Effects of task and material on hemispheric lateralisation of nonverbal memory

Adam Bentvelzen
Bachelor of Psychology (Honours)

Submitted for the degree of Doctor of Philosophy/Master of Clinical Neuropsychology

ARC Centre of Excellence in Cognition and its Disorders (CCD)
Department of Psychology
Macquarie University, Sydney, Australia

June 2016

Table of Contents

Abstract

The role of the right temporal lobe in memory function is unresolved. The material specificity model has successfully guided the detection of left temporal lobe pathology using verbal memory tests, but the detection of right temporal lobe pathology using nonverbal memory tests has been unreliable. Considering factors beyond material type per se could improve prediction of right hemispheric pathology. This thesis investigated the factors associated with right-lateralisation of memory function including i) the type of nonverbal stimulus used (i.e., abstract designs, faces, spatial arrays), ii) differences in task-related processing (e.g., encoding versus retrieval), and iii) potential lower-level stimulus confounds (i.e., memory versus perceptual processing). In a comprehensive meta-analysis of studies employing nonverbal memory testing of temporal lobe epilepsy patients (k = 152), memory for faces or spatial stimuli had superior detection of right-sided pathology than memory for abstract designs. By comparison, task demands including learning type (single versus repeated stimulus presentation) and the delay before testing memory (short versus long) had negligible effect. Following the meta-analysis two empirical papers compared the effects of material (verbal, spatial) and processing (encoding, retrieval) on lateralisation using event-related potentials (ERPs) and changes in electroencephalographic power (EEG). ERP measures showed right-lateralisation for spatial learning while processing type affected lateralisation only in the anterior region of the brain (encoding: left; retrieval: right). In the next two empirical papers using the same measures, the ERP results revealed that spatial memory contributed to right-lateralised brain activity over and above spatial perceptual processing. In both experiments EEG measures were less sensitive to the effects than were ERPs. The main findings of this thesis were that right-lateralisation of nonverbal memory is most reliably affected by the type of material, but with important contributions of task-related processing (encoding, retrieval) in the anterior brain regions, and that spatial memory affects right-lateralisation over and above the lateralising influences of perceptual processing. The findings stand to enhance understanding of right hemispheric memory functions.

Certification by candidate

The work contained in this thesis has not been submitted for a higher degree to any other university or institution. All the work was carried out during my PhD candidature under the supervision of Prof Greg Savage, Prof Genevieve McArthur, and Dr Nicholas Badcock. The studies reported in this thesis were carried out at Macquarie University from which ethical approval was granted (no. 5201100342, see Appendix at end of thesis for final approval letter). Information included in the projects was collected through direct contact and consent forms were obtained from all the participants.

I declare that the manuscripts presented in this thesis will be submitted for publication and the inclusion of coauthors reflects that the presented work came from active collaboration between researchers in a team-based context. For Chapters 3 and 4, Professors Greg Savage and Genevieve McArthur devised the experimental design based on stimuli developed by past student Dr. Stuart Lee, and Dr. Megan Willis carried out the testing of participants. However, from 2011 to 2016 I was the lead researcher and worked on all aspects of data processing, analysis, manuscript preparation and submission. In this role I made a number of key changes to the scope of the analysis, including increasing the focus on material type over other experimental variables and introducing an analysis of processing type, which had not been a previously focus of the study. I also introduced the use of EEG frequency measures for data analysis which had not been previously considered. Therefore, in a number of key aspects the study itself clearly departed from how it had been last envisioned by my collaborators, and as such the research team thought it appropriate for me to be the first author on any papers that were submitted for publication from 2011 onwards.

Aside from these considerations regarding Chapters 3 and 4, all experimental design, participant recruitment, testing, data processing, analysis, and manuscript preparation in this thesis was prepared by myself. This included the preparation and submission of the Chapter 3 manuscript for publication in an international journal and conference poster publications in

which Conference Abstract 1 covered material from Chapter 4 (and some additional data not reported in this thesis) and Conference Abstract 2 reported results from both Chapters 4 and 6 as listed below:

- Conference Abstract 1). Bentvelzen, A., McArthur, G., Johnson, B., Willis, M., Lee, S., Savage, G. (2012). Event-related EEG suggests modality rather than material specific memory lateralisation. *Clinical EEG and Neuroscience, 43* (3), 224-225.
- Conference Abstract 2). Bentvelzen, A., McArthur, G., Badcock, N., Johnson, B., Willis, M., Lee, S., & Savage, G. (2013). Right-hemisphere memory: lateralisation effects of material, modality, novelty, verbalisation and sex. *Journal of Cognitive Neuroscience, 25*, S51-51.

The manuscripts are listed by their associated thesis chapters:

1. Chapter 2: The prediction of right temporal lobe pathology by nonverbal memory tests: Meta-analysis of stimulus and task effects
2. Chapter 3: Material type and task demands interactively affect hemispheric lateralisation of early ERP measures during a memory task
3. Chapter 4: The effects of material type and memory processing type on lateralisation of event-related theta and alpha power
4. Chapter 5: Separable effects of perceptual form and memory on material-specific lateralisation during memory tasks: An ERP study
5. Chapter 6: EEG power shows right hemisphere lateralisation during memory tasks regardless of material type remembered or perceptual processing

Adam Bentvelzen (student number 41144015)

Acknowledgements

I would like to express my heartfelt gratitude to my primary supervisor Professor Greg Savage for his intellectual nous, sense of humour, empathy and patience throughout this journey. His expertise and support in both the clinical and research realms was extraordinary and necessary for me to survive the combined PhD/Masters. I would like to acknowledge Professor Genevieve McArthur for her invaluable advice on article preparation, "big picture" thinking, and for the use of the ERP lab. The contribution of Dr Nicholas Badcock was absolutely essential and I have immense gratitude for his unrelenting positive attitude and responsiveness. Professor Bill Thompson was very supportive during our initial "visual-musical" phase despite his busyness as Head of Psychology, and Dr Roy Kessels provided timely advice and positive encouragement regarding all things meta-analytic.

I would also like to thank the many fellow PhD students who have shared this long journey with me and given their support and friendship, including Lars Marstaller, Yatin Mahajan, Alissa Beath, Lena Quito, Jonathan McGuire, Robert Ross, Andrew Etchell, Astrid Zeman, Anne Jaeger, Vishnu Kaleeckal-Krishnanku, Erika Contini, and so many others I cannot list them all here. I could not have made it through the first few years without my fellow Masters cohort of 2009/2010 for their support, intelligence, and humorous stories, with special thanks to Gaius Gorham, Melissa Dickinson, and Deepa Bapat.

Special thanks to all of the MACCS/CCD staff, especially Lesley McKnight, Katie Webb, Marcus Ockenden, and Craig Richardson for their competence and enormous patience, and to the various heads of the organisation for their stewardship during my time here: Max Coltheart, Anne Castles, and (again!) Genevieve McArthur. My deepest gratitude goes to the Clinical Neuropsychology staff of the Psychology Department including Greg Savage (again!), Jenny Batchelor, Melanie Porter, Tammy Lane, and Tanya Lye, and to clinical supervisors Sharon Watt, Jane Lonie, Greg Savage (for the hat-trick!), Jonathan Payne, and Nicole Kochan for their professionalism, patience, and support.

Most importantly, words cannot express my level of appreciation for the patience and support of my long-suffering friends, family, and the love of my wonderful partner Linda Sigmundsdottir. Lastly, I'd like to thank my gorgeous cats, Professor and Pandora for providing me with welcome cat-straction to keep me sane.

Chapter 1: General Introduction

1.1 Early evidence for hemispheric subdivision of functions

A fundamental principle of human cognition is that the two hemispheres of the brain perform different functions. Classic studies suggested that language disorders such as aphasias, in which a person has difficulty speaking or understanding language, generally arise from left hemisphere lesions (e.g., Broca, 1865), while spatial neglect, in which a person completely ignores one side of space despite possessing intact vision, typically arise from right hemisphere lesions (e.g., Brain, 1941). Such observations led neurologists such as John Hughlings Jackson (1835-1911) to explicitly claim that the left and right hemispheres perform specialised functions, the left anterior lobe for linguistic abilities and the right posterior lobe for visuospatial functions (reviewed in Critchley & Critchley, 1998). These early findings suggested that the working of particular cognitive functions crucially depended on one hemisphere more than the other and led to the development of the widely accepted "material specific" framework in which the left hemisphere is specialised for language and the right hemisphere is specialised for visuospatial (or more generally, and henceforth, "nonverbal") processing. Material specificity has remained the most influential framework of the hemispheric specialisation of cognitive functions in both clinical neuropsychology and in the cognitive neurosciences.

1.2 Thesis aims

This thesis aims to investigate the different factors that promote the right hemispheric lateralisation of memory function. This chapter presents a literature review of the strengths and limitations of the material specificity model of hemispheric lateralisation as it applies to the assessment of nonverbal memory, along with alternative theories. The contents of the thesis, which is presented in a thesis-by-publication format, will be outlined at the end of this chapter.

1.3 Material-specific lateralisation of memory

Classic findings of lateralisation of language and spatial deficits were eventually shown to have parallels for memory functions. Early studies showed that patients with medically intractable temporal lobe epilepsy (TLE) who were surgically treated with bilateral temporal lobe resection had severe and lasting memory impairments for recently learned material (Milner, 1954; Scoville, 1954; Scoville & Milner, 1957). These studies suggested the critical importance of the medial temporal lobe (MTL) region for memory function (e.g. Scoville, 1968).

Milner's pioneering investigations showed that unilateral MTL resection (i.e., in the left or right hemisphere only) resulted in more selective memory deficits than bilateral resection. Specifically, patients with resection of the left temporal lobe showed selective impairment of memory for verbal materials (e.g., Milner, 1970), while patients with resection of the right temporal lobe showed selective impairment of memory for materials which were difficult to verbalise, or putatively "nonverbal" (e.g., Milner, 1965). These observations gave rise to the idea of material specificity of memory function: the left temporal lobe mediates memory for verbal material and the right temporal lobe mediates memory for nonverbal material (Milner, 1968).

1.4 Practical and clinical importance of nonverbal memory skills

The evidence that memory functions are lateralised in a material specific manner has had a profound impact on the clinical assessment of patients with lateralised brain damage, in whom the accurate clinical assessment of nonverbal memory functions has practical importance. The ability to remember nonverbal materials is a skill with many real-life consequences. These include remembering the location of items in a house, navigating between important landmarks, recognising a musical tune, and identifying a person's face. Impairment of such skills can therefore have a devastating impact on a person. For example, patients with topographical disorientation have a severe difficulty in orienting themselves in

new environments (Aguirre & D'Esposito, 1999). This disorder has been linked to deficits in spatial learning mediated by damage to the right MTL, most often on the right side (Aguirre & D'Esposito, 1999; Turriziani, Carlesimo, Perri, Tomaiuolo, & Caltagirone, 2003).

An understanding of how nonverbal memory performance relates to brain lateralisation also has diagnostic and prognostic value to patients with medically refractory unilateral temporal lobe epilepsy (TLE). These patients have debilitating and frequent seizures originating from one temporal lobe, and when anticonvulsant medication is ineffective, neurosurgical intervention is often a successful treatment option. Testing verbal and nonverbal memory function helps to confirm the laterality and location of the seizure focus at the presurgical stage, to identify postsurgical nonverbal memory deficits, and to track changes over time (Barr & Morrison, 2015). Accurate assessment of nonverbal memory, therefore, is a critical component to estimate the potential risk and benefits of surgery in patients with medically refractory TLE.

1.5 The association between verbal memory and left MTL dysfunction is reliable

Since the classic findings, deficits in verbal memory have been linked to left MTL resection, regardless of whether the material was presented aurally or visually (Blakemore & Falconer, 1967; Milner, 1967), or whether retention was tested by recall or by recognition (Milner, 1958, 1967). Over time, these findings are consistently borne out for the left-verbal part of the material specificity principle (see meta-analytic reviews by Lee, Yip, & Jones-Gotman, 2002, and Sherman et al., 2011). Specifically, unilateral left MTL lesions result in impaired memory for word lists (Hermann et al., 1996; Martin et al., 2002; Seidenberg et al., 1996), short stories (Lee et al., 2002; Sass et al., 1992) and sets of word pairs (Helmstaedter, Gleibetaner, Di Perna, & Elger, 1997; Saling et al., 1993; Savage, Saling, Davis, & Berkovic, 2002). This consistent impairment of verbal memory across different types of verbal tasks indicates a strong relationship between the left MTL and verbal memory processing.

In presurgical clinical contexts, the functional outcome of unilateral temporal lobe

surgery can be predicted by considering both presurgical verbal memory performance and the degree of MTL pathology evident on structural imaging (Chelune, 1995). Specifically, poorer verbal memory performance in presurgical patients is associated with greater left MTL pathology, and conversely, relatively intact performance is associated with less pathology (Baxendale et al., 1998; Sass et al., 1990; 1992, 1994; Trenerry et al., 1993). As a corollary finding, higher presurgical verbal memory performance is associated with greater risk of postsurgical memory decline (Chelune, Naugle, Luders, & Awad, 1991; Chelune, 1995). Taken together, it can be concluded that there is reliable and substantive evidence supporting the clinical value of verbal memory testing in assessing left MTL dysfunction.

1.6 Nonverbal memory testing does not reliably predict right MTL dysfunction

In initial findings, right MTL resection was associated with memory deficits for a broad array of nonverbal stimuli across the visual, auditory, and tactile sensory modalities. This included faces (Milner, 1968), dot patterns (Kimura, 1963), irregular nonsense patterns (Kimura, 1963), mazes (mediated by either vision or touch; Corkin, 1965), melody (Milner, 1962), and familiar musical tunes (Shankweiler, 1966). These findings suggested that nonverbal memory, regardless of the specific modality or type of test, had a strong dependence on the right MTL and in complementing the association between verbal memory and the left MTL supported a material specific (i.e., verbal-nonverbal) hemispheric division of memory functions (Milner, 1968).

These findings were associated with the development of clinical tests of nonverbal memory. Such tests include the Rey Complex Figure Test (RCFT; Rey, 1941) which presents a single complex abstract design for copying and recall after a brief and/or long delay, and the Visual Reproduction (VR) subtest from various editions of the Wechsler Memory Scale (e.g., WMS-R; Wechsler, 1987) which presents successive designs of increasing complexity which are recalled immediately after presentation and subsequently after a delay. These tests have remained the most popular kind of nonverbal memory test utilised by neuropsychologists

(RCFT: 65%, VR: 21%; Djordjevic & Jones-Gotman, 2011).

Despite their popularity, however, a large investigation of presurgical patients (N = 757) found no significant difference between left and right TLE patients using the RCFT and VR (Barr et al., 1997). In addition, presurgical performance on nonverbal memory tasks has not consistently predicted subsequent postsurgical changes (e.g., Chelune, Naugle, Luders, & Awad, 1991). Tests that require memory for abstract designs have also failed to consistently correlate with right hippocampal cell loss in presurgical patients, with findings of positive (Chelune, 1995; Trenerry et al., 1993) and negative correlations (Baxendale, Thompson, & van Paesschen, 1998; O'Brien, Bowden, Bardenhagen, & Cook, 2003; Rausch & Babb, 1993). Other investigations using design reproduction tests postsurgically have also failed to discriminate right from left MTL patients (Lee, Loring, & Thompson, 1989; Naugle, Chelune, Cheek, Luders, & Awad, 1993). More recently, large scale meta-analytic reviews suggest that on the whole, nonverbal memory tests, which mostly consist of design memory tasks, have poor clinical utility for predicting memory decline following surgery (Lee et al., 2002; Vaz, 2004; Sherman et al., 2011).

In conclusion, the poor clinical validity of nonverbal memory tests has posed a serious, ongoing and unresolved problem for clinical neuropsychologists for decades. Reflecting this, a US National Institute of Health panel for the Common Data Elements test battery recommended the “optional” inclusion of visuospatial memory tests for research in patients with epilepsy (Loring et al., 2011). While this response may reflect the difficulties faced, it is arguably an overly conservative judgment which neglects the practical importance of nonverbal memory skills (outlined in Section 1.4). Furthermore, it implies that assessment of epilepsy patients is sufficient without the consideration of nonverbal memory skills, which could be considered negligent regardless of whether nonverbal memory tests have lateralising ability or not. Most importantly, recent findings have implicated the right MTL in the Flynn effect, in which the level of intellectual functioning as measured by IQ tests or other abilities

appears to increase steadily between generations (Flynn, 1984). There is evidence in the healthy population that the Flynn effect may only occur for the learning and recall of nonverbal material but is absent for verbal memory (Baxendale, 2010). Furthermore, there may be inhibition of the Flynn effect in patients with right hippocampal pathology, for both nonverbal and verbal intellectual abilities (Baxendale & Smith, 2012). These findings suggest patients with right MTL dysfunction not only have greater risk of nonverbal memory impairment but their future verbal and nonverbal intellectual abilities are strongly compromised relative to their peers. This reinforces the importance of accurate assessment of functions mediated by the right MTL.

1.7 Problems with the construct of nonverbal memory

A number of suggestions have been made to address the poor reliability of nonverbal memory tests. The core of the problem may be theoretical, relating to the lack of specificity of the nonverbal memory construct. While the verbal construct centres on the concept of verbal skills as a single core ability with different subskills (i.e., speech, reading) and cognitive processes (i.e., phonological, orthographic, semantic), the nonverbal construct is typically defined in a negative sense, merely reflecting the absence of verbal processing. As such, the nonverbal construct can pertain to a constellation of varied abilities, stimulus types, modalities, and processing requirements, without its own unique and unifying concept.

In addition to the vagueness of the nonverbal construct itself, there is considerable evidence for overlap between the verbal and nonverbal constructs. Indeed, this viewpoint is supported by a finding that performance by elderly participants on commonly used neuropsychological memory tests cannot be distinguished into separate verbal and nonverbal factors; rather, both load onto a single "general memory" factor (Smith, Malec, & Ivnik, 1992). A meta-analytic review showed that resection of the right MTL can impair verbal memory (20% of patients declined while 14% improved), albeit less frequently than after left-sided resection (44% declined, 7% improved), while left MTL resection can impair nonverbal

memory (21% declined, 15% improved) at a rate comparable to that found with right MTL resection (23% declined, 10% improved; Baxendale, Thompson, & Duncan, 2008; Sherman et al., 2011).

This evidence suggests that the function of the MTL in each hemisphere is not symmetrically nor exclusively dissociable according to material type. It is clear that unilateral TLE patients can retain both verbal and nonverbal information, and that their memory for both kinds of material is often impaired (Dobbins, Kroll, Tulving, Knight, & Gazzaniga, 1998). This lack of specificity of the nonverbal construct has arguably contributed to the development of nonverbal memory tests with poor reliability in detecting right MTL dysfunction (Barr, 1997). Instead of continuing to be guided only by the principle of material specificity, better understanding of the causes of right hemispheric lateralisation may facilitate the development of tests with greater clinical utility.

1.8 Facial memory and spatial memory: cognitive neuroscience findings

In the investigation of more specific proficiencies of the right hemisphere, memory for faces and spatial information each have not only obvious ecological value for humans and there is ample evidence that each is processed in a right-lateralised manner. Landmark findings have suggested that processing of unfamiliar faces is strongly right-lateralised in areas including the right occipitotemporal and ventrolateral temporal cortices (Farah, 1991; Kanwisher, McDermott, & Chun, 1997; Rossion et al., 2003; Rossion & Jacques, 2008). Other studies suggest right-lateralised processing of spatial information particularly in the right parietal region (Badzakova-Trajkov, Haberling, Roberts, & Corballis, 2010; Corballis, 2003), and spatial neglect frequently correlates with lesions in the right ventral cortex, particularly the right temporoparietal junction and right superior temporal gyrus (Corbetta & Shulman, 2011; Shulman et al., 2010).

Neuroimaging techniques including positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have shown activation in the right MTL

regions for face memory tasks (e.g., Chiaravalotti & Glosser, 2004; Crane & Milner, 2002; Haxby et al., 1996; Sergent, Ohta, & Macdonald, 1992) and spatial or navigation memory tasks (e.g., Bellgowan et al., 2009; Finke, Ostendorf, Braun, & Ploner, 2011; Kuhn & Gallinat, 2014; Papanicolaou et al., 2002).

Encouragingly, there is abundant evidence that right MTL lesions selectively impair memory in experimental tasks using novel faces (Baxendale, 1997; Moscovitch & McAndrews, 2002) and spatial location (Abrahams, Pickering, Polkey, & Morris, 1997; Kessels, Hendriks, Schouten, Van Asselen, & Postma, 2004; Nunn, Polkey, & Morris, 1998; Smith & Milner, 1981; Spiers et al., 2001). A meta-analysis suggested that various kinds of experimental spatial memory tasks (object-location, maze learning, and positional memory) have also been shown to elicit poorer performance in those with right- than left-sided hippocampal damage (Kessels, de Haan, Kappelle, & Postma, 2001). The findings also suggested that memory for precise spatial information (e.g., exact positions, distances) showed the strongest association with right hippocampal damage.

Such research findings have paralleled the increased use of neuropsychological tests of face memory and spatial memory. Meta-analytic reviews support the relative superiority of tests of face memory over design memory for the purpose of detecting postsurgical memory deficits and change from presurgical performance in patients with right TLE (Sherman et al., 2011; Vaz, 2004). Some clinical tests of facial or spatial memory have failed to distinguish patients with left or right MTL lesions, however, including tests of spatial sequence learning (Araujo, Schwarze, & White, 2009; Chiaravalloti & Glosser, 2004) and novel faces (Hermann, Connell, Barr, & Wyler, 1995; Naugle et al., 1994). Taken together, these findings suggest that for face recognition and spatial/navigational tasks there is strong ipsilateral functional interdependence between right-lateralised perceptual processing in sensory association regions and right-lateralised memory processing in the right MTL. Tests of face memory and spatial memory have each shown promise for clinical purposes, although it still

remains unclear whether clinical tests are sufficiently reliable for detection of right MTL dysfunction.

