐
5. I agree to take part in the above study ☐

Participant's signature……………………………………………Date………………………….

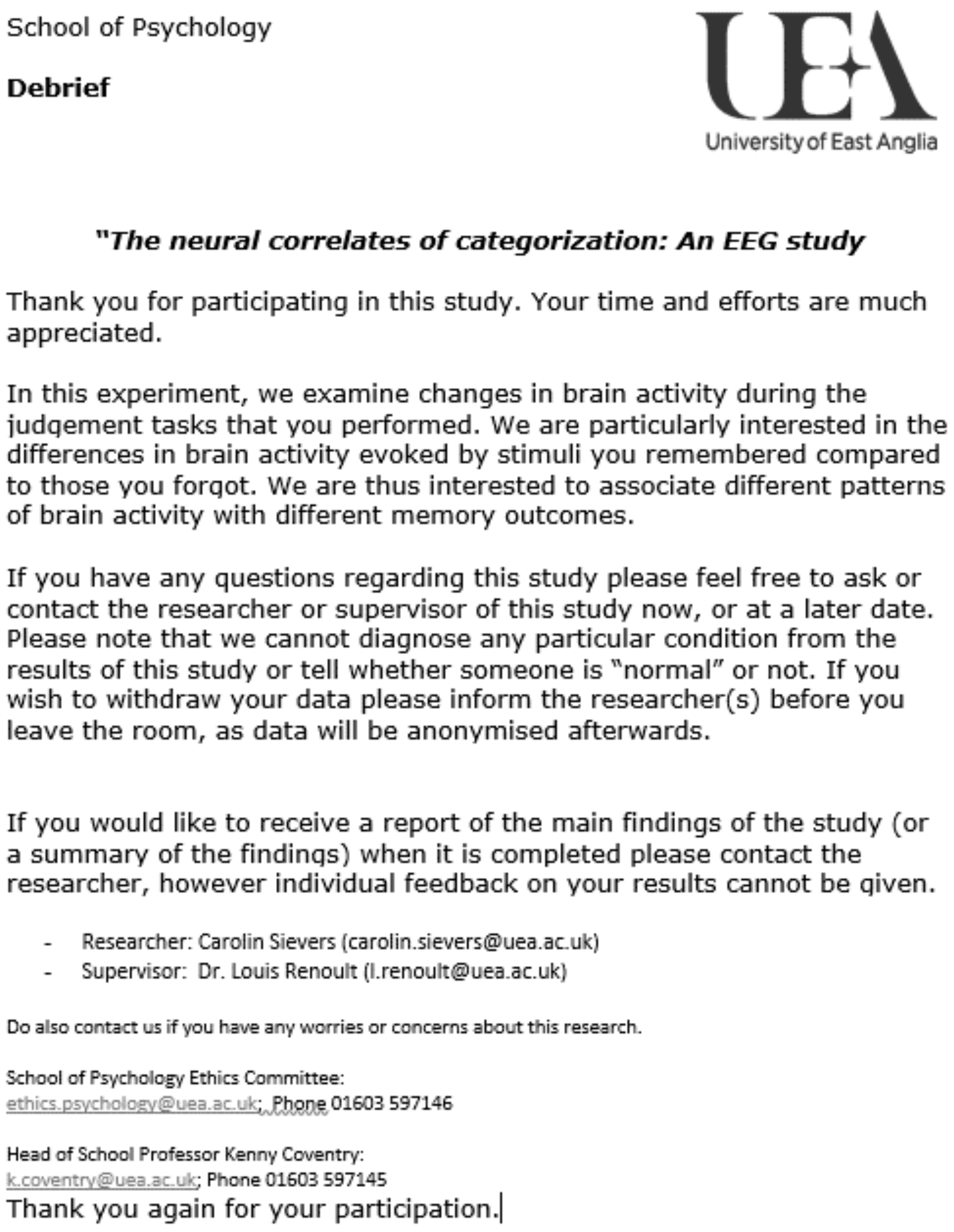
Researcher Contact details:

Carolin Sievers: **carolin.sievers@uea.ac.uk**

Do also contact us if you have any worries or concerns about this research.

School of Psychology Ethics Committee:
ethics.psychology@uea.ac.uk; Phone 01603 597146

Head of School Professor Kenny Coventry:
k.coventry@uea.ac.uk; Phone 01603 597145



School of Psychology

Debrief

"The neural correlates of categorization: An EEG study

Thank you for participating in this study. Your time and efforts are much appreciated.

In this experiment, we examine changes in brain activity during the judgement tasks that you performed. We are particularly interested in the differences in brain activity evoked by stimuli you remembered compared to those you forgot. We are thus interested to associate different patterns of brain activity with different memory outcomes.

If you have any questions regarding this study please feel free to ask or contact the researcher or supervisor of this study now, or at a later date. Please note that we cannot diagnose any particular condition from the results of this study or tell whether someone is "normal" or not. If you wish to withdraw your data please inform the researcher(s) before you leave the room, as data will be anonymised afterwards.

If you would like to receive a report of the main findings of the study (or a summary of the findings) when it is completed please contact the researcher, however individual feedback on your results cannot be given.

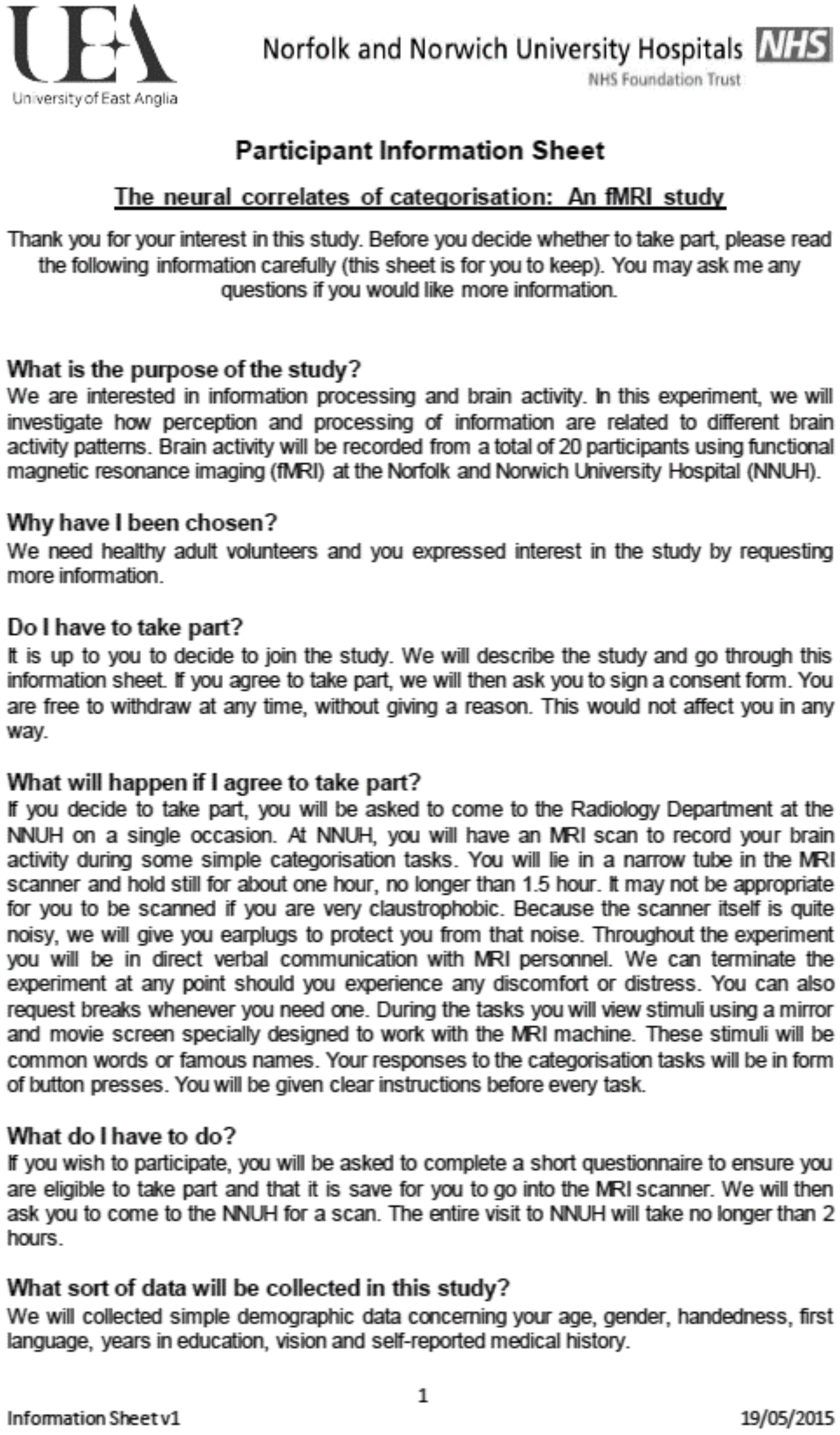
- Researcher: Carolin Sievers (carolin.sievers@uea.ac.uk)
- Supervisor: Dr. Louis Renoult (l.renoult@uea.ac.uk)

Do also contact us if you have any worries or concerns about this research.

School of Psychology Ethics Committee:
ethics.psychology@uea.ac.uk; Phone 01603 597146

Head of School Professor Kenny Coventry:
k.coventry@uea.ac.uk; Phone 01603 597145
Thank you again for your participation.