1.9 The binding versus spatial map accounts of right MTL function

As an alternative to using particular types of stimuli that elicit processing in wider right lateralised networks, there is a case for focusing on the particular proficiencies of the MTL itself. The MTL has been shown to be critical for association between multiple elements (see e.g., Eichenbaum & Bunsey, 1995; Eichenbaum, Otto, & Cohen, 1994; Mayes, Montaldi, & Migo, 2007). This function has been linked to the long-known role of the MTL region in forming episodic memories, that is memories that are rich in associations between the to-be-remembered material and the time, location, and context in which it is remembered (Eichenbaum et al., 1994). The associative role of the MTL has also been linked to material specific hemispheric lateralisation, with evidence that the left medial temporal lobe, and especially the hippocampus, is involved in tasks requiring the associations of word pairs (Rausch & Crandall, 1982; Saling et al., 1993; Saling, 2009).

In parallel with findings for the left MTL, there is evidence that the right MTL is involved in association between pairs of nonverbal stimuli, most commonly demonstrated between objects and their locations (e.g., Bohbot et al., 1998; Owen, Milner, Petrides, & Evans, 1996; Smith & Milner, 1989). A meta-analysis of patients with hippocampal damage associated right-sided damage more strongly with poorer object-location memory than left-sided damage (Kessels et al., 2001). However, effect sizes were statistically larger for positional memory tasks in which there was no binding requirement, implying that rather than a deficit in binding of objects to locations, an inability to constitute an internally coherent spatial representation or "map" of the stimuli may underpin the right-lateralisation effect for both positional memory and object-location memory (Kessels et al., 2001). Indeed, a previous review presented evidence of distinct memory processes for constructing a positional map and assigning objects to positions (Postma & de Haan, 1996).

Tasks that focus on the association between objects and locations may also have attributes that draw upon left-lateralised structures. A study using a virtual reality town found that postsurgical left TLE patients had selective impairment for context-dependent episodic memory (e.g., associations between object identity and person, place, and time) while postsurgical right-sided patients had difficulties with topographical memory tasks including navigation and scene recognition (Spiers et al., 2001). Memory for object locations also has considerable overlap with memory for "categorical" relationships between objects (i.e., knowing left from right, up from down, e.g., "the pen is to the right of the ruler"), which many studies have shown involve left-lateralisation or relatively less right-lateralisation than "coordinate" spatial processing (i.e., exact distance and positional information, e.g., "the pen is 25 centimetres from the ruler") which consistently shows strong right-lateralisation (e.g., Palermo, Bureca, Matano, & Guariglia, 2008; Kosslyn, 1987; van Asselen, Kessels, Kappelle, & Postma, 2008; van der Ham, Postma, & Laeng, 2014). Therefore, object-location association could serve to detect right MTL pathology if the task involves highly precise spatial discrimination, rather than comparing abstract relations, and when rich contextual details are not included. Indeed, a recently proposed model differentiates between distinctly lateralised memory processes for object processing (bilateral ventral), episodic memory binding and categorical object-location binding (left hippocampus), and coordinate object-location binding (right hippocampus; Postma, Kessels, & van Asselen, 2008, and see Zimmermann & Eschen, 2016, for a review that updates findings on this model).

To date there have been few clinical tests of visual associative learning. The Visual Spatial Learning Test (VSLT) assesses associations between designs and locations in a grid and one study showed a link between performance on this test and right temporal lobe pathology (Malec, Ivnik, & Hinkeldey, 1991; Trenerry et al., 1993), while another study using factor analysis failed to distinguish that it measures memory ability independently of verbal memory (Smith, Malec, & Ivnik, 1992). The recently released Designs subtest of the WMS-IV is very similar to the VSLT but has not yet been sufficiently validated (Wechsler, 2009).

A longstanding and competing view is that the MTL is crucially involved in spatial processing, particularly in the formation of a map-like representation (O'Keefe & Nadel, 1978). Monumental findings from single-cell recordings in animals specifically concerning "grid cells" which map the immediate surroundings in precise spatial coordinates, and "place cells" which encode and track the exact location of the person regardless of changes in their surroundings, have recently been replicated in humans (Burgess, 2002; Ekstrom et al., 2003). Furthermore, both of these cell types and their role in creating spatial maps, have been strongly associated with the human right hippocampal and parahippocampal regions (Burgess, 2002; Ekstrom et al., 2003; Suthana et al., 2009). Both the binding and the spatial map hypotheses, therefore, present compelling theoretical frameworks through which to investigate hemispheric lateralisation of the MTL.

Taken together, unlike the validity of paired associate learning of words in discriminating left- from right-sided MTL patients, the mere pairing together of ostensibly nonverbal information including objects and locations may not constitute a sufficiently specific test of right MTL function. A related problem is that most objects or landmarks can be easily named, hence allowing verbalisation of the ostensibly "nonverbal" stimuli. It would seem simpler to use positional memory tasks with the sole demand of spatial processing, rather than requiring explicit associative demands that may draw upon left-lateralised processing.

1.10 The confounding influence of verbalisation

Language is a universal human skill with a pervasive influence on cognitive activities including memory for visually-based material. Since the classic studies of postsurgical TLE patients, it was emphasised that to test for right-sided MTL dysfunction, nonverbal memory tasks must involve stimuli that are difficult to convert into a verbal form (Milner, 1968). An ongoing controversy of nonverbal memory tests is that the stimuli used are too easily verbalised, resulting in recruitment of left-lateralised verbal structures that reduce their

specificity to right MTL dysfunction (e.g., Lee, Loring, & Thompson, 1989). However, many clinical tests of nonverbal memory appear to have been created on the basis that if they are visual and do not contain words (i.e., do not explicitly demand verbal processing), this will be sufficiently "nonverbal" to preferentially engage the right MTL. This includes Visual Reproduction, which contains easy-to-verbalise designs (e.g., "cross with left-facing flags") and the Rey Complex Figure Test which contains verbalisable features and configurations (e.g., "face in circle", "diamond", "long cross on left side").

While many clinical tests that require memory for abstract designs are notoriously easy to verbalise, the issue of verbalisation extends beyond design memory. For example, tests of face memory such as the Warrington Recognition Memory Test for Faces (WRMT-Faces) may be confounded by the presence of readily verbalisable external features that allow identification of the face without attending to the face itself (e.g., hairstyle, ears, clothing; Testa, Schefft, Privatera, & Yeh, 2004) or the if faces themselves are not sufficiently similar to each other in terms of their configuration (e.g., big nose with wide eyes; small chin and thin eyebrows, etc.). Similarly, object-location tasks with nameable objects and an excessively easy spatial array (e.g., in a regular 4 x 4 grid as in the Designs subtest from the WMS-IV) also suffer from verbalisability confounds (e.g., "dart in middle upper left"). Even ostensibly pure tests of positional memory such as the 7/24 Spatial Recall Test (Barbizet & Caney, 1968) which simply requires memory for plain black circles in positions, could be similarly verbalised due to the use of a 6 x 4 grid. In short, merely belonging to a particular class of nonverbal stimulus in and of itself does not protect a stimulus from verbalisation. However, while the creation of a purely nonverbal stimulus or task may not be a realistic goal, it may be possible to create stimuli and memory tasks with very low susceptibility to verbalisation. A promising example is provided by the Brown Location Test which involves memory for plain circles in an asymmetrical, irregular array (Brown et al., 2007).

Despite the long-recognised contribution of verbalisation to the poor reliability of

nonverbal memory tests, surprisingly little systematic investigation of factors relating to stimulus verbalisability is available. In a neuroimaging study using fMRI it was found that different kinds of nonverbal stimuli had different levels of verbalisability (scenes > faces > abstract spatial patterns), as determined by a dual-task verbal interference behavioural test (Golby et al., 2001). In addition, higher levels of verbalisability correlated negatively with the degree of right-lateralisation of activity in the MTL and the inferior prefrontal cortex during memory encoding (spatial patterns: right; scenes and faces: symmetrical; verbal: left; Golby et al., 2001). The verbalisability and bilateral activation for faces could arguably have been due to the presence of verbalisable external features (such as hairstyle), since in this study the faces were not cropped, a common methodological problem (also see Kelley et al., 1998).

Another finding that also used verbal or visuospatial interference tasks suggested that memory for coloured 3D towers was partially dependent on verbal processing and was sensitive to amygdalohippocampectomy in both hemispheres, while memory for grey 3D towers was reliant on visuospatial processing and was sensitive and specific to right amygdalohippocampectomy (Hampstead et al., 2010). In sum, memory for spatial patterns may show a lower dependence on verbal processing than other kinds of stimuli, including scenes, and colour combinations, and possibly faces, when verbalisable features are present.

1.11 Material-specific lateralisation is relative not absolute

In the same way that verbalisation of nonverbal stimuli may confound the association between nonverbal memory and the right hemisphere, verbal tasks can themselves be influenced by unwanted involvement of right-lateralised processing. In contexts that are highly demanding of visual perceptual analysis, such as when words or letters are perceptually degraded (Sergent & Hellige, 1986), masked (Polich, 1978), or accompanied by visual distractors (Marsolek, Kosslyn, & Squire, 1992), verbal task performance has been shown to become right-lateralised. Similarly, in a continuous recognition memory task with a split visual field design, the right hemisphere was superior to the left for word memory after

long retention intervals, but after shorter intervals the left was superior (Federmeier & Benjamin, 2005). This was replicated with an event-related potential (ERP) design, showing a right-lateralised "old/new effect" (i.e., in which the amplitude of the P2 peak was larger for previously seen "old" stimuli than for novel "new" foils; Evans & Federmeier, 2007). The authors interpreted these results as reflecting the more rapid decay of, and interference between, gist-like semantic transformations of the left hemisphere, compared with the more stable retention of veridical (i.e., exact or "real") representations of the words by the right hemisphere, which is particularly important in a continuous recognition memory task in which there is constant interference from new items.

In summary, for verbal materials, the right hemisphere may outperform the left when there are strong demands for highly specific, exact representations of stimuli compared with the need to encode and retain verbal information using its semantic content. As such, right hemispheric processing of verbal stimuli does not merely reflect a degraded version of left hemispheric verbal processing but provides its own a unique contribution.

1.12 Clinical tests confound material type with stimulus and response modality

An overlooked problem of clinical tests is that material type is typically confounded with presentation modality, often in addition to the type of response required. In verbal memory tests, the stimuli (e.g., words, stories) are usually presented in an auditory spoken form and also require an auditory spoken response (e.g., the Rey Auditory-Verbal Learning Test; RAVLT). In contrast, for nonverbal memory tests, the stimuli are usually presented visually and commonly require patients to draw their response, or sometimes to indicate recognition of learned stimuli when re-presented by responding verbally (e.g., "yes" or "no") or nonverbally (e.g., point to the correct item out of a set). As a result, the comparison is ostensibly between an auditory-verbal-speech task and a visual-nonverbal-sensorimotor-constructional task, therefore it is difficult to determine what process or combination of processes are contributing to differences in performance between verbal and nonverbal tests.

There is sufficient evidence that the processes relating to speech may be more left-lateralised than those involving lexical or semantic processing per se due to a dependence on articulatory processing in the dorsal stream (for a review see Hickok & Poeppel, 2007). While the focus of this thesis is on visual materials, it is important that interpretation of lateralisation occurs within this broader context, and it is critical that these factors are controlled in both the experimental and the clinical studies of hemispheric lateralisation.

1.13 Differences in lateralisation depending on how a stimulus is processed

Differences in the way a stimulus is processed may have important effects on hemispheric lateralisation. These differences can be elicited by presenting the exact same stimulus to a participant and testing for lateralisation when performing distinct tasks. As mentioned in Section 1.9, a relational spatial judgment involving a dot and a bar (e.g., "is the dot above or below the bar?") may engage the right hemisphere less than a coordinate spatial judgment such as the exact angle between the dot and bar (Badzakova-Trajkov, Haberling, Roberts, & Corballis, 2010; Corballis, 2003). It could be argued that spatial relations are more left-lateralised than spatial coordinates, simply due to greater verbalisability as discussed in Section 1.10; however, spatial relational judgments appear to have independent left hemispheric effects over and above verbal labelling (van der Ham & Postma, 2010). Supporting this, pre-verbal infants show mainly left hemisphere activity when they make relational decisions about spatial orientations (Franklin, Catherwood, Alvarez, & Axelsson, 2010). While this relational-coordinate distinction appears particularly important within the parietal cortices, evidence has been found for the same effect in the primary visual cortex (e.g., van der Ham et al., 2012). An anatomical-functional dissociation has also been shown between parietally-mediated categorical processing and hippocampus-mediated coordinate processing (Baumann & Mattingley, 2014), and the effect has been replicated in patients with unilateral brain damage (e.g., Palermo, Bureca, Matano, & Guariglia, 2008; van Asselen, Kessels, Kappelle, & Postma, 2008).

For face stimuli the identification of a face based on its "configural" or "holistic" aspects, which pertain to the way in which multiple individual facial features are spatially integrated into a coherent whole, is strongly right-lateralised in areas including the occipitotemporal and ventrolateral temporal cortices (Farah, 1991; Kanwisher, McDermott, & Chun, 1997; Landis et al., 1988; Rossion & Jacques, 2008; Sagiv & Bentin, 2001). In contrast, homologous left hemisphere regions have been linked to recognition of highly familiar or famous faces, or when faces must be named (Gorno-Tempini et al., 1998; Levy, Trevarthen, & Sperry, 1972). In line with such findings, models of face processing have suggested a role of the left hemisphere in processing semantic information related to faces (e.g., names, physical and social attributes; Bruce & Le Voi, 1983; Rhodes, 1985).

While line drawings of abstract designs are thought to be relatively easy to verbalise, and particularly in the case of the simple designs used in tests like Visual Reproduction (Barr 1997), they may also have elements that invoke more right-lateralised processing than others. The scoring of spatial distortions in the Rey Complex Figure Test using a qualitative scoring method (Loring, Lee, & Meador, 1988) successfully discriminated more impaired right TLE patients from left TLE patients, while the standard scoring method did not distinguish the groups (Piguet, Saling, O'Shea, Berkovic, & Bladin, 1994). For an experimental task using a scene, TLE patients with extensive right hippocampal removal had impaired retention of object-location associations, while memory for object information per se was related to surgery in either hemisphere (Pigott & Milner, 1993). However, there have also been a number of negative findings, failing to show differential lateralisation of figural and spatial memory components of the RCFT (e.g., Kneebone, Lee, Wade, & Loring, 2007; McConley, Martin, Banos, Blanton, & Faught, 2006; McConley et al., 2008).

Taken together, patterns of lateralisation may differ depending on which attributes of a stimulus is required to perform a given task. There appear to be commonalities in these patterns across different kinds of nonverbal stimuli, with the right hemisphere most

implicated in tasks that involve precise or configural spatial processing, relative to greater left hemispheric involvement in tasks that require categorical spatial processing, naming, association with learned semantic information, and memory for isolated details. Hence, it is clear that the use of nonverbal stimuli per se, or a particular kind of nonverbal stimulus, is not sufficient for eliciting right-lateralisation. More general, universal kinds of cognitive processing may underlie these common hemispheric patterns across different stimulus types.

1.14 Alternative models of hemispheric asymmetries in visual processing

Material specificity has provided very influential guidance in our understanding of hemispheric specialisation of memory. However, the abundant flaws and limitations with the approach limit its application to basic and clinical research to that of a general heuristic principle. A number of alternative theories have been proposed to explain the differential hemispheric lateralisation of visual stimuli in a more parsimonious and explanatory manner. The general aim of such theories is to provide a unified account of the principles that underlie hemispheric lateralisation regardless of whether the visual processes involved are primarily perceptual or involve additional memory demands. The theories that are the most relevant to the focus of this thesis will be outlined below.

1.14.1 Analytic/configural model

One influential model of hemispheric lateralisation is the analytic/configural model (Bradshaw & Nettleton, 1981). This distinction has usually been defined as a left hemispheric orientation towards serial analysis of stimuli in which each individual feature is examined in turn, whereas the right hemisphere is oriented towards parallel analysis of stimuli with configural analysis applied holistically (Dien, 2009). According to this view the left hemispheric serial, analytic preference is suited for the sequential nature of words and the right hemispheric parallel, configural preference is suited for the simultaneous analysis of multiple facial features. This model has generally been supported by studies of face recognition, particularly in studies using face inversion designed to disrupt the parallel,

configural processing of features by the right hemisphere: For example, patients with right posterior lesions show an impairment in recognising upright faces but not inverted faces (Leehey, Carey, Diamond, & Cahn, 1978; Yin, 1970). The relative degree of analytic versus configural processing has also been considered as applicable to hemispheric lateralisation effects for object recognition more generally (e.g., Corballis, Funnel, & Gazzaniga, 2000; Gazzaniga, 2000).

The model has not been empirically supported for lateralisation of word reading, however, as the right hemisphere, but not the left, is associated with longer reaction times as the length of words increases (e.g., Bouma, 1973; Iacoboni & Zaidel, 1996). Such findings run counter to analytic/configural predictions as the left hemisphere acts in a more configural manner by quickly identifying words by the whole rather than by serial analysis of their parts, while the right hemisphere processes the words serially in a letter-by-letter fashion (for a review see Ellis, 2004). As it stands, the analytic/configural model provides an incomplete account of hemispheric asymmetries beyond its central focus on face perception.

1.14.2 Categorical/coordinate model

The categorical/coordinate model (Kosslyn et al., 1989; briefly outlined in Sections 1.9 and 1.13) distinguishes between memory for "categorical" relationships between objects (e.g., "the pen is to the right of the ruler"), is predicted to involve left-lateralisation or relatively less right-lateralisation than "coordinate" spatial processing (e.g., "the pen is 25 centimetres from the ruler"). The model has been mostly investigated for spatial processing and has been supported using different testing methodologies including visual hemifield studies, ERP, fMRI, and in unilateral TLE patients (see van der Ham et al., 2014, for a review). The model has recently has been extended to processes involved in object-location memory (Postma et al., 2008), superordinate- versus exemplar-level naming of pictures (e.g., "bird" vs. "penguin"; Laeng, Zarrinpar, & Kosslyn, 2003), spatial aspects of object representations (e.g., Brooks & Cooper, 2006), and faces (Cooper & Wojan, 2000). Therefore,

this model appears to be much more generalisable than the analytic/configural model. In addition, it may help explain failure to show right-lateralisation in clinical memory tasks that test spatial memory: the use of grids clearly divides space, potentially promoting categorical spatial processing by the left hemisphere rather than precise coordinate processing by the right hemisphere. However, it remains unclear whether or how the categorical/coordinate approach could explain different lateralisation patterns for words.

1.14.3 Spatial frequency model

The high/low spatial frequency model is arguably the leading hypothesis of perceptually based hemispheric lateralisation (Dien, 2008). In this account the left hemisphere is specialised for processing high frequency information and the right hemisphere is specialised for low frequency information (Sergent, 1982, 1983). This model has great explanatory potential because it is a universal account of visually-based lateralisation which can be used to explain other hemispheric dichotomies with respect to underlying confounds with frequency (Sergent, 1982), it provides plausible neural mechanisms by which it may be implemented, and it is easily testable. Specifically, simulations have suggested that the left hemisphere may have a bias to encode outputs from neurons with relatively small and non-overlapping receptive fields, which correspond to greater sensitivity to high spatial frequencies, whereas the right hemisphere has a bias for neurons with relatively large and overlapping receptive fields and corresponds to greater sensitivity to low spatial frequencies (Chabris & Kosslyn, 1998; Kosslyn et al., 1992).

The high/low frequency model can potentially explain material specific findings on the basis that letter recognition requires high-frequency analysis to discriminate closely spaced and sharply delimited patterns, whereas most spatial judgments require the broad, diffuse, and blurred visual changes detectable by a low spatial frequency filter (Sergent, 1982). It is argued that these processing asymmetries also explain the categorical-coordinate distinction, as large and overlapping receptive fields are required to make coordinate spatial

judgments, while processing categorical spatial relations are required to make more fine-grained segmentation of space afforded by high spatial frequencies (Ivry & Robertson, 1998; Jacobs & Kosslyn, 1994; Kosslyn et al., 1992; Okubo & Michimata, 2002, 2004; Sergent, 1982, 1983). A relative right hemispheric proficiency for low spatial frequencies also provides a potential explanation for the observed right lateralisation of the configural processing of faces (e.g., Awasthi, Sowman, Friedman, & Williams, 2013). A number of experiments have also supported the model by manipulating spatial frequencies across a range of different stimuli including basic checkerboard stimuli (Martinez et al., 2001), and scenes of natural landscapes (Peyrin, Chauvin, Chokron, & Marendaz, 2003).

The high/low spatial frequency model has become closely associated with the local/global distinction in object recognition. For example, studies of figures constructed from smaller figures, such as a T shape constructed from small E's (e.g., Navon, 1977) suggest that attention to the smaller local features is left-lateralised since they are more predominantly represented by fine features requiring analysis of high spatial frequency features, while attention to the larger global features is right-lateralised due to the predominance of low spatial frequency information. The local/global distinction is also a clinically useful heuristic that allows flexible interpretation of the RCFT, for example, with evidence that lateralisation of white matter pathways as measured by diffusion tensor imaging is associated with differences in reproducing local versus global features (Chechlacz, Mantini, Gillebert, & Humphreys, 2015). However, there is also empirical evidence that the local/global and high/low spatial frequency accounts may involve independent lateralising mechanisms, or affect lateralisation at the level of association with stored representations rather than at a lower attentional level (Dien, 2008; Lamb, Yund, & Pond, 1999). More research will be required to settle these issues.

Not all hemispheric phenomena can be explained by confounds of spatial frequency. For example, studies of case-independent repetition priming show that the 'visual word form

area', an area within the left fusiform gyrus that has been linked to word-level orthographic processing, was less sensitive to changes in the case of the letters and hence to high spatial frequencies than was the right fusiform gyrus (Dehaene et al., 2001; Dehaene et al., 2004). The original spatial frequency model has also been extended into the more complex "double filtering by frequency" model (Ivry & Robertson, 1998) which postulates three separate and sequential stages of stimulus processing involving sensory representation, attentional filtering of task-relevant information, and lateralised processing depending on the attended spatial frequency. The actual lateralisation does not occur until the second stage of attentional filtering (Ivry & Robertson, 1998). A similar hierarchical account is offered to explain the categorical/coordinate distinction using the size of attentional focus as the selection mechanism, representing a convergence of the two models (van der Ham et al., 2014). While these theories are potentially very powerful within the visual modality, it remains to be seen whether the core concepts can be translated to other modalities such as speech or music (though see the excellent review by Zatorre & Samson, 2002, for a similar approach to how auditory processes may be lateralised by complementary proficiencies for temporal and spectral frequencies in the left and right auditory cortical areas).

Despite these limitations, the high/low spatial frequency hypothesis remains a highly promising model of hemispheric lateralisation that can be readily tested in research and clinical settings. For example, the relative effects of material and spatial frequency on lateralisation could be contrasted with an experimental design that manipulated one of these factors while keeping the other constant. Broadly speaking, it appears that the weight of the evidence reviewed to date suggests that right lateralisation in the brain is related to very specific "metric" analysis of spatial information that allow us to compute precise distances and positional information.

1.15 Processing specificity and hemispheric lateralisation

The majority of research on the lateralisation of memory function, as reflected in the

outline above, has focused on lateralisation effects due to differences between the type of stimuli used or differences in the way that a given stimulus is processed. However, task demands also play an important and under-recognised role in hemispheric lateralisation. A given memory task may involve different memory processes including: encoding of stimuli into short-term memory, consolidation of this information into long-term memory over a temporal delay, elaboration and structuring of remembered information, and incidental or intentional retrieval of learned information following a delay (Kopelman, 2002; Lockhart & Craik, 1990; Watkins & Gardiner, 1979; Squire, Knowlton, & Musen, 1993; Tulving & Pearlstone, 1966). An observed memory impairment could be due to a deficit in any of these processes, or a combination of processes, and the ability to disentangle different kinds of memory deficits has great clinical importance. If particular aspects of memory processing resulted in greater lateralisation independently of, or interactively with, material type, this could add to the diagnostic accuracy and interpretive power of clinical memory tests.

Neuropsychological studies have found that verbal memory performance after a long delay may be better able to detect left TLE pathology than after a short delay (e.g., Delaney, Rosen, Mattson, & Novelly, 1980). As such the left MTL may have greater involvement in consolidation processes that are required to keep verbal information in mind after a delay, than in initial attention, working memory and encoding of verbal material, that are more predominantly tested during immediate memory trials (e.g., Saling, 2009). This pattern also appears to be borne out for nonverbal memory, with an experimental scene memory test revealing that delayed recognition of object-location associations was associated with right hippocampal removal while immediate recognition was not significantly impaired (Pigott & Milner, 1993). Similar findings have been reported for remembering 3D spatial arrangements (Hampstead et al., 2010) and arbitrary design-design and design-location associations (Smith, Bigel, & Miller, 2011). A meta-analysis of neuroimaging studies of spatial memory performance in healthy participants showed that delayed memory performance was more related to activation in the anterior MTL while immediate memory was more related to

activation in the posterior MTL (Kuhn & Gallinat, 2014). This latter finding has clinical significance since typical temporal lobe surgery involves resection of the anterior hippocampus, preserving some posterior hippocampal tissue, and suggests that testing delayed memory is of critical importance in the presurgical assessment of TLE patients. However, there have also been exceptions to this pattern, most commonly with consistent impairments regardless of the delay or type of memory testing (e.g., Brown et al., 2010).

An intriguing interaction between the type of memory task and the material type has also been reported. In this interaction, patients with right MTL pathology have impairments in the initial learning of design material (i.e., patients do not benefit from repetition of material) but have intact retention of the learned designs following a delay (Jones-Gotman, Smith, Frisk & Routhier, 1996; Jones-Gotman et al., 1997; Majdan, Sziklas & Jones-Gotman, 1996; Trenerry et al., 1993). In contrast, damage to the left MTL shows the opposite pattern with intact initial learning of verbal material but impaired retention of this previously-learned material (e.g., Jones-Gotman et al., 1997). Adding a further layer of complexity, the part of this finding that pertains to nonverbal materials appears to be dependent on the presence of multiple learning trials, since for single-trial design learning tasks (e.g., Visual Reproduction) this kind of difference has not appeared between immediate and delayed memory testing (Barr et al., 1997; Vaz, 2004). These findings suggest that the right MTL may have a strong involvement in the rapid encoding of nonverbal material, while the retention of verbal material is particularly dependent on the left MTL. However, such findings must be interpreted cautiously; when the level of initial encoding of nonverbal material is low, any further reduction during retrieval would be difficult to detect compared to the reduction in verbal memory following superior performance.

In summary, the magnitude of material specific hemispheric lateralisation in TLE patients may be increased by measuring consolidation of information into long term memory using a delayed memory testing format, rather than testing immediately following learning

which is more related to working memory and initial encoding processes. The unilateral anterior MTL regions are implicated in material specific consolidation since these regions are completely resected during a standard en bloc anterior temporal lobectomy in TLE patients. There may also be an interaction effect between the material type and processing although further investigation is required regarding the parameters of this interaction.

1.16 The hemispheric encoding retrieval asymmetry (HERA) model

In contrast to studies of TLE patients, neuroimaging allows a more direct insight into which brain regions subserve particular memory processes. One prominent model that has received considerable attention in the neuroimaging literature is the hemispheric encoding retrieval asymmetry model (HERA; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). The HERA model was developed from research in healthy participants that showed that - independent of material type (e.g., verbal, pictures, faces) - the left prefrontal cortex was differentially more involved with the initial memory-encoding of stimuli than with retrieval of previously learned stimuli, while the right prefrontal cortex shows a greater involvement in retrieval than in encoding (Habib, Nyberg, & Tulving, 2003; Tulving et al., 1994). A large collection of data across different testing modalities (i.e., PET, fMRI, EEG, and behavioural) supports this encoding/retrieval dissociation (e.g., Babiloni et al., 2006; Blanchet et al., 2001; Cabeza & Nyberg, 2000; Desgranges, Baron, & Eustache, 1998). HERA has been supported across many different types of verbal tasks (e.g., semantic tasks, verb generation, word-stem completion) and nonverbal tasks (e.g., face recognition, object identity, object position) and in addition across a variety of conditions of encoding (incidental or intentional) and retrieval (recall and recognition; see review by Nyberg, Cabeza, & Tulving, 1996).

While HERA explicitly involves the prefrontal cortex, while the material specificity model primarily applies to lateralisation within the MTL, HERA has proven sufficiently influential to be experimentally compared to material specificity accounts of lateralisation. Most of these studies have involved neuroimaging of the prefrontal cortex of healthy

participants. In one study, lateralisation of prefrontal activity as measured by fMRI depended on the specific combination of material (words, object, abstract patterns) and processing type (encoding, retrieval; Johnson, Raye, Mitchell, Greene, & Anderson, 2003). Another study found material specific lateralisation in the dorsal inferior frontal gyrus (words on the left, faces on the right) while the right frontal polar cortex showed greater activity for retrieval than encoding (McDermott, Buckner, Petersen, Kelley, & Sanders, 1999). In a large-scale whole-brain analysis it was found that distinct lateralisation patterns relating to encoding and retrieval operated within networks that were material specific (sentences, pictures) and these involved interactions between MTL, prefrontal and parietal regions (Nyberg et al., 2000).

While these studies have supported a hybrid model of hemispheric lateralisation, in which both material type and memory process affect hemispheric lateralisation in a cooperative manner, a number of other studies have found material specific, but not process specific, lateralisation of the prefrontal region (e.g., Golby et al., 2001; Kelley et al., 1998; Opitz, Mecklinger, & Friderici, 2000; Raye et al., 2000; Wagner et al., 1998). From these mixed findings, alternative proposals have emerged such that, process type, only serves to modulate material specific effects (e.g., Epstein, Sekino, Yamaguchi, Kamiya, & Ueno, 2002). It has been proposed that rather than suggesting the existence of a common left prefrontal substrate for encoding per se, the left prefrontal activation for nonverbal stimuli may have been due to attempts by participants to verbally label the stimuli (Wagner et al., 1998).

The proponents of HERA, however, point out that many of these studies did not compare encoding with retrieval directly but only compared materials while testing encoding or retrieval in isolation, and therefore did not adequately test the predictions of HERA (Habib, Nyberg, & Tulving, 2003). In addition, the latest iteration of HERA emphasises that lateralisation related to material and processing type are conceptually and empirically complementary, without one or the other necessarily having to be predominant (Habib et al., 2003). In addition, the interactions between prefrontal and MTL regions are closely

interconnected both anatomically and functionally, suggesting cross-region or within-region interactions between the lateralisation effects due to material and processing (Anderson, Rajagovindan, Ghacibeh, Meador, & Ding, 2010; Fernandez & Tendolkar, 2001; Schacter & Wagner, 1999). One fMRI study suggests both process specific and material specific lateralisation effects within the MTL itself (Kennepohl, Sziklas, Garver, Wagner, & Jones-Gotman, 2007). This study found that during encoding there was greater activation of the left than right entorhinal cortex and that this effect was independent of material type, while the expected lateralisation effects occurred for verbal stimuli in the entorhinal and perirhinal cortices and for nonverbal stimuli in the anterior and posterior hippocampus.

In summary, alongside the specific type of nonverbal material used, consideration of how these materials are processed may lead to important insights about, and superior clinical assessment of, right MTL function. The HERA model has yet to be tested using TLE patients and hence a large gap remains in the literature. Further investigation of the relative effects of processing type relative to material are required to disambiguate the relative strength of each effect and how they may interact.

1.17 Electroencephalography could contribute to lateralisation research

Neuropsychological and neuroimaging approaches have been readily applied to answering important questions about hemispheric lateralisation. An overlooked method through which to investigate the relative effects of material and process is that of electroencephalography (EEG). Event-related potentials (ERP) are measured using scalp or intracranial electrodes and are calculated from the average of neural activity following multiple repetitions of a task-related stimulus (Luck, 2005). ERPs predominantly measure neural activity evoked by sensory stimulation and are modulated by different attentional and cognitive demands (Luck, 2005).

ERPs can measure neural activity in a more direct and temporally precise manner than neuroimaging techniques such as PET and fMRI, which can only detect changes

approximately 5 seconds after the onset of a stimulus due to the delay in the haemodynamic response. As such, these techniques lack sensitivity to possible differences in onset, duration, and termination of neural activity related to different memory process. ERPs are ideally suited for tasks in which attention to stimulus features is manipulated, such as high versus low spatial frequencies, as they are extremely sensitive to such changes (Luck, 2005). There is also evidence that material specific lateralisation effects (approximately 150 to 300 ms after stimulus onset) occur earlier than processing related differences (around 300 to 1000 ms) potentially allowing for the dissociation of these factors (e.g., Maillard et al., 2011).

EEG oscillations index aspects of neural activity that ERPs filter out, including recurrent and reciprocal changes between cortical regions (Pfurtscheller & da Silva, 1999). Memory performance has been associated with patterns of oscillatory synchronisation in specific frequency bands (Klimesch, 1999). In particular, changes in oscillations in the theta frequency band (4 to 7 Hz) have been related to working memory and encoding processes, while oscillations in the alpha band (8 to 13 Hz) have been related memory retrieval and may also show material specific lateralisation (Burgess & Gruzelier, 2000). It is therefore possible that the use of ERP and frequency measures of neural activity may lead to new insights about the nature of lateralisation effects as mediated by stimulus characteristics such as spatial frequency, the type of material and the type of processing. However, there is a lack of in-depth investigations of these factors using EEG measures.

1.18 Summary

This review has discussed several unresolved issues regarding hemispheric differences in memory function, particularly concerning the role of the right MTL. Based on the clinical literature, it is possible that memory for different kinds of nonverbal stimuli may differentially correlate with right MTL pathology. Findings from clinical and neuroscientific studies converge on several factors that could increase the accuracy of assessing MTL processing: the use of spatial or facial materials, increasing the demand for highly precise spatial processing,

and validation that the stimuli are difficult to verbalise. Alternative theoretical accounts to material specificity, such as the categorical/coordinate model and the spatial frequency model may have better explanatory power than material specificity in accounting for patterns of lateralisation in visual processing, and in turn could potentially be applied to clinical assessment of right TLE.

An additional factor raised in this review, arguably overlooked in the clinical context, is the type of memory process (e.g., encoding, consolidation, and retrieval). In general, right-lateralisation of memory function is likely to be influenced by independent and interactive contributions of these discussed factors. Experimental designs that systematically control for and manipulate these factors may lead to more substantive insights into the causes of right hemisphere lateralisation.

1.19 Aims and contextual overview of the thesis

This thesis sought to investigate the association of different attributes of nonverbal memory tasks to the degree of right hemispheric lateralisation, in order to clarify and build upon previous literature and potentially enhance clinical practice. It is presented in the form of five manuscripts (formatted for publication), involving a meta-analysis of published studies (Chapter 2), and four experimental chapters conducted with two samples of healthy participants (Sample 1: Chapters 3 and 4; Sample 2: Chapters 5 and 6). Each manuscript addresses specific issues raised in this introduction including: i) the factors that mediate the efficiency of clinical neuropsychological visual memory tests in diagnosing right temporal lobe pathology (Chapter 2), ii) the relative role of material type and type of memory processing on right-lateralisation of neural activity in healthy participants as measured by event-related potentials (ERPs; Chapter 3) and power measures (Chapter 4), and iii) a comparison between the effects of material specific stimulus processing, material specific memory processing, and verbalisability of materials on the right-lateralisation of ERP measures (Chapter 5) and power measures (Chapter 6). This format of thesis-by-publications

necessarily involves some repetition of information but redundancy has been minimised wherever possible.

References

Abrahams, S., Pickering, A., Polkey, C. E., & Morris, R. G. (1997). Spatial memory deficits in patients with unilateral damage to the right hippocampal formation. *Neuropsychologia, 35*(1), 11-24. doi: 10.1016/s0028-3932(96)00051-6

Aguirre, G. K., & D'Esposito, M. (1999). Topographical disorientation: a synthesis and taxonomy. *Brain, 122*(9), 1613-1628.

Anderson, K. L., Rajagovindan, R., Ghacibeh, G. A., Meador, K. J., & Ding, M. Z. (2010). Theta Oscillations Mediate Interaction between Prefrontal Cortex and Medial Temporal Lobe in Human Memory. *Cerebral Cortex, 20*(7), 1604-1612. doi: 10.1093/cercor/bhp223

Araujo, D., De Araujo, D. B., Pontes-Neto, O. M., Escorsi-Rosset, S., Simao, G. N., Wichert-Ana, L., . . . Santos, A. C. (2006). Language and motor fMRI activation in polymicrogyric cortex. *Epilepsia, 47*(3), 589-592. doi: 10.1111/j.1528-1167.2006.00473.x

Awasthi, B., Friedman, J., & Williams, M. A. (2011). Faster, stronger, lateralized: Low spatial frequency information supports face processing. *Neuropsychologia, 49*(13), 3583-3590. doi: 10.1016/j.neuropsychologia.2011.08.027

Babiloni, C., Vecchio, F., Cappa, S., Pasqualetti, P., Rossi, S., Miniussi, C., & Rossini, P. M. (2006). Functional frontoparietal connectivity during encoding and retrieval processes follows HERA model - A high-resolution study. *Brain Research Bulletin, 68*(4), 203-212. doi: 10.1016/j.brainresbull.2005.04.019

Badzakova-Trajkov, G., Häberling, I. S., Roberts, R. P., & Corballis, M. C. (2010). Cerebral asymmetries: complementary and independent processes. *PLoS One, 5*(3), e9682.

Barbizet, J., & Cany, E. (1967). Clinical and psychometrical study of a patient with memory disturbances. *International Journal of Neurology, 7*(1), 44-54.

Barr, W. B. (1997). Examining the right temporal lobe's role in nonverbal memory. *Brain and Cognition, 35*(1), 26-41.

Barr, W. B., Chelune, G. J., Hermann, B. P., Loring, D. W., Perrine, K., Strauss, E., . . . Westerveld, M. (1997). The use of figural reproduction tests as measures of nonverbal memory in epilepsy surgery candidates. *Journal of the International Neuropsychological Society, 3*(5), 435-443.

Barr, W. B. (2015). *Handbook on the Neuropsychology of Epilepsy* (Vol. pp. 1-36). London: Springer.

Baumann, O., & Mattingley, J. B. (2013). Dissociable roles of the hippocampus and parietal cortex in processing of coordinate and categorical spatial information. *Frontiers in Human Neuroscience, 8*, 73-73.

Baxendale, S. A. (1997). The role of the hippocampus in recognition memory. *Neuropsychologia, 35*(5), 591-598. doi: 10.1016/s0028-3932(96)00123-6

Baxendale, S. (2010). The Flynn effect and memory function. *Journal of Clinical and Experimental Neuropsychology, 32*(7), 699-703.

Baxendale, S. A., Van Paesschen, W., Thompson, P. J., Duncan, J. S., Shorvon, S. D., & Connelly, A. (1997). The relation between quantitative MRI measures of hippocampal structure and the intracarotid amobarbital test. *Epilepsia, 38*(9), 998-1007. doi:10.1111/j.1528-1157.1997.tb01482.x

Baxendale, S. A., Thompson, P. J., & Van Paesschen, W. (1998). A test of spatial memory and its clinical utility in the pre-surgical investigation of temporal lobe epilepsy patients. *Neuropsychologia, 36*(7), 591-602. doi: 10.1016/s0028-3932(97)00163-2

Baxendale, S. A., Van Paesschen, W., Thompson, P. J., Duncan, J. S., Harkness, W. F., & Shorvon, S. D. (1998). Hippocampal cell loss and gliosis: Relationship to preoperative and postoperative memory function. *Neuropsychiatry Neuropsychology and Behavioral Neurology, 11*(1), 12-21.

Baxendale, S. A., Thompson, P. J., & Duncan, J. S. (2008). Improvements in memory function following anterior temporal lobe resection for epilepsy. Neurology, 71(17), 1319-1325. doi: 10.1212/01.wnl.0000319699.04265.fd

Baxendale, S., & Smith, N. (2012). Right hippocampal pathology inhibits the Flynn effect in temporal lobe epilepsy. *Journal of Clinical and Experimental Neuropsychology, 34*(10), 1033-1040. doi: 10.1080/13803395.2012.711812

Bellgowan, P. S. F., Buffalo, E. A., Bodurka, J., & Martin, A. (2009). Lateralized spatial and object memory encoding in entorhinal and perirhinal cortices. *Learning & Memory, 16*(7), 433-438. doi: 10.1101/lm.1357309

Blanchet, S., Desgranges, B., Denise, P., Lechevalier, B., Eustache, F., & Faure, S. (2001). New questions on the hemispheric encoding/retrieval asymmetry (HERA) model assessed by divided visual-field tachistoscopy in normal subjects. *Neuropsychologia, 39*(5), 502-509. doi:10.1016/s0028-3932(00)00119-6

Blakemore, C. B., & Falconer, M. A. (1967). Long-term effects of anterior temporal lobectomy on certain cognitive functions. *Journal of Neurology, Neurosurgery, and Psychiatry, 30*(4), 364-367.

Bohbot, V. D., Iaria, G., & Petrides, M. (2004). Hippocampal function and spatial memory: Evidence from functional neuroimaging in healthy participants and performance of patients with medial temporal lobe resections. *Neuropsychology, 18*(3), 418-425. doi: 10.1037/0894-4105.18.3.418

Bouma, H. (1973). Visual interference in the parafoveal recognition of initial and final letters of words. *Vision research, 13*(4), 767-782.

Bradshaw, J. L., & Nettleton, N. C. (1981). The nature of hemispheric specialization in man. *Behavioral and Brain Sciences, 4*(01), 51-63.

Brain, W. R. (1941). Visual orientation with special reference to lesions of the right cerebral hemisphere. *Brain: A Journal Of Neurology*.

Broca, P. (1865). Sur le siège de la faculté du langage articulé. *Bulletins de la Société d'Anthropologie de Paris, 6*(1), 377-393.

Brooks, B. E., & Cooper, E. E. (2006). What types of visual recognition tasks are mediated by the neural subsystem that subserves face recognition? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 32*(4), 684.

Brown, F. C., Roth, R. M., Saykin, A. J., & Beverly-Gibson, G. (2007). A new measure of visual location learning and memory: Development and psychometric properties for the brown location test (blt). *Clinical Neuropsychologist, 21*(5), 811-825. doi: 10.1080/13854040600878777

Brown, F. C., Tuttle, E., Westerveld, M., Ferraro, F. R., Chmielowiec, T., Vandemore, M., . . . Spencer, S. S. (2010). Visual memory in patients after anterior right temporal lobectomy and adult normative data for the Brown Location Test. *Epilepsy & Behavior, 17*(2), 215-220. doi: 10.1016/j.yebeh.2009.11.026

Bruce, V., & Le Voi, M. (1983). Recognizing faces [and discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 302*(1110), 423-436.