Appendix E – Information sheet, consent form, debrief (fMRI)



University of East Anglia

Norfolk and Norwich University Hospitals NHS
NHS Foundation Trust

Participant Information Sheet

The neural correlates of categorisation: An fMRI study

Thank you for your interest in this study. Before you decide whether to take part, please read the following information carefully (this sheet is for you to keep). You may ask me any questions if you would like more information.

What is the purpose of the study?
We are interested in information processing and brain activity. In this experiment, we will investigate how perception and processing of information are related to different brain activity patterns. Brain activity will be recorded from a total of 20 participants using functional magnetic resonance imaging (fMRI) at the Norfolk and Norwich University Hospital (NNUH).

Why have I been chosen?
We need healthy adult volunteers and you expressed interest in the study by requesting more information.

Do I have to take part?
It is up to you to decide to join the study. We will describe the study and go through this information sheet. If you agree to take part, we will then ask you to sign a consent form. You are free to withdraw at any time, without giving a reason. This would not affect you in any way.

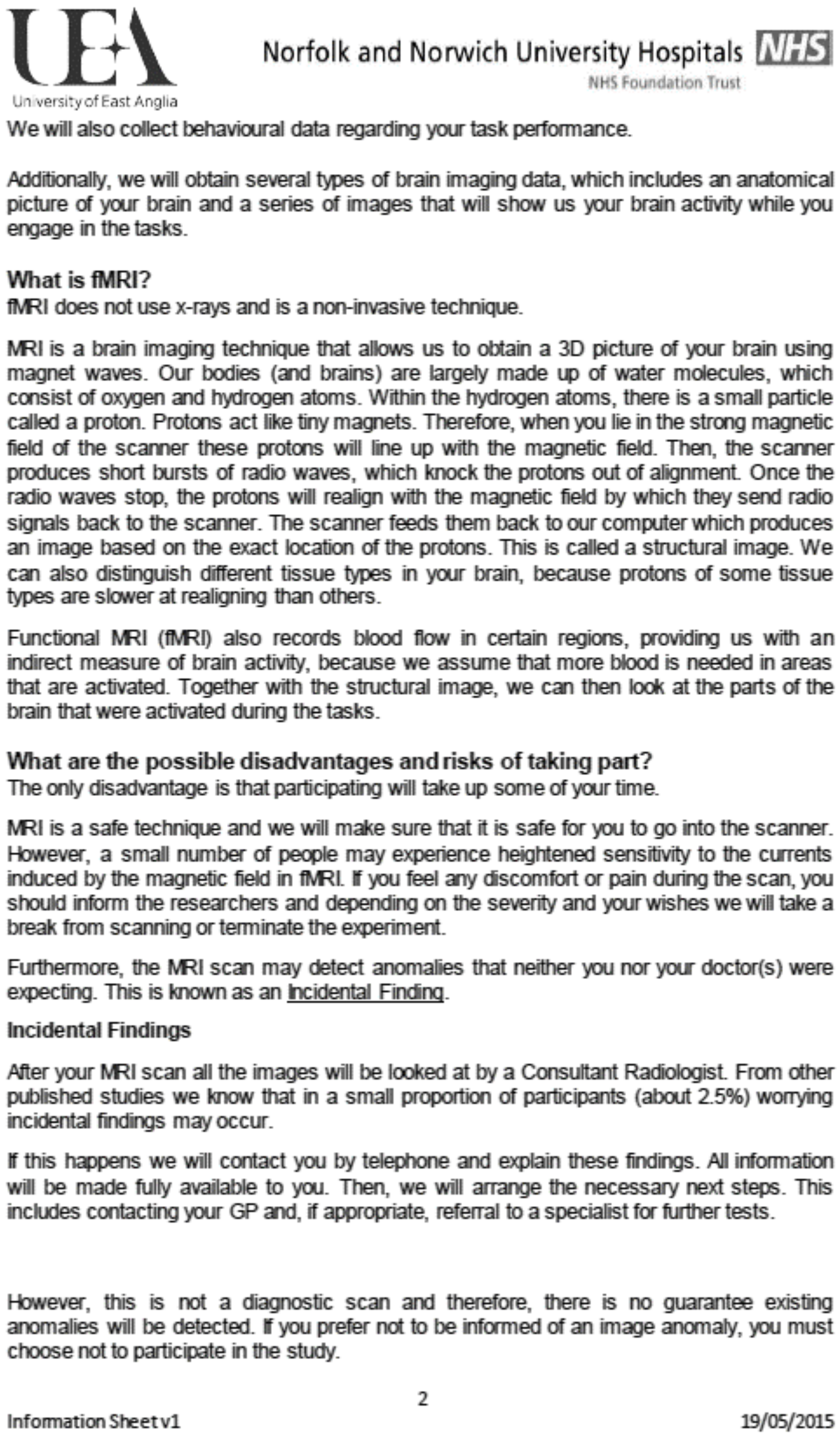
What will happen if I agree to take part?
If you decide to take part, you will be asked to come to the Radiology Department at the NNUH on a single occasion. At NNUH, you will have an MRI scan to record your brain activity during some simple categorisation tasks. You will lie in a narrow tube in the MRI scanner and hold still for about one hour, no longer than 1.5 hour. It may not be appropriate for you to be scanned if you are very claustrophobic. Because the scanner itself is quite noisy, we will give you earplugs to protect you from that noise. Throughout the experiment you will be in direct verbal communication with MRI personnel. We can terminate the experiment at any point should you experience any discomfort or distress. You can also request breaks whenever you need one. During the tasks you will view stimuli using a mirror and movie screen specially designed to work with the MRI machine. These stimuli will be common words or famous names. Your responses to the categorisation tasks will be in form of button presses. You will be given clear instructions before every task.