Burgess, N. (2002). The hippocampus, space, and viewpoints in episodic memory. *The Quarterly Journal of Experimental Psychology: Section A, 55*(4), 1057-1080.

Burgess, A. P., & Gruzelier, J. H. (2000). Short duration power changes in the EEG during recognition memory for words and faces. *Psychophysiology, 37*(5), 596-606.

Bussey, T. J., Saksida, L. M., & Murray, E. A. (2003). Impairments in visual discrimination after perirhinal cortex lesions: testing 'declarative'vs.'perceptual-mnemonic'views of perirhinal cortex function. *European Journal of Neuroscience, 17*(3), 649-660.

Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience, 12*(1), 1-47. 0034054982&partnerID=40&md5=5481058aaa7f13ea7c44d79e7ffd2a06

Chabris, C. F., & Kosslyn, S. M. (1998). How do the cerebral hemispheres contribute to encoding spatial relations? *Current Directions in Psychological Science, 7*(1), 8-14.

Chechlacz, M., Mantini, D., Gillebert, C. R., & Humphreys, G. W. (2015). Asymmetrical white matter networks for attending to global versus local features. *Cortex, 72*, 54-64.

Chelune, G. J. (1995). Hippocampal adequacy versus functional reserve: predicting memory functions following temporal lobectomy. *Archives of Clinical Neuropsychology, 10*(5), 413-432.

Chelune, G. J., Naugle, R. I., Luders, H., & Awad, I. A. (1991). Prediction of cognitive change as a function of preoperative ability status among temporal lobectomy patients seen at 6-month follow-up. *Neurology, 41*(3), 399-404.

Chiaravalloti, N. D., & Glosser, G. (2004). Memory for faces dissociates from memory for location following anterior temporal lobectomy. *Brain and Cognition, 54*(1), 35-42. doi:10.1016/s0278-2626(03)00257-4

Cooper, E. E., & Wojan, T. J. (2000). Differences in the coding of spatial relations in face identification and basic-level object recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26*(2), 470.

Corballis, M. C. (2003). From mouth to hand: Gesture, speech, and the evolution of right-handedness. *Behavioral and Brain Sciences, 26*(2), 199-208; discussion 208-160.

Corballis, P. M., Funnell, M. G., & Gazzaniga, M. S. (2000). An evolutionary perspective on hemispheric asymmetries. *Brain and Cognition, 43*(1-3), 112-117.

Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. In S. E. Hyman, T. M. Jessell, C. J. Shatz, C. F. Stevens, & H. Y. Zoghbi (Eds.), *Annual Review of Neuroscience, Vol 34* (Vol. 34, pp. 569-599).

Corkin, S. (1965). Tactually-guided maze learning in man: Effects of unilateral cortical excisions and bilateral hippocampal lesions. *Neuropsychologia, 3*(4), 339-351.

Crane, J., & Milner, B. (2002). Do I know you? Face perception and memory in patients with selective amygdalo-hippocampectomy. *Neuropsychologia, 40*(5), 530-538. doi: 10.1016/s0028-3932(01)00131-2

Critchley, M., & Critchley, E. A. (1998). *John Hughlings Jackson: Father of English Neurology: Father of English Neurology*: Oxford University Press, USA.

Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J.-F., Poline, J.-B., & Rivière, D. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience, 4*(7), 752-758.

Dehaene, S., Jobert, A., Naccache, L., Ciuciu, P., Poline, J.-B., Le Bihan, D., & Cohen, L. (2004). Letter binding and invariant recognition of masked words behavioral and neuroimaging evidence. *Psychological Science, 15*(5), 307-313.

Delaney, R. C., Rosen, A. J., Mattson, R. H., & Novelly, R. A. (1980). Memory function in focal epilepsy: a comparison of non-surgical, unilateral temporal lobe and frontal lobe samples. *Cortex, 16*(1), 103-117.

Desgranges, B., Baron, J. C., & Eustache, F. (1998). The functional neuroanatomy of episodic memory: The role of the frontal lobes, the hippocampal formation, and other areas. *Neuroimage, 8*(2), 198-213. doi: 10.1006/nimg.1998.0359

Dien, J. (2008). Looking both ways through time: The Janus model of lateralized cognition. *Brain and Cognition, 67*(3), 292-323.

Dien, J. (2009). A tale of two recognition systems: implications of the fusiform face area and the visual word form area for lateralized object recognition models. *Neuropsychologia, 47*(1), 1-16.

Djordjevic, J., & Jones-Gotman, M. (2011). Inquiry on assessments across epilepsy centers in different countries. In C. Helmstaedter, B. Hermann, M. Lassonde, P. Kahane, & A. Arzimanoglou (Eds.), Neuropsychology in the care of people with epilepsy. Montrouge, FR: John Libbey Eurotext.

Dobbins, I. G., Kroll, N. E., Tulving, E., Knight, R. T., & Gazzaniga, M. S. (1998). Unilateral medial temporal lobe memory impairment: type deficit, function deficit, or both? *Neuropsychologia, 36*(2), 115-127.

Eichenbaum, H., & Bunsey, M. (1995). On the binding of associations in memory: Clues from studies on the role of the hippocampal region in paired-associate learning. *Current Directions in Psychological Science, 4*(1), 19-23.

Eichenbaum, H., Otto, T., & Cohen, N. J. (1994). Two functional components of the hippocampal memory system. *Behavioral and Brain Sciences, 17*(3), 449-472.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., & et al. (2003). Cellular networks underlying human spatial navigation. *Nature, 425*(6954), 184-188.

Epstein, C. M., Sekino, M., Yamaguchi, K., Kamiya, S., & Ueno, S. (2002). Asymmetries of prefrontal cortex in human episodic memory: effects of transcranial magnetic stimulation on learning abstract patterns. *Neuroscience Letters, 320*(1–2), 5-8. doi: http://dx.doi.org/10.1016/S0304-3940(01)02573-3

Evans, K. M., & Federmeier, K. D. (2007). The memory that's right and the memory that's left: Event-related potentials reveal hemispheric asymmetries in the encoding and retention of verbal information. *Neuropsychologia, 45*(8), 1777-1790. doi: 10.1016/j.neuropsychologia.2006.12.014

Farah, M. J. (1991). Cognitive neuropsychology: Patterns of co-occurrence among the associative agnosias: Implications for visual object representation. *Cognitive Neuropsychology, 8*(1), 1-19.

Federmeier, K. D., & Benjamin, A. S. (2005). Hemispheric asymmetries in the time course of recognition memory. *Psychonomic Bulletin & Review, 12*(6), 993-998.

Finke, C., Ostendorf, F., Braun, M., & Ploner, C. J. (2011). Impaired representation of geometric relationships in humans with damage to the hippocampal formation. *Plos One, 6*(5).

Flynn, J. R. (1984). The mean IQ of Americans: Massive gains 1932 to 1978. *Psychological Bulletin, 95*(1), 29.

Franklin, A., Catherwood, D., Alvarez, J., & Axelsson, E. (2010). Hemispheric asymmetries in categorical perception of orientation in infants and adults. *Neuropsychologia, 48*(9), 2648-2657.

Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication. *Brain, 123*(7), 1293-1326.

Gorno-Tempini, M. L., Price, C. J., Josephs, O., Vandenberghe, R., Cappa, S. F., Kapur, N., & Frackowiak, R. S. (1998). The neural systems sustaining face and proper-name processing. *Brain, 121 (Pt 11),* 2103-2118.

Golby, A. J., Poldrack, R. A., Brewer, J. B., Spencer, D., Desmond, J. E., Aron, A. P., & Gabrieli, J. D. E. (2001). Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. *Brain, 124*, 1841-1854. doi: 10.1093/brain/124.9.1841

Habib, R., Nyberg, L., & Tulving, E. (2003). Hemispheric asymmetries of memory: the HERA model revisited. *Trends in Cognitive Sciences, 7*(6), 241-245. doi:10.1016/s1364-6613(03)00110-4

Hampstead, B. M., Lacey, S., Ali, S., Phillips, P. A., Stringer, A. Y., & Sathian, K. (2010). Use of complex three-dimensional objects to assess visuospatial memory in healthy individuals and patients with unilateral amygdalohippocampectomy. *Epilepsy and Behavior, 18*(1-2), 54-60.

Haxby, J. V., Ungerleider, L. G., Horwitz, B., Maisog, J. M., Rapoport, S. I., & Grady, C. L. (1996). Face encoding and recognition in the human brain. *Proceedings of the National Academy of Sciences of the United States of America, 93*(2), 922-927. doi: 10.1073/pnas.93.2.922

Helmstaedter, C., Gleißner, U., Di Perna, M., & Elger, C. E. (1997). Relational verbal memory processing in patients with temporal lobe epilepsy. *Cortex, 33*(4), 667-678.

Hermann, B. P., Seidenberg, M., Haltiner, A., & Wyler, A. R. (1995). Relationship of age at onset, chronologic age, and adequacy of preoperative performance to verbal memory change after anterior temporal lobectomy. *Epilepsia, 36*(2), 137-145.

Hermann, B. P., Seidenberg, M., Wyler, A., Davies, K., Christeson, J., Moran, M., & Stroup, E. (1996). The effects of human hippocampal resection on the serial position curve. *Cortex, 32*(2), 323-334.

Hickok, G., & Poeppel, D. (2007). Opinion - The cortical organization of speech processing. *Nature Reviews Neuroscience, 8*(5), 393-402. doi: 10.1038/nrn2113

Iacoboni, M., & Zaidel, E. (1996). Hemispheric independence in word recognition: Evidence from unilateral and bilateral presentations. *Brain and Language, 53*, 121-140.

Ivry, R. B., & Robertson, L. C. (1998). *The Two Sides of Perception*. Cambridge, Massachusetts: The MIT Press.

Jacobs, R. A., & Kosslyn, S. M. (1994). Encoding shape and spatial relations: The role of receptive field size in coordinating complementary representations. *Cognitive science, 18*(3), 361-386.

Johnson, M. K., Raye, C. L., Mitchell, K. J., Greene, E. J., & Anderson, A. W. (2003). fMRI evidence for an organization of prefrontal cortex by both type of process and type of information. *Cerebral Cortex, 13*(3), 265-273. doi:10.1093/cercor/13.3.265

Jones-Gotman, M., Smith, M. L., Frisk, V., & Routhier, N. (1996). Learning and retention of connected prose before and after surgical resection from a temporal lobe. *Epilepsia, 37*(S5), 120-120.

Jones-Gotman, M., Zatorre, R. J., Olivier, A., Andermann, F., Cendes, F., Staunton, H., . . . Wieser, H. G. (1997). Learning and retention of words and designs following excision from medial or lateral temporal-lobe structures. Neuropsychologia, 35(7), 963-973. doi: 10.1016/s0028-3932(97)00024-9

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17*(11), 4302-4311.

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., . . . Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron, 20*(5), 927-936. doi: 10.1016/s0896-6273(00)80474-2

Kennepohl, S., Sziklas, V., Garver, K. E., Wagner, D. D., & Jones-Gotman, M. (2007). Memory and the medial temporal lobe: Hemispheric specialization reconsidered. *Neuroimage, 36*(3), 969-978. doi: 10.1016/j.neuroimage.2007.03.049

Kessels, R. P. C., de Haan, E. H. F., Kappelle, L. J., & Postma, A. (2001). Varieties of human spatial memory: a meta-analysis on the effects of hippocampal lesions. *Brain Research Reviews, 35*(3), 295-303.

Kessels, R. P. C., Hendriks, M., Schouten, J., Van Asselen, M., & Postma, A. (2004). Spatial memory deficits in patients after unilateral selective amygdalohippocampectomy. *Journal Of The International Neuropsychological Society: JINS, 10*(6), 907-912.

Kimura, D. (1963). Right temporal-lobe damage. *Archives of Neurology, 8*, 264-271.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews, 29*(2-3), 169-195. doi: 10.1016/s0165-0173(98)00056-3

Kneebone, A. C., Lee, G. P., Wade, L. T., & Loring, D. W. (2007). Rey Complex Figure: figural and spatial memory before and after temporal lobectomy for intractable epilepsy. *Journal of the International Neuropsychological Society, 13*(04), 664-671.

Kosslyn, S. M. (1987). Seeing and Imagining in the Cerebral Hemispheres: A Computational Approach. *Psychological Review, 94*(2), 148-175.

Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. D. (1989). Evidence for two types of spatial representations: hemispheric specialization for

categorical and coordinate relations. *Journal of experimental psychology: human perception and performance, 15*(4), 723.

Kosslyn, S. M., Chabris, C. F., Marsolek, C. J., & Koenig, O. (1992). Categorical versus coordinate spatial relations: Computational analyses and computer simulations. *Journal of experimental psychology: human perception and performance, 18*(2), 562.

Kuhn, S., & Gallinat, J. (2014). Segregating Cognitive Functions Within Hippocampal Formation: A Quantitative Meta-analysis on Spatial Navigation and Episodic Memory. *Human Brain Mapping, 35*(4), 1129-1142. doi: 10.1002/hbm.22239

Laeng, B., Zarrinpar, A., & Kosslyn, S. M. (2003). Do separate processes identify objects as exemplars versus members of basic-level categories? Evidence from hemispheric specialization. *Brain and Cognition, 53*(1), 15-27.

Lamb, M. R., Yund, E. W., & Pond, H. M. (1999). Is attentional selection to different levels of hierarchical structure based on spatial frequency? *Journal of Experimental Psychology: General, 128*(1), 88.

Lee, G. P., Loring, D. W., & Thompson, J. L. (1989). Construct validity of material-specific memory measures following unilateral temporal lobe ablations. *Psychological Assessment, 1*(3), 192.

Lee, T. M. C., Yip, J. T. H., & Jones-Gotman, M. (2002). Memory deficits after resection from left or right anterior temporal lobe in humans: A meta-analytic review. *Epilepsia, 43*(3), 283-291

Leehey, S., Carey, S., Diamond, R., & Cahn, A. (1978). Upright and inverted faces: The right hemisphere knows the difference. *Cortex, 14*(3), 411-419.

Levy, J., Trevarthen, C., & Sperry, R. W. (1972). Perception of bilateral chimeric figures following hemispheric deconnexion. *Brain, 95*(1), 61-78.

Lockhart, R. S., & Craik, F. I. (1990). Levels of processing: A retrospective commentary on a framework for memory research. *Canadian Journal of Psychology/Revue canadienne de psychologie, 44*(1), 87.

Loring, D. W., Lee, G. P., & Meador, K. J. (1988). Revising the Rey-Osterrieth: Rating right hemisphere recall. *Archives of Clinical Neuropsychology, 3*(3), 239-247.

Loring, D. W., Lowenstein, D. H., Barbaro, N. M., Fureman, B. E., Odenkirchen, J., Jacobs, M. P., . . . Gaillard, W. D. (2011). Common data elements in epilepsy research: development and implementation of the NINDS epilepsy CDE project. *Epilepsia, 52*(6), 1186-1191.

Luck, S. (2005). *An Introduction To The Event-Related Potential Technique*. Cambridge, Massachusetts: The MIT Press.

Maillard, L., Barbeau, E. J., Baumann, C., Koessler, L., Benar, C., Chauvel, P., & Liegeois-Chauvel, C. (2011). From Perception to Recognition Memory: Time Course and Lateralization of Neural Substrates of Word and Abstract Picture Processing. *Journal of Cognitive Neuroscience, 23*(4), 782-800. doi:10.1162/jocn.2010.21434

Majdan, A., Sziklas, V., & JonesGotman, M. (1996). Performance of healthy subjects and patients with resection from the anterior temporal lobe on matched tests of verbal and visuoperceptual learning. *Journal of Clinical and Experimental Neuropsychology, 18*(3), 416-430. doi:10.1080/01688639608408998

Malec, J. F., Ivnik, R. J., & Hinkeldey, N. S. (1991). Visual spatial learning test. *Psychological Assessment: A Journal of Consulting and Clinical Psychology, 3*(1), 82.

Marsolek, C. J., Kosslyn, S. M., & Squire, L. R. (1992). Form-specific visual priming in the right cerebral hemisphere. *Journal of Experimental Psychology-Learning Memory and Cognition, 18*(3), 492-508. doi:10.1037//0278-7393.18.3.492

Martinez, A., Di Russo, F., Anllo-Vento, L., & Hillyard, S. A. (2001). Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clinical Neurophysiology, 112*(11), 1980-1998.

McConley, R., Martin, R., Banos, J., Blanton, P., & Faught, E. (2006). Global/local scoring modifications for the Rey-Osterrieth Complex Figure: Relation to unilateral temporal

lobe epilepsy patients. *Journal of the International Neuropsychological Society, 12*(3), 383-390. doi:10.1017/s1355617706060413

McConley, R., Martin, R., Palmer, C. A., Kuznieck, R., Knowlton, R., & Faught, E. (2008). Rey Osterrieth complex figure test spatial and figural scoring: Relations to seizure focus and hippocampal pathology in patients with temporal lobe epilepsy. *Epilepsy & Behavior, 13*(1), 174-177. doi:10.1016/j.yebeh.2008.03.003

McDermott, K. B., Buckner, R. L., Petersen, S. E., Kelley, W. M., & Sanders, A. L. (1999). Set- and code-specific activation in the frontal cortex: An fMRI study of encoding and retrieval of faces and words. *Journal of Cognitive Neuroscience, 11*(6), 631-640. doi:10.1162/089892999563698

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

Martin, R. C., Kretzmer, T., Palmer, C., Sawrie, S., Knowlton, R., Faught, E., . . . Kuzniecky, R. (2002). Risk to verbal memory following anterior temporal lobectomy in patients with severe left-sided hippocampal sclerosis. *Archives of Neurology, 59*(12), 1895-1901. doi:10.1001/archneur.59.12.1895

Milner, B. (1954). Intellectual function of the temporal lobes. *Psychological Bulletin, 51*(1), 42.

Milner, B. (1962). *Laterality effects in audition*. Baltimore: The John Hopkins Press.

Milner, B. (1965). Visually-guided maze learning in man: Effects of bilateral hippocampal, bilateral frontal, and unilateral cerebral lesions. *Neuropsychologia, 3*(4), 317-338.

Milner, B. (1967). Brain mechanisms suggested by studies of temporal lobes *Brain mechanisms underlying speech and language* (pp. 122-145). New York: Grune & Stratton.

Milner, B. (1958). Psychological defects produced by temporal lobe excision. *Research publications - Association for Research in Nervous and Mental Disease, 36*, 244-257.

Milner, B. (1970). Memory and the medial temporal regions of the brain. In B. Pribram K.H., D.E. (Ed.), *Biology of Memory*. New York: Academic Press.

Milner, B. (1968). Visual recognition and recall after right temporal-lobe excision in man. *Neuropsychologia, 6*(3), 191-209. doi:10.1016/0028-3932(68)90019-5

Moscovitch, D. A., & McAndrews, M. P. (2002). Material-specific deficits in "remembering" in patients with unilateral temporal lobe epilepsy and excisions. *Neuropsychologia, 40*(8), 1335-1342. doi:10.1016/s0028-3932(01)00213-5

Naugle, R. I., Chelune, G. J., Cheek, R., Luders, H., & Awad, I. A. (1993). Detection of changes in material-specific memory following temporal lobectomy using the Wechsler Memory Scale-Revised. *Archives of Clinical Neuropsychology, 8*(5), 381-395. doi:10.1016/0887-6177(93)90002-i

Naugle, R. I. (1994). Recognition Memory for Words and Faces Before and After Temporal Lobectomy. *Assessment, 1*(4), 373-381.

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive psychology, 9*(3), 353-383.

Nunn, J. A., Polkey, C. E., & Morris, R. G. (1998). Selective spatial memory impairment after right unilateral temporal lobectomy. *Neuropsychologia, 36*(9), 837-848.

Nyberg, L., Cabeza, R., & Tulving, E. (1996). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin & Review, 3*(2), 135-148. doi:10.3758/bf03212412

Nyberg, L., Persson, J., Habib, R., Tulving, E., McIntosh, A. R., Cabeza, R., & Houle, S. (2000). Large scale neurocognitive networks underlying episodic memory. *Journal of Cognitive Neuroscience, 12*(1), 163-173.

O'Brien, C. E., Bowden, S. C., Bardenhagen, F. J., & Cook, M. J. (2003). Neuropsychological correlates of hippocampal and rhinal cortex volumes in patients with mesial temporal sclerosis. *Hippocampus, 13*(8), 892-904. doi:10.1002/hipo.10128

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map* (Vol. 3): Clarendon Press Oxford.

Okubo, M., & Michimata, C. (2002). Hemispheric processing of categorical and coordinate spatial relations in the absence of low spatial frequencies. *Journal of Cognitive Neuroscience, 14*(2), 291-297.

Okubo, M., & Michimata, C. (2004). The role of high spatial frequencies in hemispheric processing of categorical and coordinate spatial relations. *Journal of Cognitive Neuroscience, 16*(9), 1576-1582.

Opitz, B., Mecklinger, A., & Friederici, A. D. (2000). Functional asymmetry of human prefrontal cortex: Encoding and retrieval of verbally and nonverbally coded information. *Learning & Memory, 7*(2), 85-96. doi:10.1101/lm.7.2.85

Owen, A. M., Milner, B., Petrides, M., & Evans, A. C. (1996). A specific role for the right parahippocampal gyrus in the retrieval of object-location: A positron emission tomography study. *Journal of Cognitive Neuroscience, 8*(6), 588-602.

Palermo, L., Bureca, I., Matano, A., & Guariglia, C. (2008). Hemispheric contribution to categorical and coordinate representational processes: A study on brain-damaged patients. *Neuropsychologia, 46*(11), 2802-2807.

Papanicolaou, A. C., Simos, P. G., Castillo, E. M., Breier, J. I., Katz, J. S., & Wright, A. A. (2002). The hippocampus and memory of verbal and pictorial material. *Learning & Memory, 9*(3), 99-104. doi:10.1101/lm.44302

Peyrin, C., Chauvin, A., Chokron, S., & Marendaz, C. (2003). Hemispheric specialization for spatial frequency processing in the analysis of natural scenes. *Brain and Cognition, 53*(2), 278-282. doi:10.1016/s0278-2626(03)00126-x

Pfurtscheller, G., & da Silva, F. H. L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical Neurophysiology, 110*(11), 1842-1857. doi:10.1016/s1388-2457(99)00141-8

Pigott, S., & Milner, B. (1993). Memory for different aspects of complex visual scenes after unilateral temporal- or frontal-lobe resection. *Neuropsychologia, 31*(1), 1-15.

Piguet, O., Saling, M. M., Oshea, M. F., Berkovic, S. F., & Bladin, P. F. (1994). Rey figure distortions reflect nonverbal recall differences between right and left foci in unilateral temporal lobe epilepsy. *Archives of Clinical Neuropsychology, 9*(5), 451-460. doi:10.1016/0887-6177(94)90007-8

Polich, J. M. (1978). Hemispheric differences in stimulus identification. *Perception and Psychophysics, 24*(1), 49-57. doi:10.3758/bf03202973

Postma, A., & DeHaan, E. H. F. (1996). What was where? Memory for object locations. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology, 49*(1), 178-199. doi:10.1080/027249896392856

Postma, A., Kessels, R. P., & van Asselen, M. (2008). How the brain remembers and forgets where things are: The neurocognition of object–location memory. *Neuroscience & Biobehavioral Reviews, 32*(8), 1339-1345.

Rausch, R., & Babb, T. L. (1993). Hippocampal neuron loss and memory scores before and after temporal lobe surgery for epilepsy. *Archives of Neurology, 50*(8), 812-817.

Rausch, R., & Crandall, P. H. (1982). Psychological status related to surgical control of temporal lobe seizures. *Epilepsia, 23*(2), 191-202.

Raye, C. L., Johnson, M. K., Mitchell, K. J., Nolde, S. F., & D'Esposito, M. (2000). fMRI investigations of left and right PFC contributions to episodic remembering. *Psychobiology, 28*(2), 197-206.

Rey, A. (1941). L'examen psychologique dans les cas d'encéphalopathie traumatique. *Archives de psychologie, 28*, 286-340.

Rhodes, G. (1985). Perceptual asymmetries in face recognition. *Brain and Cognition, 4*(2), 197-218.

Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform

gyrus is necessary for normal face processing. *Brain, 126*(11), 2381-2395. doi: 10.1093/brain/awg241

Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage, 39*(4), 1959-1979.

Sagiv, N., & Bentin, S. (2001). Structural encoding of human and schematic faces: holistic and part-based processes. *Cognitive Neuroscience, Journal of, 13*(7), 937-951.

Saling, M. M., Berkovic, S. F., O'Shea, M. F., Kalnins, R. M., Darby, D. G., & Bladin, P. F. (1993). Lateralization of verbal memory and unilateral hippocampal sclerosis: evidence of task-specific effects. *Journal of Clinical and Experimental Neuropsychology, 15*(4), 608-618.

Saling, M. M. (2009). Verbal memory in mesial temporal lobe epilepsy: beyond material specificity. *Brain, 132*, 570-582. doi:10.1093/brain/awp012

Sass, K. J., Spencer, D. D., Kim, J. H., Westerveld, M., Novelly, R. A., & Lencz, T. (1990). Verbal memory impairment correlates with hippocampal pyramidal cell density. *Neurology, 40*(11), 1694-1697.

Sass, K. J., Sass, A., Westerveld, M., Lencz, T., Novelly, R. A., Kim, J. H., & Spencer, D. D. (1992). Specificity in the Correlation of Verbal Memory and Hippocampal Neuron Loss: Dissociation of Memory, Language, and Verbal Intellectual Ability. *Journal of Clinical and Experimental Neuropsychology, 14*(5), 662-672.

Sass, K. J., Westerveld, M., Buchanan, C. P., Spencer, S. S., Kim, J. H., & Spencer, D. D. (1994). Degree of hippocampal neuron loss determines the severity of verbal memory decrease after left anteromesiotemporal lobectomy. *Epilepsia, 35*(6), 1179-1186. doi:10.1111/j.1528-1157.1994.tb01786.x

Savage, G. R., Saling, M. M., Davis, C. W., & Berkovic, S. F. (2002). Direct and indirect measures of verbal relational memory following anterior temporal lobectomy. *Neuropsychologia, 40*(3), 302-316. doi:10.1016/s0028-3932(01)00092-6

Schacter, D. L., & Wagner, A. D. (1999). Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus, 9*(1), 7-24. doi:10.1002/(sici)1098-1063(1999)9:1<7::aid-hipo2>3.0.co;2-k

Scoville, W. B. (1954). The limbic lobe in man. *Journal of Neurosurgery, 11*(1), 64-66. doi:10.3171/jns.1954.11.1.0064

Scoville, W. B. (1968). Amnesia after bilateral mesial temporal-lobe excision: Introduction to Case H.M. *Neuropsychologia, 6*(3), 211-213. doi:10.1016/0028-3932(68)90020-1

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

Seidenberg, M., Hermann, B. P., Dohan, F. C., Jr., Wyler, A. R., Perrine, A., & Schoenfeld, J. (1996). Hippocampal Sclerosis and Verbal Encoding Ability following Anterior Temporal Lobectomy. *Neuropsychologia, 34*(7), 699-708.

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation. *Journal of Experimental Psychology-Human Perception and Performance, 8*(2), 253-272. doi:10.1037/0096-1523.8.2.253

Sergent, J. (1983). Role of the input in visual hemispheric asymmetries. *Psychological Bulletin, 93*(3), 481-512.

Sergent, J., & Hellige, J. B. (1986). Role of input factors in visual-field asymmetries. *Brain and Cognition, 5*(2), 174-199.

Sergent, J., Ohta, S., & Macdonald, B. (1992). Functional neuroanatomy of face and object processing. *Brain, 115*(1), 15-36.

Shankweiler, D. (1966). Effects of temporal-lobe damage on perception of dichotically presented melodies. *Journal of Comparative and Physiological Psychology, 62*(1), 115-119. doi:10.1037/h0023470

Sherman, E. M. S., Wiebe, S., Fay-McClymont, T. B., Tellez-Zenteno, J., Metcalfe, A., Hernandez-Ronquillo, L., . . . Jette, N. (2011). Neuropsychological outcomes after

epilepsy surgery: Systematic review and pooled estimates. *Epilepsia, 52*(5), 857-869. doi:10.1111/j.1528-1167.2011.03022.x

Shulman, G. L., Pope, D. L. W., Astafiev, S. V., McAvoy, M. P., Snyder, A. Z., & Corbetta, M. (2010). Right Hemisphere Dominance during Spatial Selective Attention and Target Detection Occurs Outside the Dorsal Frontoparietal Network. *Journal of Neuroscience, 30*(10), 3640-3651. doi:10.1523/jneurosci.4085-09.2010

Smith, M. L., & Milner, B. (1981). The role of the right hippocampus in the recall of spatial location. *Neuropsychologia, 19*(6), 781-793.

Smith, M. L., Bigel, M., & Miller, L. A. (2011). Visual paired-associate learning: In search of material-specific effects in adult patients who have undergone temporal lobectomy. *Epilepsy and Behavior, 20*(2), 326-330.

Smith, M. L., & Milner, B. (1989). Right hippocampal impairment in the recall of spatial location: Encoding deficit or rapid forgetting? *Neuropsychologia, 27*(1), 71-81.

Smith, G. E., Malec, J. F., & Ivnik, R. J. (1992). Validity of the construct of nonverbal memory: A factor-analytic study in a normal elderly sample. *Journal of Clinical and Experimental Neuropsychology, 14*(2), 211-221. doi:10.1080/01688639208402824

Spiers, H. J., Burgess, N., Maguire, E. A., Baxendale, S. A., Hartley, T., Thompson, P. J., & O'Keefe, J. (2001). Unilateral temporal lobectomy patients show lateralized topographical and episodic memory deficits in a virtual town. *Brain, 124*, 2476-2489. doi:10.1093/brain/124.12.2476

Squire, L. R., Knowlton, B., & Musen, G. (1993). The structure and organization of memory. *Annual Review of Psychology, 44*(1), 453-495.

Suthana, N. A., Ekstrom, A. D., Moshirvaziri, S., Knowlton, B., & Bookheimer, S. Y. (2009). Human Hippocampal CA1 Involvement during Allocentric Encoding of Spatial Information. *Journal of Neuroscience, 29*(34), 10512-10519. doi:10.1523/jneurosci.0621-09.2009

Testa, S. M., Schefft, B. K., Privatera, M. D., & Yeh, H. S. (2004). Warrington's recognition memory for faces: interpretive strategy and diagnostic utility in temporal lobe epilepsy. *Epilepsy & Behavior, 5*(2), 236-243. doi:10.1016/j.yebeh.2003.12.011

Trenerry, M. R., Jack, C. R., Ivnik, R. J., Sharbrough, F. W., Cascino, G. D., Hirschorn, K. A., . . . Meyer, F. B. (1993). MRI hippocampal volumes and memory function before and after temporal lobectomy. *Neurology, 43*(9), 1800-1805.

Tulving, E., & Pearlstone, Z. (1966). Availability versus accessibility of information in memory for words. *Journal of Verbal Learning and Verbal Behavior, 5*(4), 381-391.

Tulving, E., Kapur, S., Craik, F. I. M., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding / retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences of the United States of America, 91*(6), 2016-2020. doi:10.1073/pnas.91.6.2016

Turriziani, P., Carlesimo, G. A., Perri, R., Tomaiuolo, F., & Caltagirone, C. (2003). Loss of spatial learning in a patient with topographical disorientation in new environments. *Journal of Neurology, Neurosurgery & Psychiatry, 74*(1), 61-69. doi:10.1136/jnnp.74.1.61

van Asselen, M., Kessels, R. P., Kappelle, L. J., & Postma, A. (2008). Categorical and coordinate spatial representations within object-location memory. *Cortex, 44*(3), 249-256.

van der Ham, I. J., & Postma, A. (2010). Lateralization of spatial categories: A comparison of verbal and visuospatial categorical relations. *Memory & Cognition, 38*(5), 582-590.

van der Ham, I. J., Duijndam, M. J., Raemaekers, M., Van Wezel, R. J., Oleksiak, A., & Postma, A. (2012). Retinotopic mapping of categorical and coordinate spatial relation processing in early visual cortex. *Plos One, 7*(6), e38644.

van der Ham, I. J. M., Postma, A., & Laeng, B. (2014). Lateralized perception: The role of attention in spatial relation processing. *Neuroscience and Biobehavioral Reviews, 45*, 142-148. doi:10.1016/j.neubiorev.2014.05.006

Vaz, S. A. M. (2004). Nonverbal memory functioning following right anterior temporal lobectomy: a meta-analytic review. *Seizure-European Journal of Epilepsy, 13*(7), 446-452. doi:10.1016/j.seizure.2003.12.004

Wagner, A. D., Poldrack, R. A., Eldridge, L. L., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. *Neuroreport, 9*(16), 3711-3717.

Watkins, M. J., & Gardiner, J. M. (1979). An appreciation of generate-recognize theory of recall. *Journal of Verbal Learning and Verbal Behavior, 18*(6), 687-704.

Wechsler, D. (1997). *Wechsler memory scale (WMS-III)*: Psychological Corporation.

Yin, R. K. (1970). Face recognition by brain-injured patients: a dissociable ability? *Neuropsychologia, 8*(4), 395-402.

Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: music and speech. *Trends in Cognitive Sciences, 6*(1), 37-46. doi:10.1016/s1364-6613(00)01816-7

Zimmermann, K., & Eschen, A. (2016). Brain regions involved in subprocesses of small-space episodic object-location memory: a systematic review of lesion and functional neuroimaging studies. *Memory*, 1-33.

Chapter 2: The prediction of right temporal lobe pathology by nonverbal memory tests: Meta-analysis of stimulus and task effects

Adam Bentvelzen[1,2], Roy Kessels[3,] Nicholas A. Badcock[1,4], Greg Savage[1,2].

[1] ARC Centre of Excellence in Cognition and its Disorders, Macquarie University, NSW, 2109, Australia;

[2] Department of Psychology, Macquarie University, NSW, 2109, Australia;

[3] Centre for Cognition, Donders Institute for Brain, Cognition and Behaviour, Radboud University, 6500 HE Nijmegen, The Netherlands;

[4] Department of Cognitive Science, Macquarie University, NSW, 2109, Australia.

Key words: temporal lobe epilepsy, nonverbal memory, lateralisation, meta-analysis, neuropsychology.

Corresponding author: Adam Bentvelzen. ARC Centre of Excellence in Cognition and its Disorders, and Department of Psychology, Macquarie University, NSW, 2109, Australia.
Email: adam.bentvelzen@students.mq.edu.au

Acknowledgements

This work was funded by an Australian Postgraduate Award (APA) to Adam Bentvelzen and a Macquarie University Research Development Grant, and supported by the Australian Research Council Centre of Excellence for Cognition and its Disorders (CE110001021) http://www.ccd.edu.au

Abstract

Nonverbal memory tests do not reliably detect pathology in the right temporal lobe. This is associated with a lack of clarity on the factors that contribute to right-lateralised memory functions. Previous meta-analytic reviews have suggested that memory for facial or spatial stimulus materials may correlate more strongly with right temporal lobe pathology than tests of memory for abstract designs. Other findings have suggested that lateralisation may be affected by task demands including the type of learning, and the amount of delay before testing. Here we update previous reviews and expand their scale to allow comparison of these multiple features of memory tests simultaneously. In a comprehensive meta-analysis (152 studies) different neuropsychological tests of nonverbal memory were categorised by the type of nonverbal material (designs, faces, spatial arrays) and task demands (type of learning, delay before testing), to compare the impact of these factors in identifying right versus left temporal lobe pathology. To assess the relative effects of temporal lobe pathology and surgery we compared patients prior to surgery, subsequent to surgery, and the degree of postsurgical change. Results revealed that in presurgical patients effect sizes were uniformly small (*ds* ~ 0.2) and not affected by the type of material or task demands. By contrast, postsurgical patients showed an effect of stimulus type, with tests of face and spatial memory showing superior capacity to discriminate right-sided postsurgical patients from their left-sided counterparts (*ds* ~ 0.5) compared to design memory tests (*ds* ~ 0.2). Face memory tests also discriminated postsurgical change in right- versus left-resected patients, with the faces subtest of the Warrington Recognition Memory Test also showing this significant pattern. In contrast, task demands had minimal effect on discrimination of the resected side. The results are discussed in the context of affected brain regions and extent of damage due to epilepsy versus resection. The ramifications of these findings for the assessment of unilateral temporal lobe epilepsy patients are detailed.

1. Introduction

The role of the right temporal lobe in forming memories for nonverbal experiences remains unresolved. While there is consistent evidence that the left temporal lobe plays a crucial role in forming verbally-mediated memories, as shown by many studies in temporal lobe epilepsy (TLE) patients following left temporal lobe resection (e.g., Alpherts et al., 2006; Rausch et al., 2003), analogous investigations in patients with right-sided resection have not shown reliable declines in nonverbal memory (Barr, 1997a; Bell & Davies, 1998). Indeed, the evidence suggests that the functions of each hemisphere are not symmetrically dissociated by material type, since right-sided resection can impair verbal memory functions, albeit less frequently than left-sided resection, while conversely left-sided resection can improve nonverbal memory function (Baxendale, Thompson, & Duncan, 2008; Sherman et al., 2011). In addition, patients with right- compared with left-sided temporal resection, may have only a small or negligible increase in risk of nonverbal memory decline following surgery (Sherman et al., 2011; Vaz, 2004).

The accurate assessment of right temporal lobe function has arguably been compromised by the inadequacy of the tests used to measure nonverbal memory. Large-scale studies and reviews have demonstrated that the two most popular clinical tests of nonverbal memory - Visual Reproduction (VR; from various editions of the Wechsler Memory Scale, WMS) and the Rey Complex Figure Test (RCFT) - are not useful for lateralising the side of memory function in patients with medically refractory temporal lobe epilepsy (Barr et al., 1997; Lee, Yip, & Jones-Gotman, 2002). Based on such findings, a National Institute of Health panel recommended the omission of nonverbal memory tests from the Common Data Elements research test battery for evaluation of patients with epilepsy (Loring et al., 2011). While this recommendation reflects the difficulties faced in assessing the right medial temporal lobe, the blanket removal of nonverbal memory tests disregards the critical importance of nonverbal memory abilities in the everyday life of a patient, such as the ability to remember the face of new people, or how to navigate a recently learned route. In addition,

it also ignores decades of research from the clinical neuropsychological and cognitive neuroscience literatures that suggest the degree of right-lateralisation may differ by the type of nonverbal stimulus and by task demands. These findings may help improve the assessment of right temporal lobe pathology.

For instance, a previous meta-analytic review found that performance on the Face Recognition subtest from the Warrington Recognition Memory Test battery (WRMT-Faces) was the only test to show a consistent decline (Cohen's d = - 0.31) after right temporal lobe surgery, unlike other tests that were predominantly tested memory for abstract designs (Vaz, 2004). A more recent meta-analytic review showed an increased proportion of right-sided versus left-sided TLE patients with clinically significant decline in performance on WRMT-Faces following surgery (Sherman et al., 2011). A meta-analysis of multiple spatial memory tasks (object location, maze learning, and positional memory) showed that they are performed more poorly by patients with right hippocampal pathology than by their left hippocampal counterparts (Kessels et al., 2001). These findings in TLE patients are supported by neuroimaging evidence of right-lateralised activity in the medial temporal lobe when healthy participants encoded faces into memory (e.g., Kelley et al., 1998) or retrieved previously navigated routes (see meta-analysis by Kuhn & Gallinat, 2014). Furthermore, there is evidence that higher levels of verbalisability (scenes > faces > abstact spatial patterns) correlates negatively with the degree of right-lateralisation of medial temporal lobe and inferior prefrontal activity during memory encoding (Golby et al., 2001). In summary, the particular type of nonverbal stimulus employed and its resistance to verbalisability may have an important effect on the prediction of right-sided temporal lobe pathology.

In addition to the type of nonverbal stimulus, different task demands may affect the capacity of nonverbal memory tests to detect right temporal lobe pathology. One task demand is whether the set of to-be-learned stimuli are presented only once or multiple times. It has been argued that, for tasks with a single learning trial, factors unrelated to memory itself such as attentional lapses or poor comprehension, may lead to poor performance when memory

itself is intact (e.g., Jones-Gotman, Harnadek, & Kubu, 2000). In contrast, with multiple stimulus presentations these transient factors are minimised, providing more opportunity for accurate comprehension, making it more likely that poor performance across multiple trials indicates a memory deficit. Supporting this view, a recent meta-analysis of postsurgical change in TLE patients, showed that among tests of design memory, a test with multiple learning trials (Nonverbal Selective Reminding Task; NVSRT) detected a greater proportion of right-sided than left-sided patients that had reliable differences in memory change, while tests with a single learning trial (e.g., VR, RCFT, and the Benton Visual Retention Test; BVRT), did not detect this difference (Sherman et al., 2011). Other design memory tests with multiple learning trials have also shown an ability to discriminate postsurgical change in right versus left TLE patients (e.g., Bonelli et al., 2010).

In addition to the type of nonverbal material, other studies have suggested that lateralised temporal lobe pathology may be associated with a pattern of impairment best described as an interaction between material and task demands. Specifically, patients with right-sided damage had impairments in the initial learning of visual designs, as shown by an inability to benefit from repeated learning trials, while after a delay they had intact retention of the limited number of designs that were learned (Jones-Gotman, Smith, Frisk, & Routhier, 1996; Jones-Gotman et al., 1997; Majdan, Sziklas, & Jones-Gotman, 1996; Trennery et al., 1993). In contrast, left-sided damage showed the opposite pattern of intact initial learning of verbal material but impaired retention of this material (e.g., Jones-Gotman et al., 1997). Therefore, left-sided temporal pathology was associated with verbal retrieval and right-sided temporal pathology, with nonverbal encoding and consolidation processes. However, since this finding is predominantly observed in tasks with multiple learning trials, its parsimony is unclear and requires further systematic investigation.

Another task factor, the length of the delay before memory is tested, may also affect the extent of lateralisation elicited by nonverbal memory tasks. This task-related factor may be mediated by the intra-hemispheric location of the epilepsy-related or surgical damage to

the medial temporal lobe. A meta-analysis of neuroimaging studies in healthy participants suggested that the anterior region of the medial temporal lobe is more responsible for the retrieval of spatially navigated routes following a delay than immediately after learning, while the posterior region is more responsible for immediate memory than delayed memory (Kuhn & Gallinat, 2014). This analysis also showed greater right-lateralisation for navigational memory than for non-spatial episodic memory tasks (e.g., using words, pictures). Given that typical temporal lobe surgery involves resection of the anterior hippocampus, preserving some posterior hippocampal tissue, it is possible that nonverbal memory tested following a long delay may be more impaired, and hence show greater right-lateralisation, than nonverbal memory tested after a short delay.