What do I have to do?
If you wish to participate, you will be asked to complete a short questionnaire to ensure you are eligible to take part and that it is save for you to go into the MRI scanner. We will then ask you to come to the NNUH for a scan. The entire visit to NNUH will take no longer than 2 hours.

What sort of data will be collected in this study?
We will collected simple demographic data concerning your age, gender, handedness, first language, years in education, vision and self-reported medical history.

1

Information Sheet v1 19/05/2015



We will also collect behavioural data regarding your task performance.

Additionally, we will obtain several types of brain imaging data, which includes an anatomical picture of your brain and a series of images that will show us your brain activity while you engage in the tasks.

What is fMRI?

fMRI does not use x-rays and is a non-invasive technique.

MRI is a brain imaging technique that allows us to obtain a 3D picture of your brain using magnet waves. Our bodies (and brains) are largely made up of water molecules, which consist of oxygen and hydrogen atoms. Within the hydrogen atoms, there is a small particle called a proton. Protons act like tiny magnets. Therefore, when you lie in the strong magnetic field of the scanner these protons will line up with the magnetic field. Then, the scanner produces short bursts of radio waves, which knock the protons out of alignment. Once the radio waves stop, the protons will realign with the magnetic field by which they send radio signals back to the scanner. The scanner feeds them back to our computer which produces an image based on the exact location of the protons. This is called a structural image. We can also distinguish different tissue types in your brain, because protons of some tissue types are slower at realigning than others.

Functional MRI (fMRI) also records blood flow in certain regions, providing us with an indirect measure of brain activity, because we assume that more blood is needed in areas that are activated. Together with the structural image, we can then look at the parts of the brain that were activated during the tasks.

What are the possible disadvantages and risks of taking part?

The only disadvantage is that participating will take up some of your time.

MRI is a safe technique and we will make sure that it is safe for you to go into the scanner. However, a small number of people may experience heightened sensitivity to the currents induced by the magnetic field in fMRI. If you feel any discomfort or pain during the scan, you should inform the researchers and depending on the severity and your wishes we will take a break from scanning or terminate the experiment.