This pattern of greater right-lateralisation for delayed memory than for immediate memory of nonverbal materials appears to be borne out in TLE patients. In an experimental scene memory task, patients with extensive right hippocampal removal had impaired object-location memory after a delay but not immediately after learning (Pigott & Milner, 1993). Memory for 3D spatial arrangements only showed diagnostic sensitivity and specificity for right versus left MTL function when memory was tested following a delay (Hampstead et al., 2010). Similarly, memory for novel design-design and design-spatial associations were impaired for delayed recognition but not during initial learning (Smith, Bigel, & Miller, 2010). However, not all findings support this pattern, since single-trial design learning tasks (e.g., VR) have not shown a lateralisation difference between immediate and delayed memory testing (Barr et al., 1997; Lee, Banks, & Jones-Gotman, 2002; Vaz, 2004). While this may be due to the poor ability of single-trial design memory tests to detect right-lateralised dysfunction per se, other findings with facial memory and positional memory tasks contradict this pattern, suggesting it may not be completely reliable (Brown et al., 2010; Dade & Jones-Gotman, 2001). In sum, a meta-analysis of findings comparing delayed to immediate memory testing may help clarify the reliability of this task-related factor in detecting right TLE pathology.

Taken together, the reviewed evidence suggests that, nonverbal memory tasks may have greater sensitivity to right temporal lobe dysfunction if they employ facial or spatial materials with multiple learning trials and a delayed memory test, rather than design materials with a single learning trial and immediate memory test. In this context, the primary aim of this meta-analytic review was to examine nonverbal memory tests to determine whether the type of stimulus material (designs, faces, spatial arrays) and task demands (type of learning trial, delay before memory testing) affect their sensitivity to right temporal lobe pathology compared with left-sided pathology. This was tested by grouping neuropsychological tests of nonverbal memory into overarching categories by material, subcategorised by demands. We then compared the effects of left- and right-sided temporal lobe pathology on nonverbal memory performance separately in pre- and post-surgical TLE patients, and also determined the degree of postsurgical change in memory performance in left-sided and right-sided patients. Extending previous reviews (Lee et al., 2002; Sherman et al., 2011; Vaz, 2004) that only analysed performance in postsurgical patients or postsurgical change, we also evaluated presurgical data to help account for possible floor effects (i.e., extremely poor performance) at the presurgical stage (Baxendale et al., 2008), and, more generally, to help distinguish lateralisation effects due to TLE per se from effects due to the combination of TLE plus surgery.

2. Methods

2.1 Inclusion of studies

Studies were selected by means of a literature search in Medline, ProQuest, Web of Science, and Scopus (January 1990 to June 2015) using the following search terms: 1) *epilepsy* AND *neuropsych** AND *temporal lobe*; and 2) *epilepsy* AND *memory* AND *temporal lobe*. Additional studies were identified by examining reference lists of the identified studies, from neuropsychological texts (Lezak, 2012; Strauss, Sherman, & Spreen, 2006), and from published manuals for neuropsychological tests and batteries (e.g. Wechsler, 2009). Papers meeting the following criteria were included for review:

1. Full-text peer reviewed publications.
2. Participant population with a diagnosis of medically refractory unilateral temporal lobe epilepsy (TLE), with lateralisation exclusively to a unilateral temporal lobe region having been confirmed via standard clinical investigations including video-EEG monitoring, intracranial EEG recordings in the temporal lobe region, results from the Wada/IAT, identification of pathology as determined by magnetic resonance imaging (MRI), neuropsychological testing, or a combination of these methods. Multiple TLE aetiologies were permitted (e.g., medial temporal sclerosis, low-grade tumours, cortical dysgenesis, or cryptogenic).
3. Original data reported from neuropsychological tests of nonverbal memory, with raw test scores or standardised scores (e.g. *SS*, *z*, *T* etc.) presented for both the left and right TLE patients in order to calculate an effect size (i.e., means and standard deviations or alternatively exact *p, t,* or *F* values).

Patients with other major medical and/or psychiatric conditions known to affect neuropsychological function were excluded, with the exception of depression, which is the most common psychiatric comorbidity in TLE patients (Fuller-Thomson & Brennenstuhl, 2009). Based on estimates of the prevalence of non-dominant language lateralisation in temporal lobe epilepsy patients (Gaillard et al., 2002; Janszky et al., 2003; Springer et al., 1999) we excluded patient samples with greater than 20% of patients with bilateral representation or right-lateralisation of speech/language functions as determined by fMRI, Wada, handedness, or dichotic listening task to maximise the external validity of the findings. As the focus of this study was on adults we excluded patients aged less than 14 or greater than 65 years. Patient samples were also excluded if they had: estimated intellectual functioning (i.e., IQ, FSIQ) less than 70 or poor postsurgical seizure control. Data on patient age at testing and the age of epilepsy onset were collected and when the age of epilepsy onset was not reported this was estimated, where possible, by subtraction of patient age at testing from epilepsy duration.

Nonverbal memory tests were included if they had published manuals or journal articles containing normative data in healthy or clinical samples, and/or psychometric validation data specifically in patients with unilateral TLE (e.g., test-retest reliability, convergent validity with other memory tests, factor structure, etc.). Tests with elements that may be nameable (e.g., the simple designs in Visual Reproduction or the colours in the design-colour stimuli in Visual Paired Associates from WMS-R) were included since the material itself was not explicitly verbal, whereas tests containing explicitly verbal material were excluded (e.g., face-name associations in Loring et al., 2000).

2.2 Categorisation of studies by type of material and task

Nonverbal memory tests reported in reviewed studies were categorised according to two main factors: 1) type of material (*designs*, *faces*, *mazes, navigational, positions, scene*), and 2) task demands which were comprised of the subcategories a) type of learning trial (*single*, *repeated*) and b) delay before memory testing (*immediate, learning, retention, delayed*). Within material types, design stimuli could be either abstract or simple, but were excluded if they involved drawings of known and easily nameable objects or places since such stimuli strongly draw upon verbal memory. Similarly, mazes, navigational, and scene memory tasks could not involve demands to remember verbally labelled items (e.g., to recall street names). Face materials could not be those of famous people, nor could the memory task involve recognition of emotional expression.

Within task demands, the *designs* category was further subdivided by the type of learning trial. For example, stimuli exposed for a single trial such as the Rey Complex Figure Test were categorised as *designs-single*, while stimuli repeatedly exposed across multiple trials such as the Rey Visual Design Learning Test (RVDLT; Rey, 1999) were categorised as *designs-repeated*. Design memory was further subdivided by the delay before memory testing. For example, VR I which tests memory immediately after presentation was included within *designs-single-immediate* while VR II, which tests memory after a delay, was included within *designs-single-delayed*, while percent retention measures were included as *designs-*

single-retention. Unlike *designs-single*, for *design-repeated* measures there were often a mixture of recall and recognition measures, therefore the delay before memory testing was also indicated as *recall* or *recognition* as appropriate. The same subcategories were applied to the remaining material types where applicable. For completeness, in addition to these categories, composite index scores of nonverbal memory involving a mixture of material types and task demands (e.g., faces and scenes from the WMS-III) were analysed and reported separately.

Many of the included studies presented data from multiple nonverbal memory tests. Hereafter, "test" refers to a particular clinical memory test (e.g., VR) while "measures" refers to a particular measure of a test (e.g., VR I). If a study reported multiple measures from tests that differed by material type (e.g., VR II and Faces II), they were each included into their respective separate categories. Similarly, if a paper reported different measures from a particular test that belonged to separate subcategories, as the data were never combined we permitted inclusion of each measure into their respective subcategories (for example, VR I into *designs-single-immediate* and VR II into *designs-single-delayed*). However, when a particular study reported multiple measures of the same test that also belonged within the same subcategory (e.g., Correct and Errors scores from the Benton Visual Retention Test [BVRT] both fit into *designs-single-immediate*), we selected only one of the scores for inclusion into that subcategory. The outcome measure chosen was determined by its relative similarity with other measures in the subcategory, prevalence in the neuropsychological and epilepsy literature and on psychometric grounds (i.e., the Correct score for BVRT would be chosen over Errors due to its greater similarity to other measures within *designs-single-immediate*). When patients were tested multiple times following surgery, the follow-up closest to one year was selected. For studies that featured subgroups of TLE patients, only subgroups that satisfied our selection criteria were included. If multiple within-study subgroups satisfied inclusion criteria, these data were pooled into one group using the following formulae:

$$M_{\text{pooled}} = M1.\left(\frac{n1}{n1+n2}\right) + M2.\left(\frac{n2}{n1+n2}\right) \quad (1)$$

$$SD_{\text{pooled}} = \sqrt{([SD1^2.(n1-1) + SD2^2.(n2-1)]/[n1+n2-2])} \quad (2)$$

where M_{pooled} and SD_{pooled} are the pooled mean and standard deviation, respectively, and $M1$, $SD1$, $n1$ and $M2$, $SD2$, $n2$ are the means, standard deviations, and sample size of the first and second groups, respectively. When more than two within-study groups were pooled, this process was repeated until all groups were combined.

We included all presurgical data into the same dataset, regardless of whether the study also presented postsurgical data, and vice versa for the postsurgical data. As a result, presurgical, postsurgical, and postsurgical change datasets did not contain completely independent patient samples. However, we considered this preferable to an alternative in which the rejection of datasets had to be determined post hoc in order for patient groups to be fully independent.

2.3 Statistical analysis

For each included nonverbal memory measure, pooled standardised mean differences (Cohen's *d*; Cohen, 1977) and pooled variance were calculated for: 1) left- versus right-hemisphere presurgical patients, 2) left- versus right-hemisphere postsurgical patients, 3) presurgical versus postsurgical left-hemisphere patients, and 4) presurgical versus postsurgical right-hemisphere patients. The direction of the effect size was negative if the right hemisphere patients performed worse than the left hemisphere patients, or if performance declined following surgery.

From these *d* values, meta-analyses of each subcategory and individual test was then performed separately for the presurgical, postsurgical, postsurgical change (left TLE), and postsurgical change (right TLE) samples. The pooled *d* value weighted by sample size, was calculated using a random-effects model since we anticipated clinical and test-related heterogeneity among the studies (Hunter & Schmidt, 2000), along with the standard error,

95% confidence intervals, and significance testing (z with p values). However, when a meta-analysis comprised only a single study the fixed-effects model (weighted for sample size) was used to calculate a study-specific d, since by definition the effect of study is fixed because there is no variation. The magnitude of effect sizes was appraised according to the review of Lipsey and Wilson (2001): (i.e., small: less than 0.3, medium: 0.3 to 0.7, large: > 0.7).

Heterogeneity was estimated using the Q-statistic and for meta-analyses, which used the random-effects method, we also calculated I^2, the percentage of the total variability in the effect size estimates (which is composed of heterogeneity and sampling variability) that can be attributed to heterogeneity among the true effects, using restricted maximum-likelihood estimation (see Viechtbauer, 2005 for details). To determine the possible impact of bias due to the selective publication of significant over non-significant results, fail-safe N values were calculated for each meta-analysis, using the following formula: $N_{fs} = k(d - d_c) / d_c$, where k = the number of studies in the meta-analysis, d = the average effect size for the studies synthesised, and d_c = the criterion value selected that d would equal when some knowable number of hypothetical studies N_{fs} were added to the meta-analysis (Orwin, 1983). The value of d_c was set at 0.01 since based on previous reviews effect sizes were expected to range from only small to medium for most analyses (e.g., Vaz, 2004). The resulting measure, N_{fs}, therefore represents the number of unpublished studies with effect size of 0.01 that would be needed to be added to the meta-analysis to make the significant effect nonsignificant. All analyses were conducted using R (version 3.2.2, Windows) using the *metafor* package.

3. Results

Figure 1 shows a summary of the literature search that resulted in 152 relevant studies. Details of all included studies are in Supplementary Table 1 in the Appendix, including the neuropsychological tests in each, the number of participants per study and their age at testing and the age of epilepsy onset. Of the studies included (k = 152), the breakdown by patient type was as follows: presurgical (k = 129), postsurgical (k = 79), postsurgical change (k = 56). There were few tests within each of the *mazes, navigational,* and *positions* material types, so

these were combined into a single group (*spatial)* which were subdivided further into *spatial-learning* and *spatial-delayed* subcategories. For scene memory the included data was almost exclusively from the Family Pictures subtest of the WMS-III, so these data were analysed as individual tests.

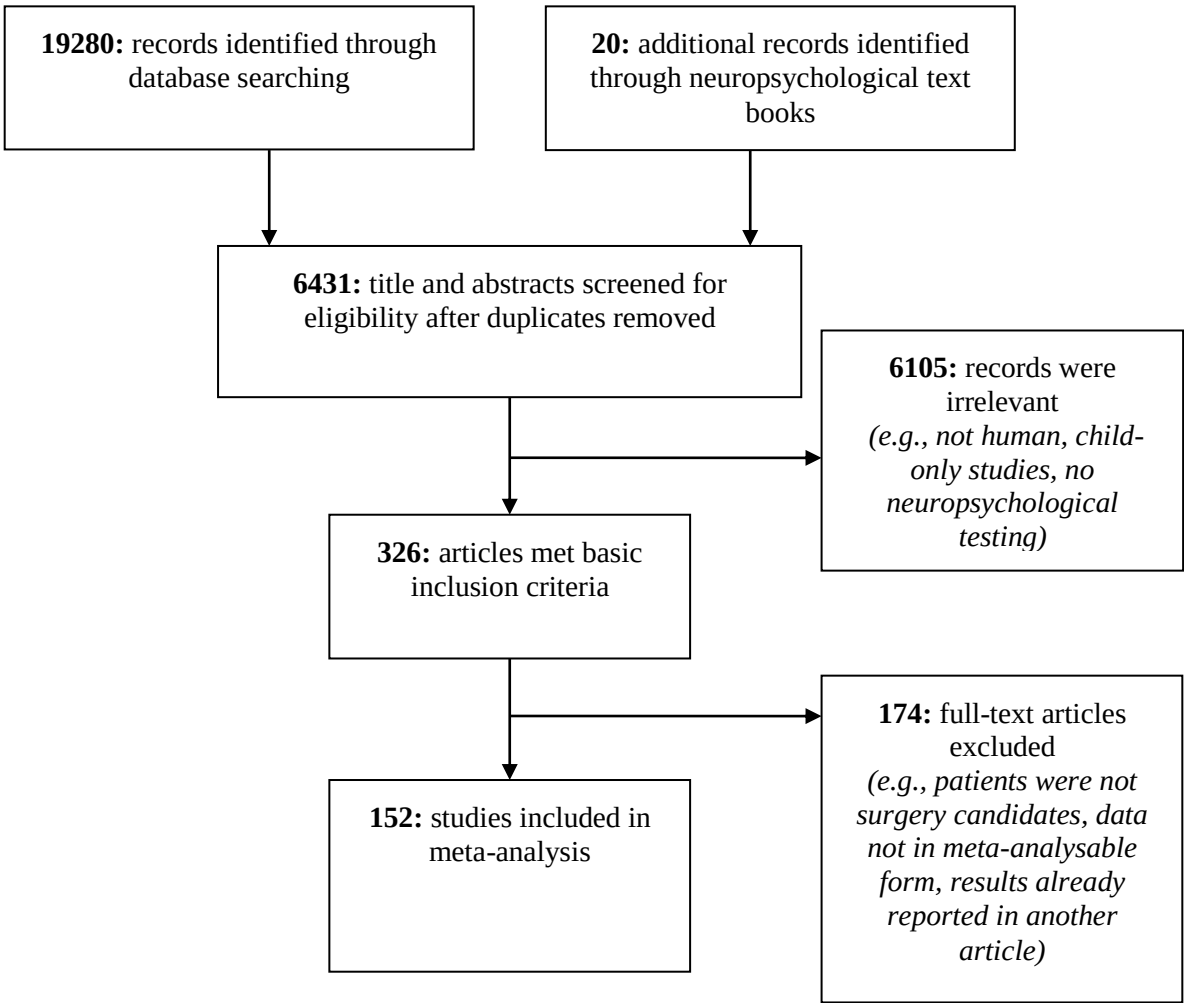

Fig 1. Summary of the literature search and process of inclusion and exclusion of studies (numbers of records in bold).

3.1 Results grouped by category of material and task demands

3.1.1 Presurgical patients

Figure 2A shows mean pooled *d* values and confidence intervals for each category of nonverbal memory test for presurgical patients, along with *k*, *N, Z, p, Q,* and I^2 (see Supplementary Table 2 in Appendix of complete descriptive and test statistics for presurgical data). The figure shows that across all material types and subcategories therein, right-sided TLE presurgical patients demonstrated a lowered performance compared to left-sided patients (range of *d* from −0.04 to −0.60), though the effect sizes were predominantly small (overall value was $d = -0.16$). The effect sizes showed significant lateralisation (left > right performance) for *designs-single-delayed,* $d = -0.14$, $p = .008$, *designs-repeated-learning,* $d = -0.25$, $p < .001$, and *designs-repeated-delayed recall,* $d = -0.27$, $p = .03$, and *faces-immediate,* $d = -0.22$, $p = .002$. In contrast, while *spatial-learning* showed by far the largest mean effect size, $d = -0.60$, this was not significant, $p = .09$. Taken together, the small performance difference in favour of left-over right-sided presurgical patients for nonverbal memory did not appear to be strongly affected by the type of material or by task demands (either the type of learning trial or delay before memory testing).

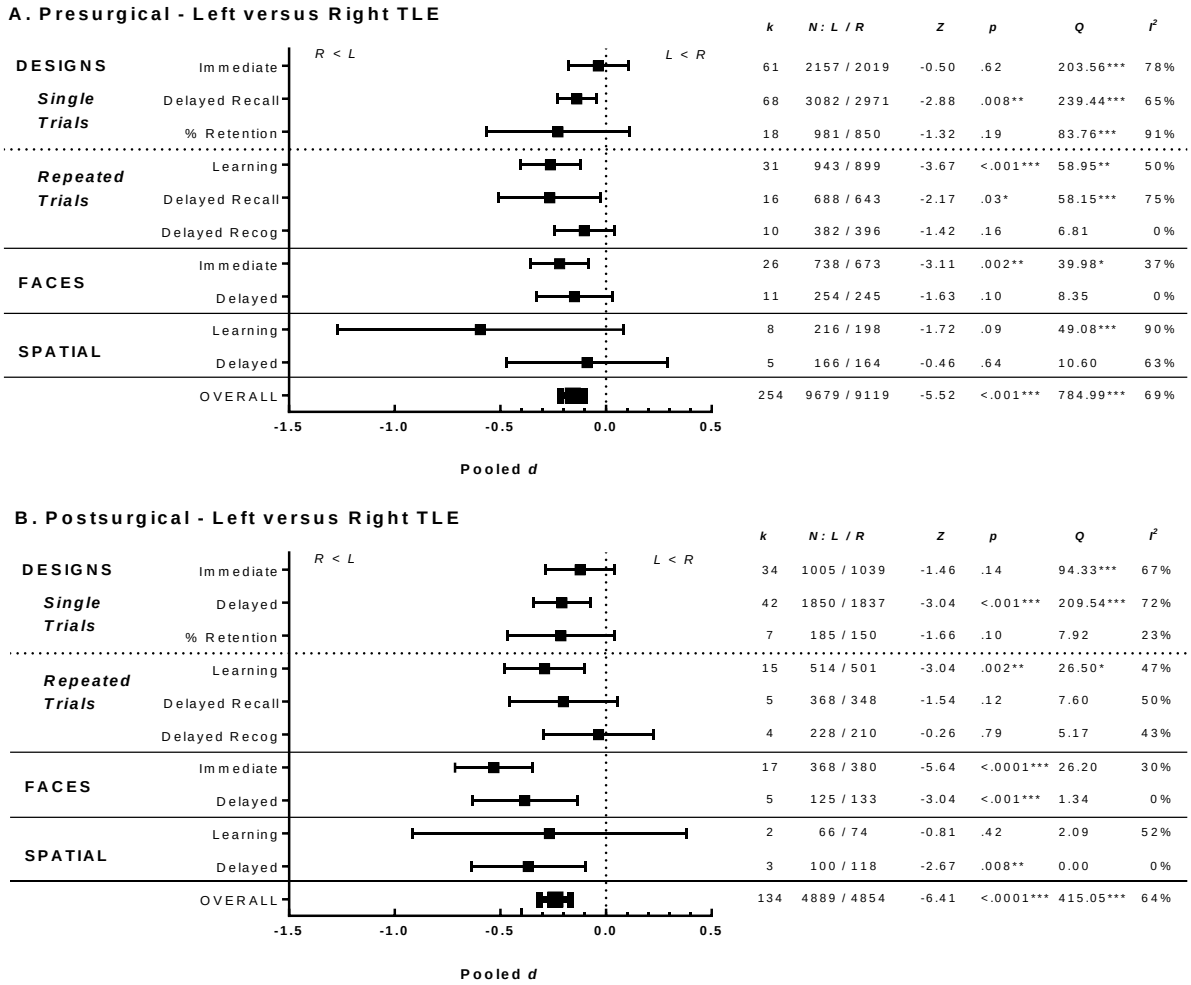

Fig 2. Standardised effect sizes (Cohen's *d*) and 95% CIs for nonverbal memory tests, categorised by material (and by type of learning trial for design materials) then by the delay before memory testing. A: presurgical patients. B: postsurgical patients. Negative effect sizes indicate poorer performance for right-sided than left-sided TLE patients. Sample size (*k*, studies and *N*, patients), inferential statistics (*Z*, *z*-value test statistic, *p*, p-value of significance test) and heterogeneity statistics (*Q*, heterogeneity test, I^2, percentage heterogenity attributable to true effects) are provided on the right. * $p < .05$, ** $p < .01$, *** $p < .001$.

3.1.2 Postsurgical patients

Meta-analyses of nonverbal memory data from postsurgical patients revealed that mean *d* ranged from −0.04 to −0.53, with an average of -0.24 overall (see Supplementary Table 3 in Appendix for complete postsurgical results). Figure 2B shows that for design memory, the size and pattern of *d* was similar to presurgical patients, and the effect sizes for *designs-single-delayed,* $d = -0.12$, $p = .002$, and *designs-repeated-learning,* $d = -0.29$, $p = .002$, were significant. Notably, the effect sizes for face and spatial (delayed) memory

were on average larger than those for design memory, specifically: *faces-immediate, d* = −0.53, $p < .001$, *faces-delayed*, $d = -0.38$, $p = .002$, and *spatial-delayed, d* = −0.37, $p = .008$, were significant while *spatial-learning*, $d = -0.27$, $p = .42$ was not significant. Overall, for postsurgical patients the effect sizes of lateralisation (left > right) were medium in size for face memory and spatial delayed memory, while they were small in size for design memory. However, there was no clear-cut effect of task demands within or across material types.

3.1.3 Postsurgical change

Figures 3A and 3B present the pooled effect sizes for pre-post differences in memory performance for left-and right-resected patients, respectively, for each category of nonverbal memory test (see Supplementary Table 4 in Appendix for complete pre-post results). For left-resected patients the overall pattern indicated a small improvement in nonverbal memory due to surgery, $d = -0.37$, $p < .001$, which was significant for *faces-immediate*, $d = 0.29$, $p = .002$, *faces-delayed, d* = 0.40, $p = .02$, and *designs-single-delayed, d* = 0.13, $p = .04$. For right-resected patients the overall pattern showed no change, $d = -0.02$, $p = .45$, with only categories of tests with significant effect sizes were *designs-repeated-delayed recognition, d* = 0.26, $p = .008$ (postsurgical improvement), and *designs-repeated-learning, d* = −0.24, $p = .009$ (postsurgical decline). The *spatial-delayed* group showed the numerically largest mean decline for right-resected patients $d = -0.26$, but consistent with the similar right-lateralised pattern in postsurgical data this did not reach significance, $p = .10$.

When comparing the postsurgical changes between left-and right-sided patients, only *faces-immediate* showed non-overlapping estimates (left: 0.11 to 0.47, $p = .02$; right: −0.33 to 0.02, $p = .09$). Overall, the data showed a subtle improvement in nonverbal memory following left-sided surgery especially for face memory, and a lack of change following right-sided surgery (with the exception of a mixed pattern of improvement and decline between different design-repeated tasks). These postsurgical changes did not appear to be strongly affected by the type of nonverbal material or task demands with the exception that *faces-immediate*, but not *faces-delayed,* showed a significant difference between left- and right-sided patients.

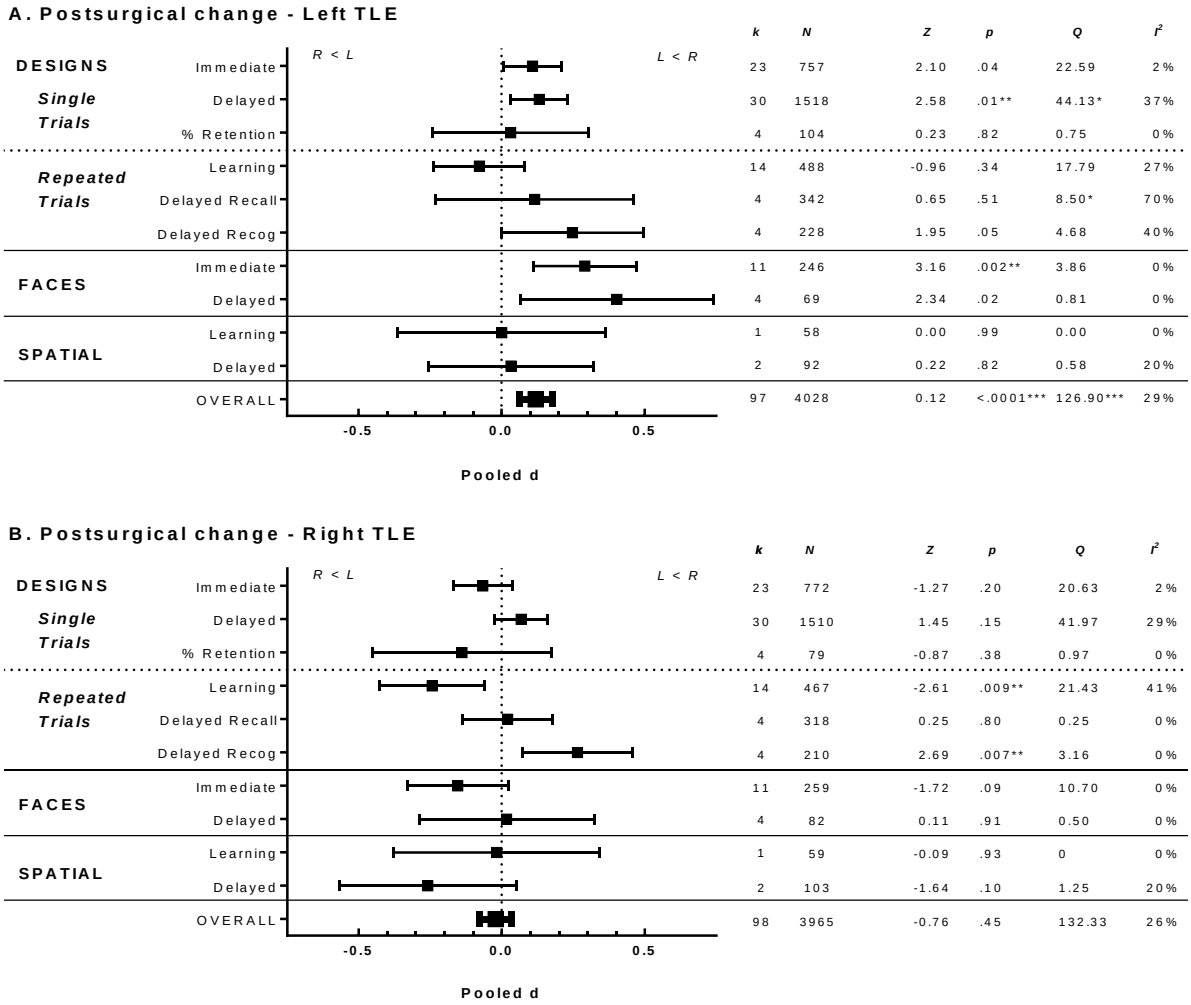

Fig 3. Standardised effect sizes (Cohen's *d*) and 95% CIs for nonverbal memory tests, categorised by material (and by type of learning trial for design materials) then by the delay before memory testing. A: postsurgical change, left TLE patients. B: postsurgical change, right TLE patients. Negative effect sizes indicate a decline in postsurgical performance. Sample size (*k,* studies and *N*, patients), inferential statistics (*Z*, *z*-value test statistic, *p*, p-value of significance test) and heterogeneity statistics (*Q*, heterogeneity test, I^2, percentage heterogenity attributable to true effects) are provided on the right. * $p < .05$, ** $p < .01$, *** $p < .001$.

3.2 Results by individual tests

Due to their prohibitive numbers, meta-analyses of individual tests are not presented graphically and are instead summarised here (see appropriate Supplementary Tables in Appendix for complete results).

3.2.1 Design memory (single trials)

For single trial design memory, there were thousands of patients with most tested by

VR, RCFT or both. Despite frequently showing highly significant effect sizes the magnitude of the effect sizes (left – right) for these tests were generally small (e.g., $d = -0.18$, $p < .001$ for VR II in postsurgical patients) suggesting the significance levels derived largely from the size of the samples than necessarily from the reliability of the effect. Postsurgical change was also small and did not differ between left-and right-sided patients. The BVRT showed predominantly small and unreliable differences and the only significant change was a postsurgical decline for right-sided patients, $d = -0.31$, $p = .02$).

3.2.2 Design memory (multiple learning trials)

For repeated trial design memory, there was a wide variety of tests and considerable variability in the effect sizes. For measures in the *learning* subcategory (most commonly, the measure was the sum total of all learning trials), the Design Learning subtest from the Adult Memory and Information Processing battery (DL-AMIPB) showed a medium-sized right-lateralisation effect in presurgical patients, $d = -0.49$, $p < .0001$, and postsurgical patients, $d = -0.48$, $p < .0001$. In contrast, DL-AMIPB learning measures showed very small and nonsignificant postsurgical changes for both left- and right-sided patients (i.e., *ds* between 0 and −0.05), while learning measures from the Diagnostikum für Cerebralschädigung (DCS) test showed significant decline for right-sided patients, $d = -0.49$, $p = .01$. The learning measure from the Figure Learning subtest (FL-AMIPB) showed a large and significant effect for presurgical patients, $d = -1.40$, $p < .01$; however, this was based on a single study with a small sample. Despite some other medium-to-large effect sizes, no other individual test from this category showed a significant effect.

A number of measures in the *delayed* subcategory showed significant effect sizes in presurgical patients: FL-AMIPB, $d = -0.74$, $p < .001$; DL-AMIPB, $d = -0.47$, $p = .02$; DCS, $d = -0.86$, $p = .04$, and the Rey Visual Design Test (RVDT), $d = -0.86$, $p < .03$. However, caution is urged for interpreting the DCS and RVDT findings since they are each based on one study. Delayed memory measures from the Rey Visual Design Learning Test (RVDLT, not to be confused with the RVDT) showed a significant pre-post improvement in left-sided

patients, $d = 0.32$, $p < .01$, but no difference for any other patient group.

Results from the *delayed recognition* subcategory measures were mixed. For the RVDLT, right-sided postsurgical patients performed significantly more poorly than their left-sided counterparts, $d = -0.29$, $p = .04$, but left-sided pre-post patients showed a significant improvement, $d = 0.49$, $p < .001$. In contrast the recognition measure of the DCS showed significant improvement for right-sided pre-post patients, $d = 0.47$, $p < .01$.

3.2.3 Face memory

In the *immediate* subcategory WRMT-Faces showed a marginally significant difference in presurgical patients, $d = -0.17$, $p = .06$, a medium-sized difference in postsurgical patients, $d = -0.59$, $p < .0001$, and small improvement in left-sided postsurgical patients, $d = 0.23$ [0.02 to 0.44], $p = .03$, that did not overlap with a small-to-medium decline in right-sided postsurgical patients, $d = -0.30$ [−0.51 to −0.08], $p < .01$. Other face memory tests showed medium-to-large differences in presurgical patients (Dade Face Learning Test, $d = -1.05$, $p < .01$, Denman Facial Recognition Test, $d = -0.50$, $p = .01$; $k = 1$ in both of these), and in postsurgical patients: Faces I subtest of the WMS-III, $d = -0.56$, $p = .03$; Graduate Hospital Facial Memory Test (GHFMT), $d = -0.49$, $p = .02$. As on the WRMT-Faces, left-sided pre-post patients showed significant improvement on the GHFMT, $d = 0.50$, $p = .02$. For *faces-delayed* measures only Faces II (WMS-III) showed significant right-lateralisation for postsurgical patients, $d = -0.37$, $p = .02$.

3.2.4 Spatial memory

For measures in the *learning* subcategory the following tests showed significant effects in presurgical patients: Austin Maze, $d = -0.86$, $p = .02$; Brown Location Test (BLT), $d = -1.56$, $p < .01$; and the Route Learning Test, $d = -2.65$, $p < .0001$. However, there were no significant effects in postsurgical or pre-post patients. Among *delayed* measures, the BLT showed a significant effect for presurgical patients, $d = -1.04$, $p = .04$, but despite the overall significance of the *spatial-delayed* category for postsurgical patients none of the individual

tests reached significance in isolation (though the 7-24 Spatial Learning Test was marginal at $p = .05$). Right-sided patients had significant postsurgical decline on the Nonverbal Selective Reminding Test, $d = -0.44$, $p = .04$.

3.2.5 Uncategorised tests

In this section results are summarised from tests that did not fit into the categories above. The only notable findings among this group was the very large effect size of the Doors test (best categorised as scene memory) in postsurgical patients, $d = -2.00$, $p < .0001$, and a large effect size for the total score of Designs I (design-location association) from the WMS-IV, $d = -1.00$, $p = .03$, both from single studies. In contrast, the Family Pictures (I and II) subtests from the WMS-III, (scene memory), and Visual Paired Associates (VPA) I and II subtest from the WMS-R (design-colour association) did not show any significant lateralised effects (see Supplementary Table 5 in Appendix for complete results).

3.3 Composite measures

From the WMS-III the Visual Immediate index (VII) and the Visual Delayed index (VDI) showed significant effect sizes for presurgical and postsurgical patients (*ds* from −0.24 to −0.45, *ps* < .02), but not for postsurgical change. Results from single studies indicated a large effect for a customised combination of Wechsler subtests (VPA II and WMS-III measures - VR-II, Faces II, Family Pictures II) in postsurgical patients, $d = -0.87$, $p = .01$ (see footnotes to Supplementary Table 6 in Appendix for details and complete results for composite measures). None of the composite measures showed significant effect sizes for postsurgical change.

3.4 Heterogeneity

In general, there was a high level of heterogeneity within the different categories of nonverbal memory test, as reflected by highly significant *Q* values in Figures 2 and 3 (see Supplementary Tables 2 to 6 in Appendix for equivalent measures for individual tests). These must be interpreted with the caveat that estimates of heterogeneity become highly imprecise

with small sample size (Viechtbauer, 2005). The pattern of I^2 values indicated that, for many categories, the majority of the heterogeneity was explained by true variation in the effect size, relative to variability between the study samples. Categories of test in postsurgical patients with a reasonable sample size (i.e., $k > 15$) and relatively small I^2 values (hence, relatively consistent effect sizes) include *designs-repeated-learning* ($Q = 29.47$, $p = .01$, $I^2 = 49\%$) and *faces-immediate* ($Q = 26.20$, $p = .05$, $I^2 = 30\%$). Notably, the latter only demonstrated borderline significant heterogeneity, conceivably due to the predominance of studies of WRMT-Faces (11/17) in this category. By comparison, *designs-single-immediate* had approximately double the sample size ($k = 34$) but greater heterogeneity which in addition was predominantly explained by variance in the effect size ($Q = 94.33$, $p < .001$, $I^2 = 67\%$).

3.5 Publication bias

For each significant effect size, the calculated fail-safe *N* (the estimated number of additional studies with effect size of 0.01 to reverse the significance of the effect) was well in excess of the number of unpublished studies reasonably hypothesised to exist that had such a low effect size (see Supplementary Tables in Appendix). This indicates that each of the observed significant effects are highly unlikely to be explained by publication bias.

4. Discussion

The goal of this paper was to examine whether different attributes of neuropsychological tests of nonverbal memory influenced their ability to discriminate right- from left-sided temporal lobe patients. The overall pattern of results showed four things 1) Patients with right TLE performed worse on all types of nonverbal memory tests than patients with left TLE, in both the presurgical and postsurgical patient groups, but overall the effect sizes were small. 2) For presurgical patients, effect sizes were consistently small for all types of nonverbal memory test; however, for postsurgical patients the differences were medium-sized for face memory and spatial (delayed) memory. 3) Postsurgical changes showed an overall pattern of mild improvement in left-sided patients and no change in right-sided patients, with only face memory tasks clearly dissociating left-sided patients who improved

more than right-sided patients who showed a marginally significant trend to decline. And 4), there was no consistent effect of task demands (type of learning trial or delay before memory testing) in any patient group. Our results update and expand upon similar findings from previous meta-analyses showing greater sensitivity of face memory tests to right temporal lobe pathology compared with design memory (Sherman et al., 2011; Vaz, 2004). The results also support previous evidence that experimental spatial memory tasks have an ability to detect right hippocampal pathology and extend these findings to clinical tests of spatial memory (e.g., Kessels et al., 2001). The data further suggest that task demands such as the type of learning trial or delay before memory testing may have comparatively little impact on lateralisation (cf. Majdan et al., 1996).

Results from individual tests are now considered to further explore these category-level findings. For face memory different tests showed medium-sized right-lateralisation effects in presurgical patients (Dade Face Learning Test; Denman Facial Recognition Test) in postsurgical patients (WRMT-Faces; Faces I and II; Graduate Hospital Facial Memory Test) and for differences in postsurgical change (WRMT-Faces). Notably, the WRMT-Faces was the only individual test to show a significant hemispheric dissociation in postsurgical change. Individual tests of spatial memory were mostly supported by single studies, with the 7/24 Spatial Learning Test appearing in only two studies. Within the spatial memory category, there was a wide range of effect sizes, including some within the large range (e.g., in presurgical patients, Austin Maze, $d = -0.86$, BLT, $d = -1.56$, Route Learning Test, $d = -2.65$), despite only marginal significance of the spatial learning category overall. Conversely, for postsurgical patients, despite the overall significance of the spatial delayed memory category, none of the individual measures within this category reached significance (7/24 Spatial Learning Test was marginal at $p = .05$). In sum, although our results suggest the promise of spatial memory tests for assessing right temporal lobe damage, particularly in presurgical patients for which there is the biggest clinical need, more replication is required to consider them appropriate for clinical use.

For design memory, it was notable that consistent with an earlier review (Sherman et al., 2011) the only tests to show significant and medium-sized right-lateralisation effects were those with multiple learning trials: DL-AMIPB (learning and delayed recall measures) in both presurgical and postsurgical patients and DCS (learning) for postsurgical decline in right-sided patients. There were mixed findings from the many other tests with multiple learning trials and we speculate that differences in the particular stimuli (e.g., novelty of designs), or testing method (e.g. recall or recognition), may have contributed to the mixed findings. While supported by a very large number of studies, design memory tests with single learning trials (e.g., VR, RCFT) failed to show any significant effects of medium or large size. Consistent with previous reviews (Vaz, 2004), the immediate memory subcategory of design memory tests performed numerically the worst ($ds < 0.12$ for all patient groups). For tests that were not classified there were mixed results (i.e., large effects for Doors test, and no effect for Family Pictures or Visual Paired Associates).

In general, taken across all three types of nonverbal material, there was no consistent advantage of using delayed memory measures over immediate memory measures, or in using tests with multiple learning trials over tests with single learning trials. For example, in postsurgical patients, testing memory for faces immediately after learning showed better categorisation of postsurgical change due to right-sided versus left-sided resection compared to delayed memory, while spatial delayed memory was able to distinguish right- from left-sided postsurgical patients than spatial learning. These findings suggest that material type is more important in eliciting right temporal lobe involvement than the task demands, or any specific combination of stimulus type and task demands (c.f. Majdan et al., 1996). Caution is urged in extrapolating these findings to clinical situations, however, as the effect of task demands were only grouped within subcategories of stimulus types rather than as a cross-stimulus category (e.g., “immediate memory” including abstract design and face stimuli versus “delayed memory” including designs, faces, and spatial stimuli). It was believed that the inevitable confounding of stimulus type with task demands, and the overt numerical

dominance of designs per se, prevented a sensible interpretation of this type of grouping. There may also be complex interactions between the type of stimulus and task demands that are not yet understood.

This study updated and expanded upon previous meta-analyses, and the novel contribution of this work was its inclusion of a wider variety and number of neuropsychological tests, and the use of presurgical, postsurgical and pre-post samples. The latter allowed clearer inferences to be made regarding the differential impact of the epilepsy-related pathology itself versus the impact of surgery, both of which are important considerations for the clinician in assessing the risk of memory decline. Specifically, presurgical right TLE patients showed poorer nonverbal memory than left-sided patients, but these effects were small and were not moderated by the particular type of material or task demand. By contrast, the combined impact of TLE and surgery itself is associated with a larger decline in face and spatial memory than design memory.

One possible explanation for the difference may be that the postsurgical sample had more severe temporal lobe dysfunction prior to surgery than did the presurgical sample. This could occur for two reasons. Firstly, while studies of presurgical patients were only included if patients had been tested to assess their appropriateness for surgical intervention, in some studies it was not known whether they eventually underwent surgery. The much larger number of studies with presurgical compared with postsurgical patients supports the notion that not all presurgical patients eventually underwent surgery. Secondly, it is possible that patients were more likely to be tested following surgery if they were at higher risk of memory loss, compared to patients with lower risk of memory loss. The combined effects of one or both of these potential sampling biases within the studies included in this meta-analysis may have led to an overall greater severity of dysfunction in postsurgical than presurgical samples, in turn leading to an increased ability to detect differences in performance between the different types of stimuli. To test between these possibilities future studies could compare presurgical patients with and without hippocampal damage, since the former would be expected to

perform relatively more poorly with face and spatial memory tasks than with design memory tasks. Similarly, a comparison of patients following standard anterior temporal lobectomy, which typically removes some ventrolateral structures, to those following selective amygdalohippocampectomy (SAH) techniques, could also cast more light on this issue.