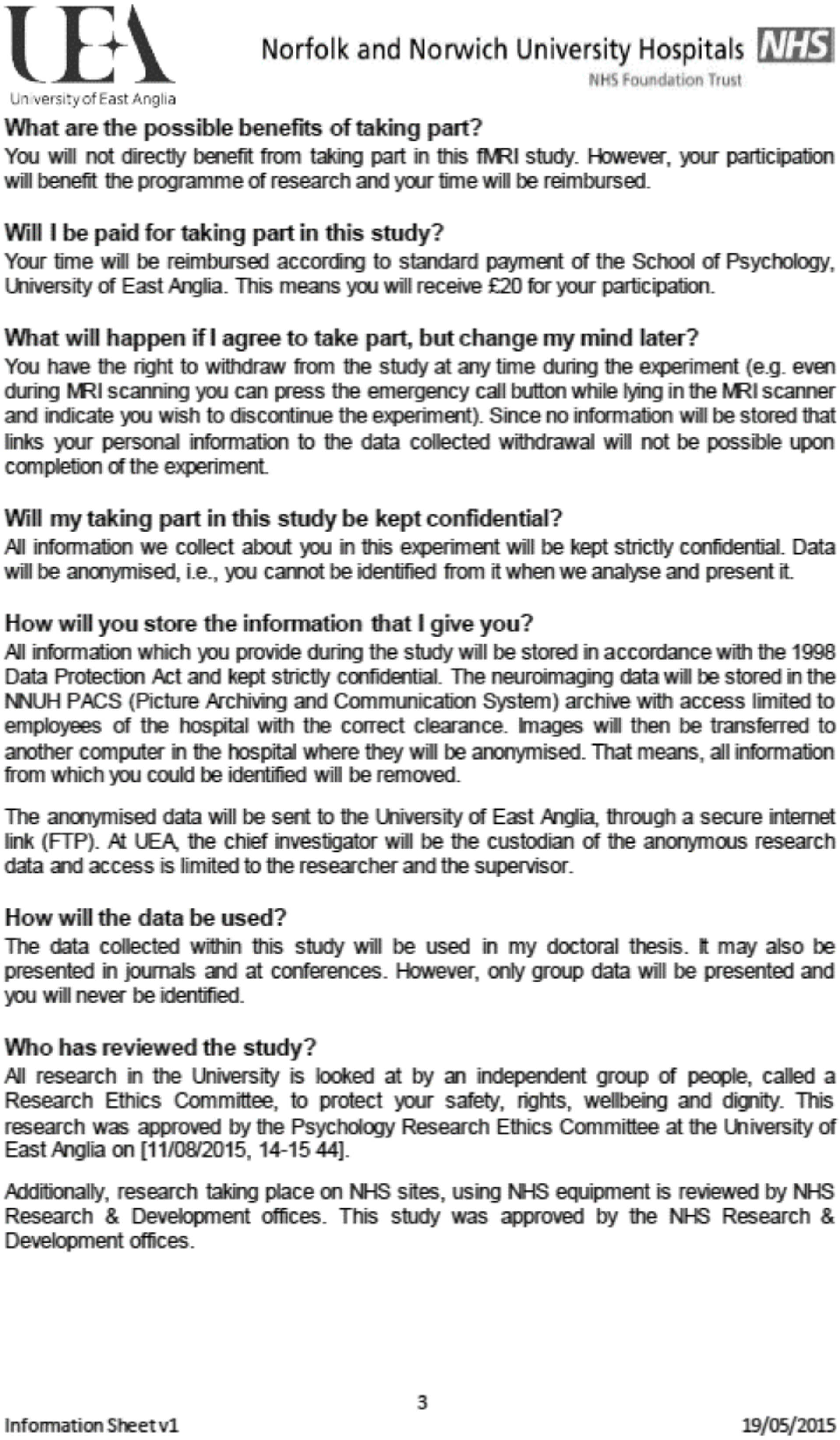
Furthermore, the MRI scan may detect anomalies that neither you nor your doctor(s) were expecting. This is known as an Incidental Finding.

Incidental Findings

After your MRI scan all the images will be looked at by a Consultant Radiologist. From other published studies we know that in a small proportion of participants (about 2.5%) worrying incidental findings may occur.

If this happens we will contact you by telephone and explain these findings. All information will be made fully available to you. Then, we will arrange the necessary next steps. This includes contacting your GP and, if appropriate, referral to a specialist for further tests.

However, this is not a diagnostic scan and therefore, there is no guarantee existing anomalies will be detected. If you prefer not to be informed of an image anomaly, you must choose not to participate in the study.



What are the possible benefits of taking part?

You will not directly benefit from taking part in this fMRI study. However, your participation will benefit the programme of research and your time will be reimbursed.

Will I be paid for taking part in this study?

Your time will be reimbursed according to standard payment of the School of Psychology, University of East Anglia. This means you will receive £20 for your participation.

What will happen if I agree to take part, but change my mind later?

You have the right to withdraw from the study at any time during the experiment (e.g. even during MRI scanning you can press the emergency call button while lying in the MRI scanner and indicate you wish to discontinue the experiment). Since no information will be stored that links your personal information to the data collected withdrawal will not be possible upon completion of the experiment.

Will my taking part in this study be kept confidential?

All information we collect about you in this experiment will be kept strictly confidential. Data will be anonymised, i.e., you cannot be identified from it when we analyse and present it.

How will you store the information that I give you?

All information which you provide during the study will be stored in accordance with the 1998 Data Protection Act and kept strictly confidential. The neuroimaging data will be stored in the NNUH PACS (Picture Archiving and Communication System) archive with access limited to employees of the hospital with the correct clearance. Images will then be transferred to another computer in the hospital where they will be anonymised. That means, all information from which you could be identified will be removed.

The anonymised data will be sent to the University of East Anglia, through a secure internet link (FTP). At UEA, the chief investigator will be the custodian of the anonymous research data and access is limited to the researcher and the supervisor.

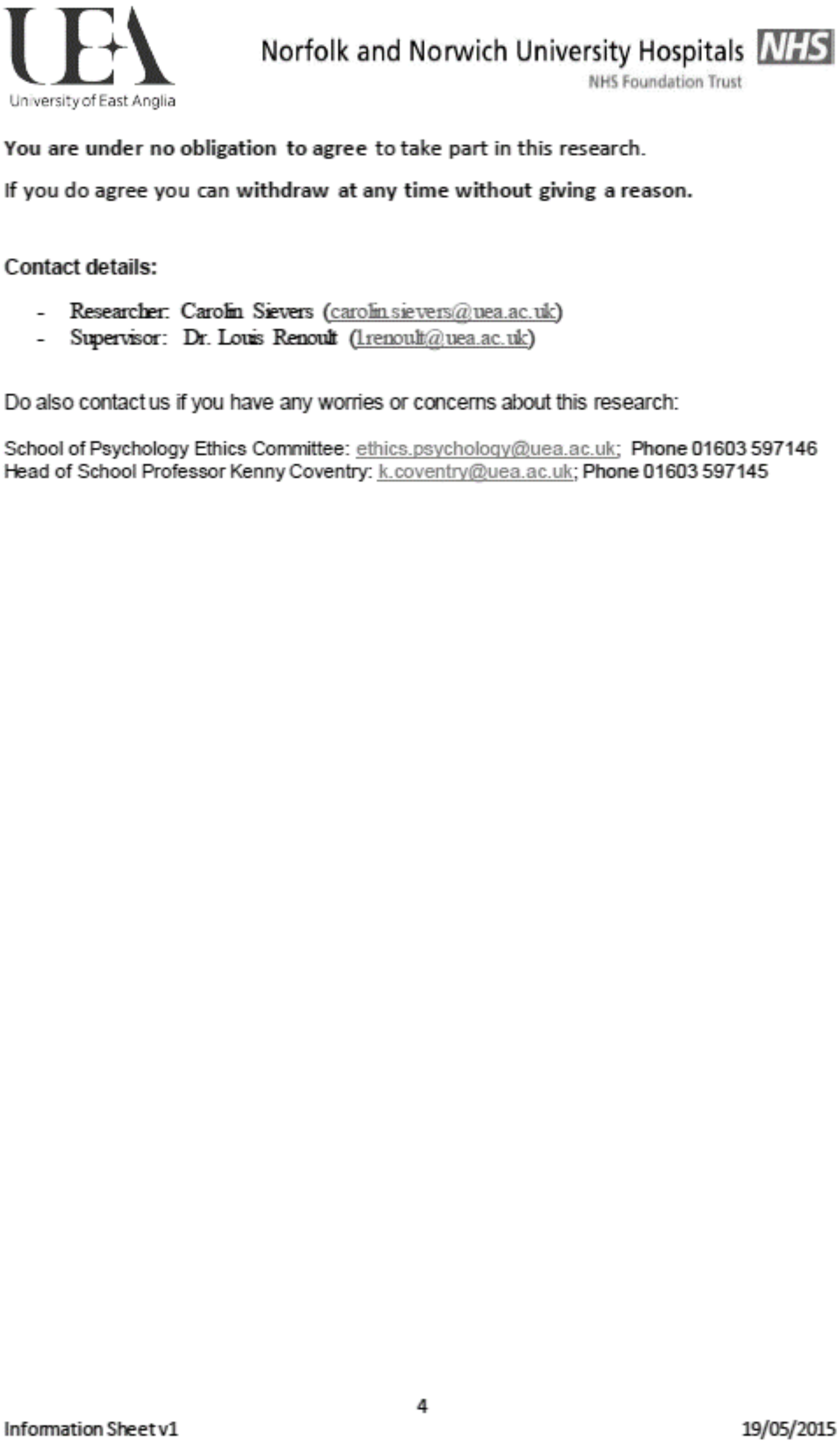
How will the data be used?

The data collected within this study will be used in my doctoral thesis. It may also be presented in journals and at conferences. However, only group data will be presented and you will never be identified.

Who has reviewed the study?

All research in the University is looked at by an independent group of people, called a Research Ethics Committee, to protect your safety, rights, wellbeing and dignity. This research was approved by the Psychology Research Ethics Committee at the University of East Anglia on [11/08/2015, 14-15 44].

Additionally, research taking place on NHS sites, using NHS equipment is reviewed by NHS Research & Development offices. This study was approved by the NHS Research & Development offices.



University of East Anglia

Norfolk and Norwich University Hospitals NHS
NHS Foundation Trust

You are under no obligation to agree to take part in this research.

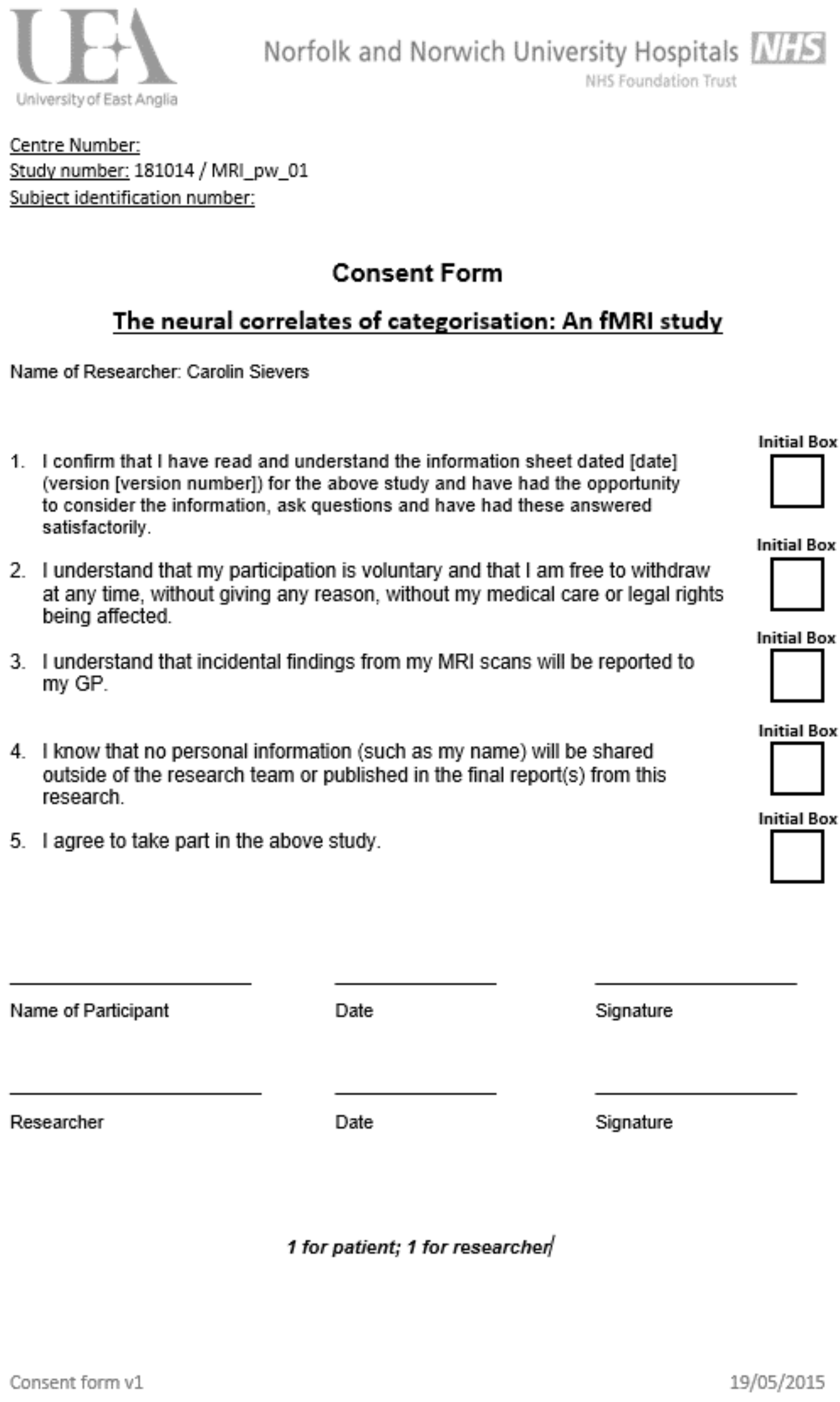
If you do agree you can withdraw at any time without giving a reason.

Contact details:

- Researcher: Carolin Sievers (carolin.sievers@uea.ac.uk)
- Supervisor: Dr. Louis Renoult (l.renoult@uea.ac.uk)

Do also contact us if you have any worries or concerns about this research:

School of Psychology Ethics Committee: ethics.psychology@uea.ac.uk; Phone 01603 597146
Head of School Professor Kenny Coventry: k.coventry@uea.ac.uk; Phone 01603 597145



University of East Anglia

Norfolk and Norwich University Hospitals NHS
NHS Foundation Trust

Centre Number:
Study number: 181014 / MRI_pw_01
Subject identification number:

Consent Form

The neural correlates of categorisation: An fMRI study

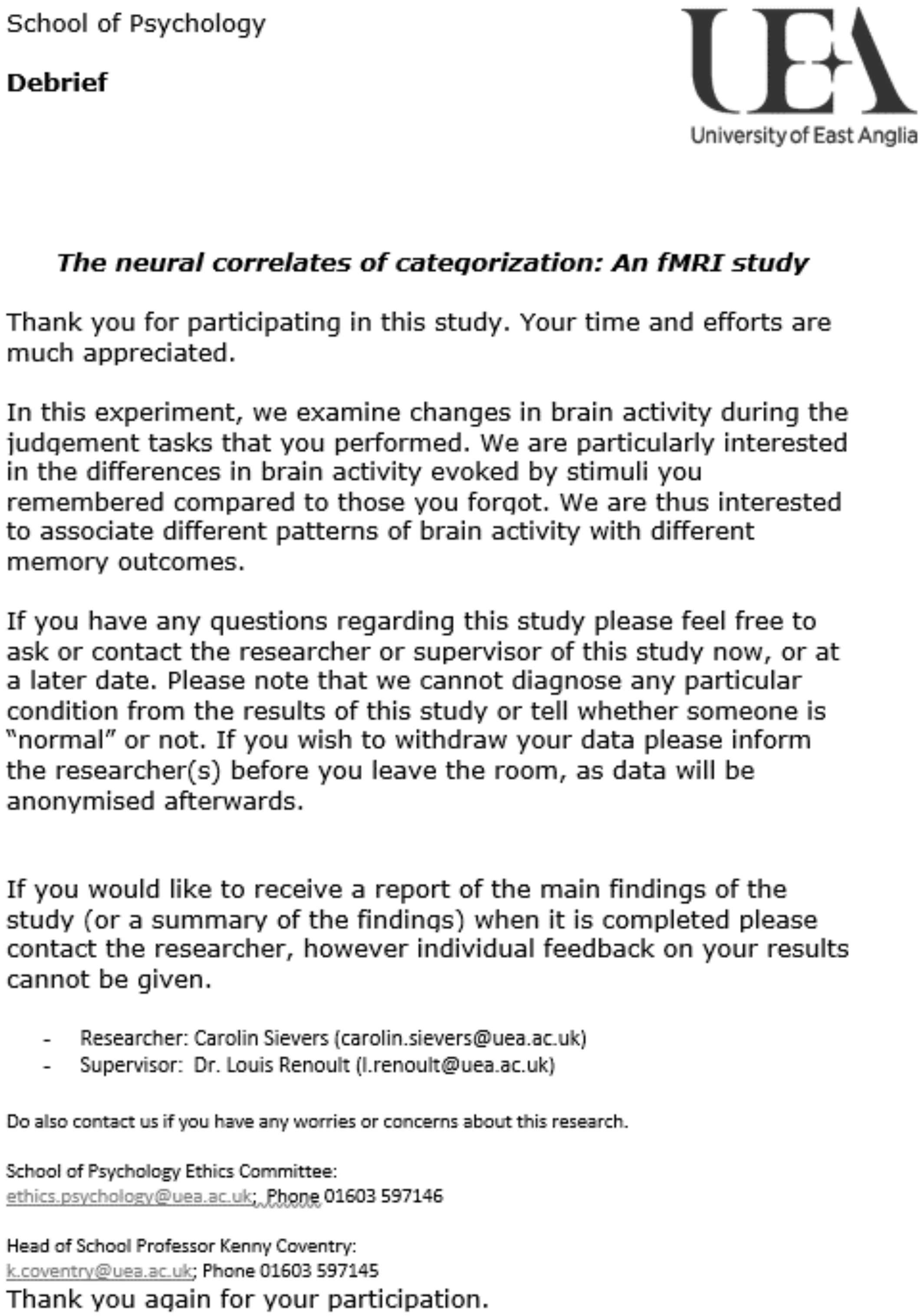
Name of Researcher: Carolin Sievers

1. I confirm that I have read and understand the information sheet dated [date] (version [version number]) for the above study and have had the opportunity to consider the information, ask questions and have had these answered satisfactorily. **Initial Box** ☐
2. I understand that my participation is voluntary and that I am free to withdraw at any time, without giving any reason, without my medical care or legal rights being affected. **Initial Box** ☐
3. I understand that incidental findings from my MRI scans will be reported to my GP. **Initial Box** ☐
4. I know that no personal information (such as my name) will be shared outside of the research team or published in the final report(s) from this research. **Initial Box** ☐
5. I agree to take part in the above study. **Initial Box** ☐

Name of Participant	Date	Signature
Researcher	Date	Signature

1 for patient; 1 for researcher

Consent form v1 19/05/2015



School of Psychology

Debrief

University of East Anglia

The neural correlates of categorization: An fMRI study

Thank you for participating in this study. Your time and efforts are much appreciated.

In this experiment, we examine changes in brain activity during the judgement tasks that you performed. We are particularly interested in the differences in brain activity evoked by stimuli you remembered compared to those you forgot. We are thus interested to associate different patterns of brain activity with different memory outcomes.

If you have any questions regarding this study please feel free to ask or contact the researcher or supervisor of this study now, or at a later date. Please note that we cannot diagnose any particular condition from the results of this study or tell whether someone is "normal" or not. If you wish to withdraw your data please inform the researcher(s) before you leave the room, as data will be anonymised afterwards.

If you would like to receive a report of the main findings of the study (or a summary of the findings) when it is completed please contact the researcher, however individual feedback on your results cannot be given.

- Researcher: Carolin Sievers (carolin.sievers@uea.ac.uk)
- Supervisor: Dr. Louis Renoult (l.renoult@uea.ac.uk)

Do also contact us if you have any worries or concerns about this research.

School of Psychology Ethics Committee:
ethics.psychology@uea.ac.uk; Phone 01603 597146

Head of School Professor Kenny Coventry:
k.coventry@uea.ac.uk; Phone 01603 597145
Thank you again for your participation.