Another important consideration is that standard anterior temporal lobectomy may damage functional tissue that is not affected by seizures within and outside of the medial temporal lobe. Among these the right ventrolateral temporal cortex, which contains the inferior temporal and fusiform gyrus, has been linked to the perception of unfamiliar faces (e.g., Kanwisher, McDermott, & Chun, 1997). Therefore, a primary or concurrent face perception deficit due to surgery may confound or at least contribute to the greater face memory deficits for right-sided postsurgical patients, relative to presurgical patients. However, since damage exclusively to the right hippocampus has also been linked to deficits in face memory the removal of adjacent structures cannot be assumed to confound the results (e.g., Haxby et al., 1996). For spatial memory, most evidence implicates right parietal rather than right temporal regions in lower-level spatial processes (Langner & Eickhoff, 2013; van der Ham, Postma, & Laeng, 2014), although interestingly there is increasing evidence of the critical involvement of right ventrolateral regions in spatial attention (Shulman et al., 2010). In general, the performance of a memory task for faces or spatial material relies on a distributed network of brain areas, and surgical resection may disrupt this network by the removal and/or disconnection of tissue that are functionally important.

Although not the primary focus of this study, for patients in which postsurgical change was measured, we found mild improvements in nonverbal memory following left-sided temporal lobe resection. This result supports previous findings and also complements reports of improvement in verbal memory function after right-sided resection (Baxendale, Thompson, & Duncan, 2008). However, in our analysis the improvement appeared larger for faces than designs or spatial memory. Taken together, these improvements conceivably occur through an increased ability of the right side to process the material (particularly faces) following the

elimination of uncontrolled seizures that spread from the left to the right hemisphere (e.g., see Novelly et al., 2004). Alternatively, they may indicate that faces are more verbalisable than designs or spatial arrays, since left-sided pathology presumably impairs the ability to verbally encode a nonverbal stimulus. This important question merits further investigation, perhaps using the transcranial magnetic stimulation method in which the left or right side of the temporal lobe of healthy participants could be given a temporary 'virtual lesion' in order to assess their differential ability to verbalise different types of nonverbal materials. In any case, these improvements in face memory highlight a potential positive outcome following left-sided surgery, contrasting with the risk of decline to verbal memory (Sherman et al., 2011).

One potential limitation of our study was the partial repetition of memory testing in some patients, specifically in those tested at both presurgical and postsurgical stages. In addition, there was repetition of different memory tests within the same patients, as well as repetition of multiple measures within specific memory tests (e.g., immediate and delayed recall measures from the WMS) in some instances. However, we considered correction for multiple comparisons (e.g., Bonferroni) inappropriate for the meta-analysis for a number of reasons. Firstly, we focused on the size of effects rather than statistical significance per se, as the former is more clinically relevant, while the latter, in the context of very large samples, was predominantly an index of sample size. Indeed, many of the highly significant results derived from very large samples but were associated with the smallest effect sizes (e.g., for design memory tasks with single learning trials), which indicated that while the effects were very reliably small, they were not of a clinically meaningful magnitude. We attempted to maximise the interpretability of our data by showing data for postsurgical change in addition to data from the overall presurgical and postsurgical groups. In this vein, we did not also compare performance of patients on nonverbal memory tests with verbal memory tests, since we considered this outside the scope of this review.

4.1 Conclusion

In sum, this meta-analysis revealed that particular kinds of neuropsychological tests of

nonverbal memory showed greater ability to detect right temporal lobe damage due to surgery, namely tests of face memory and spatial memory compared to design memory. By contrast, task demands including the type of learning trial and the delay before memory testing had no meaningful effect on the degree of lateralisation. The only individual test to reliably lateralise postsurgical memory changes was the Warrington Recognition Memory Test for Faces. Our findings have ramifications for the choice of measure in the clinical assessment of unilateral temporal lobe epilepsy patients and also on the design of future measures for this purpose.

References

* Asterisks indicate studies that were included in the meta-analysis

*Abrahams, S., Morris, R. G., Polkey, C. E., Jarosz, J. M., Cox, T. C., Graves, M., & Pickering, A. (1999). Hippocampal involvement in spatial and working memory: a structural MRI analysis of patients with unilateral mesial temporal lobe sclerosis. *Brain and Cognition, 41*(1), 39-65.

*Adda, C. C., Castro, L. H. M., Além-Mar e Silva, L. C., de Manreza, M. L. G., & Kashiara, R. (2008). Prospective memory and mesial temporal epilepsy associated with hippocampal sclerosis. *Neuropsychologia, 46*(7), 1954-1964. doi: 10.1016/j.neuropsychologia.2008.01.016

*Akanuma, N., Alarcon, G., Lum, F., Kissani, N., Koutroumanidis, M., Adachi, N., . . . Morris, R. G. (2003). Lateralizing value of neuropsychological protocols for presurgical assessment of temporal lobe epilepsy (vol 44, pg 408, 2003). *Epilepsia, 44*(7), 990-990. doi: 10.1046/j.1528-1157.2003.44702.x

*Alessio, A., Bonilha, L., Rorden, C., Kobayashi, E., Min, L. L., Damasceno, B. P., & Cendes, F. (2006). Memory and language impairments and their relationships to hippocampal and perirhinal cortex damage in patients with medial temporal lobe epilepsy. *Epilepsy & Behavior, 8*(3), 593-600. doi:10.1016/j.yebeh.2006.01.007

*Alessio, A., Pereira, F. R., Sercheli, M. S., Rondina, J. M., Ozelo, H. B., Bilevicius, E., . . . Cendes, F. (2013). Brain plasticity for verbal and visual memories in patients with mesial temporal lobe epilepsy and hippocampal sclerosis: An fMRI study. *Human Brain Mapping, 34*(1), 186-199.

Alpherts, W. C. J., Vermeulen, J., van Rijen, P. C., da Silva, F. H. L., van Veelen, C. W. M., & Dutch Collaborative Epilepsy, S. (2006). Verbal memory decline after temporal epilepsy surgery? A 6-year multiple assessments follow-up study. *Neurology, 67*(4), 626-631. doi:10.1212/01.wnl.0000230139.45304.eb

*Araujo, G. C., Schwarze, N. J., & White, D. A. (2009). Lateralizing seizure focus in presurgical patients with temporal lobe epilepsy: Utility of the Ruff-Light Trail Learning Test. *Epilepsy & Behavior, 15*(4), 496-499. doi: 10.1016/j.yebeh.2009.06.002

*Baker, G. A., Austin, N. A., & Downes, J. J. (2003). Validation of the Wechsler Memory Scale-III in a population of people with intractable temporal lobe epilepsy. *Epilepsy research, 53*(3), 201-206. doi: 10.1016/s0920-1211(03)00023-8

*Bandt, S. K., Werner, N., Dines, J., Rashid, S., Eisenman, L. N., Hogan, R. E., . . . Dowling, J. (2013). Trans-middle temporal gyrus selective amygdalohippocampectomy for medically intractable mesial temporal lobe epilepsy in adults: Seizure response rates, complications, and neuropsychological outcomes. *Epilepsy & Behavior, 28*(1), 17-21.

*Barnett, A. J., Park, M. T. M., Pipitone, J., Chakravarty, M. M., & McAndrews, M. P. (2015). Functional and structural correlates of memory in patients with mesial temporal lobe epilepsy. *Frontiers in Neurology, 6*(MAY). doi:10.3389/fneur.2015.00103

*Barr, W., Morrison, C., Zaroff, C., & Devinsky, O. (2004). Use of the Brief Visuospatial Memory Test-Revised (BVMT-R) in neuropsychological evaluation of epilepsy surgery candidates. *Epilepsy & Behavior, 5*(2), 175-179. doi: 10.1016/j.yebeh.2003.12.010

*Barr, W. B. (1997a). Examining the right temporal lobe's role in nonverbal memory. *Brain and Cognition, 35*(1), 26-41.

*Barr, W. B. (1997b). Receiver operating characteristic curve analysis of Wechsler Memory Scale-Revised scores in epilepsy surgery candidates. *Psychological Assessment, 9*(3), 171-176.

*Barr, W. B., Chelune, G. J., Hermann, B. P., Loring, D. W., Perrine, K., Strauss, E., . . . Westerveld, M. (1997). The use of figural reproduction tests as measures of nonverbal memory in epilepsy surgery candidates. *Journal of the International Neuropsychological Society, 3*(5), 435-443.

*Baxendale, S., Thompson, P. J., & Duncan, J. S. (2008). Improvements in memory function following anterior temporal lobe resection for epilepsy. *Neurology, 71*(17), 1319-1325. doi: 10.1212/01.wnl.0000319699.04265.fd

*Baxendale, S., Thompson, P. J., & Duncan, J. S. (2012). Neuropsychological function in patients who have had epilepsy surgery: A long-term follow-up. *Epilepsy & Behavior, 23*(1), 24-29. doi: 10.1016/j.yebeh.2011.10.021

*Baxendale, S. A. (1997). The role of the hippocampus in recognition memory. *Neuropsychologia, 35*(5), 591-598. doi: 10.1016/s0028-3932(96)00123-6

*Baxendale, S. A., Thompson, P. J., & Kitchen, N. D. (2000). Postoperative hippocampal remnant shrinkage and memory decline - A dynamic process. *Neurology, 55*(2), 243-249.

*Baxendale, S. A., Thompson, P. J., & Van Paesschen, W. (1998). A test of spatial memory and its clinical utility in the pre-surgical investigation of temporal lobe epilepsy patients. *Neuropsychologia, 36*(7), 591-602. doi: 10.1016/s0028-3932(97)00163-2

Bell, B. D., & Davies, K. G. (1998). Anterior temporal lobectomy, hippocampal sclerosis, and memory: Recent neuropsychological findings. *Neuropsychology Review, 8*(1), 25-41. doi:10.1023/a:1025679122911

*Bell, B. D., Fine, J., Dow, C., Seidenberg, M., & Hermann, B. P. (2005). Temporal lobe epilepsy and the selective reminding test: The conventional 30-minute delay suffices. *Psychological Assessment, 17*(1), 103-109. doi: 10.1037/1040-3590.17.1.103

*Bianchin, M. M., Velasco, T. R., Coimbra, E. R., Gargaro, A. C., Escorsi-Rosset, S. R., Wichert-Ana, L., . . . Sakamoto, A. C. (2013). Cognitive and Surgical Outcome in Mesial Temporal Lobe Epilepsy Associated with Hippocampal Sclerosis Plus Neurocysticercosis: A Cohort Study. *PLoS One, 8*(4). doi: 10.1371/journal.pone.0060949

*Bigras, C., Shear, P. K., Vannest, J., Allendorfer, J. B., & Szaflarski, J. P. (2013). The effects of temporal lobe epilepsy on scene encoding. *Epilepsy and Behavior, 26*(1), 11-21.

*Binder, J. R., Sabsevitz, D. S., Swanson, S. J., Hammeke, T. A., Raghavan, M., & Mueller, W. M. (2008). Use of preoperative functional MRI to predict verbal memory decline after temporal lobe epilepsy surgery. *Epilepsia, 49*(8), 1377-1394.

*Bjornaes, H., Stabell, K. E., Roste, G. K., & Bakke, S. J. (2005). Changes in verbal and nonverbal memory following anterior temporal lobe surgery for refractory seizures: effects of sex and laterality. *Epilepsy & Behavior, 6*(1), 71-84. doi: 10.1016/j.yebeh.2004.10.011

*Blake, R. V., Wroe, S. J., Breen, E. K., & McCarthy, R. A. (2000). Accelerated forgetting in patients with epilepsy - Evidence for an impairment in memory consolidation. *Brain, 123*, 472-483. doi: 10.1093/brain/123.3.472

*Bonelli, S. B., Powell, R. H. W., Yogarajah, M., Samson, R. S., Symms, M. R., Thompson, P. J., . . . Duncan, J. S. (2010). Imaging memory in temporal lobe epilepsy: predicting the effects of temporal lobe resection. *Brain, 133*, 1186-1199. doi: 10.1093/brain/awq006

*Breier, J. I., Plenger, P. M., Castillo, R., Fuchs, K., Wheless, J. W., Thomas, A. B., . . . Papanicolaou, A. (1996). Effects of temporal lobe epilepsy on spatial and figural aspects of memory for a complex geometric figure. *Journal of the International Neuropsychological Society, 2*(6), 535-540.

*Breier, J. I., Thomas, A. B., Plenger, P. M., Wheless, J. W., Brookshire, B. L., Papanicolaou, A., & Willmore, L. J. (1997). Asymmetries in the effect of side of seizure onset on recognition memory following intracarotid amobarbital injection. *Epilepsia, 38*(11), 1209-1215. doi: 10.1111/j.1528-1157.1997.tb01218.x

*Brown, F. C., Tuttle, E., Westerveld, M., Ferraro, F. R., Chmielowiec, T., Vandemore, M., . . . Spencer, S. S. (2010). Visual memory in patients after anterior right temporal lobectomy and adult normative data for the Brown Location Test. *Epilepsy & Behavior, 17*(2), 215-220. doi: 10.1016/j.yebeh.2009.11.026

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron, 35*(4), 625-641. doi:10.1016/s0896-6273(02)00830-9

*Busch, R. M., Dulay, M. F., Kim, K. H., Chapin, J. S., Jehi, L., Kalman, C. C., . . . Najm, I. M. (2011). Pre-Surgical Mood Predicts Memory Decline after Anterior Temporal Lobe Resection for Epilepsy. *Archives of Clinical Neuropsychology, 26*(8), 739-745. doi:10.1093/arclin/acr067

*Carvajal, F., Rubio, S., Martin, P., Serrano, J. M., & Garcia-Sola, R. (2009). Perception and recall of faces and facial expressions following temporal lobectomy. *Epilepsy & Behavior, 14*(1), 60-65. doi:10.1016/j.yebeh.2008.08.016

*Castro, L. H., Silva, L. C. A. M., Adda, C. C., Banaskiwitz, N. H. C., Xavier, A. B., Jorge, C. L., . . . Nitrini, R. (2013). Low prevalence but high specificity of material-specific memory impairment in epilepsy associated with hippocampal sclerosis. *Epilepsia, 54*(10), 1735-1742. doi: 10.1111/epi.12343

*Chelune, G. J., Naugle, R. I., Luders, H., & Awad, I. A. (1991). Prediction of cognitive change as a function of preoperative ability status among temporal lobectomy patients seen at 6-month follow-up. *Neurology, 41*(3), 399-404.

*Chelune, G. J., Naugle, R. I., Lüders, H., Sedlak, J., & Awad, I. A. (1993). Individual Change After Epilepsy Surgery: Practice Effects and Base-Rate Information. *Neuropsychology, 7*(1), 41-52.

*Chiaravalloti, N. D., Tulsky, D. S., & Glosser, G. (2004). Validation of the WMS-III facial memory subtest with the Graduate Hospital Facial Memory Test in a sample of right and temporal lobectomy left anterior patients. *Journal of Clinical and Experimental Neuropsychology, 26*(4), 484-497. doi: 10.1080/13803390490496623

Cohen, J. (1977). *Statistical power for behavioural sciences (revised edition).* New York: Academic Press.

*da Costa Neves, R. S., Silva Tudesco, I. d. S., Jardim, A. P., Sales Ferreira Caboclo, L. O., Lancellotti, C., Ferrari-Marinho, T., . . . Targas Yacubian, E. M. (2012). Granule cell dispersion is associated with memory impairment in right mesial temporal lobe

epilepsy. *Seizure-European Journal of Epilepsy, 21*(9), 685-690. doi: 10.1016/j.seizure.2012.07.008

*Dade, L. A., & Jones-Gotman, M. (2001). Face learning and memory: The twins test. *Neuropsychology, 15*(4), 525-534. doi: 10.1037/0894-4105.15.4.525

*Dige, N., & Wik, G. (2001). A visual learning and memory test for preoperative evaluation of patients with temporal lobe epilepsy. *International Journal of Neuroscience, 111*(3-4), 167-174. doi: 10.3109/00207450108994228

*Dodrill, C. B., & Ojemann, G. A. (2007). Do recent seizures and recent changes in antiepileptic drugs impact performances on neuropsychological tests in subtle ways that might easily be missed? *Epilepsia, 48*(10), 1833-1841. doi: 10.1111/j.1528-1167.2007.01140.x

*Doss, R. C., Chelune, G. J., & Naugle, R. I. (2000). Comparability of the expanded WMS-III standardization protocol to the published WMS-III among right and left temporal lobectomy patients. *Clinical Neuropsychologist, 14*(4), 468-473.

*Doss, R. C., Chelune, G. J., & Naugle, R. I. (2004). WMS-III performance in epilepsy patients following temporal lobectomy. *Journal of the International Neuropsychological Society, 10*(2), 173-179. doi: 10.1017/s1355617704102026

*Doucet, G., Osipowicz, K., Sharan, A., Sperling, M. R., & Tracy, J. I. (2013). Extratemporal functional connectivity impairments at rest are related to memory performance in mesial temporal epilepsy. *Human Brain Mapping, 34*(9), 2202-2216. doi: 10.1002/hbm.22059

*Doucet, G. E., Rider, R., Taylor, N., Skidmore, C., Sharan, A., Sperling, M., & Tracy, J. I. (2015). Presurgery resting-state local graph-theory measures predict neurocognitive outcomes after brain surgery in temporal lobe epilepsy. *Epilepsia, 56*(4), 517-526. doi: 10.1111/epi.12936

*Dulay, M. F., Levin, H. S., York, M. K., Li, X. Q., Mizrahi, E. M., Goldsmith, I., . . . Yoshor, D. (2009). Changes in individual and group spatial and verbal learning characteristics

after anterior temporal lobectomy. *Epilepsia, 50*(6), 1385-1395. doi: 10.1111/j.1528-1167.2008.01730.x

*Dulay, M. F., Levin, H. S., York, M. K., Mizrahi, E. M., Verma, A., Goldsmith, I., . . . Yoshor, D. (2009). Predictors of individual visual memory decline after unilateral anterior temporal lobe resection. *Neurology, 72*(21), 1837-1842.

*Dulay, M. F., Schefft, B. K., Testa, S. M., Fargo, J. D., Privitera, M., & Yeh, H.-s. (2002). What does the family pictures subtest of the Wechsler Memory Scale-III measure? Insight gained from patients evaluated for epilepsy surgery. *The Clinical Neuropsychologist, 16*(4), 452-462.

*Dupont, S., Duron, E., Samson, S., Denos, M., Volle, E., Delmaire, C., . . . Baulac, M. (2010). Functional MR Imaging or Wada Test: Which Is the Better Predictor of Individual Postoperative Memory Outcome? *Radiology, 255*(1), 128-134. doi: 10.1148/radiol.09091079

Eichenbaum, H., Otto, T., & Cohen, N. J. (1994). Two functional components of the hippocampal memory system. Behavioral and Brain Sciences, 17(3), 449-472.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature, 425*(6954), 184-188.

*Focke, N. K., Thompson, P. J., & Duncan, J. S. (2008). Correlation of cognitive functions with voxel-based morphometry in patients with hippocampal sclerosis. *Epilepsy & Behavior, 12*(3), 472-476. doi: 10.1016/j.yebeh.2007.12.011

*Frank, J. E., & Tomaz, C. (2003). Lateralized impairment of the emotional enhancement of verbal memory in patients with amygdala-hippocampus lesion. *Brain and Cognition, 52*(2), 223-230.

Fuller-Thomson, E., & Brennenstuhl, S. (2009). The association between depression and epilepsy in a nationally representative sample. *Epilepsia, 50*(5), 1051-1058. doi:10.1111/j.1528-1167.2008.01803.x

Gaillard, W. D., Balsamo, L., Xu, B., Grandin, C. B., Braniecki, S. H., Papero, P. H., et al. (2002). Language dominance in partial epilepsy patients identified with an fMRI reading task. *Neurology, 59*(2), 256–265.

*Gargaro, A. C., Sakamoto, A. C., Bianchin, M. M., Geraldi, C. D. L., Scorsi-Rosset, S., Coimbra, E. R., . . . Velasco, T. R. (2013). Atypical neuropsychological profiles and cognitive outcome in mesial temporal lobe epilepsy. *Epilepsy & Behavior, 27*(3), 461-469. doi: 10.1016/j.yebeh.2013.03.002

*Giovagnoli, A. R., Casazza, M., Ciceri, E., Avanzini, G., & Broggi, G. (2007). Preserved memory in temporal lobe epilepsy patients after surgery for low-grade tumour. A pilot study. *Neurological Sciences, 28*(5), 251-258. doi: 10.1007/s10072-007-0831-z

*Gleissner, U., Helmstaedter, C., Schramm, J., & Elger, C. (2002). Memory Outcome after Selective Amygdalohippocampectomy: A Study in 140 Patients with Temporal Lobe Epilepsy. *Epilepsia, 43*(1), 87-95. doi: http://dx.doi.org/10.1046/j.1528-1157.2002.24101.x

*Glogau, S., Ellgring, H., Elger, C. E., & Helmstaedter, C. (2004). Face and facial expression memory in temporal lobe epilepsy patients: Preliminary results. *Epilepsy & Behavior, 5*(1), 106-112. doi:10.1016/j.yebeh.2003.11.014

*Glosser, G., Cole, L., Khatri, U., DellaPietra, L., & Kaplan, E. (2002). Assessing nonverbal memory with the Biber Figure Learning Test - Extended in temporal lobe epilepsy patients. *Archives of Clinical Neuropsychology, 17*(1), 25-35.

*Goldstein, L. H., & Polkey, C. E. (1992). Behavioural memory after temporal lobectomy or amygdalo-hippocampectomy. *The British Journal Of Clinical Psychology, 31 (Pt 1)*, 75-81.

*Goldstein, L. H., & Polkey, C. E. (1993). Short-term cognitive changes after unilateral temporal lobectomy or unilateral amygdalo-hippocampectomy for the relief of temporal lobe epilepsy. *Journal of neurology, neurosurgery, and psychiatry, 56*(2), 135-140.

*Grammaldo, L. G., Di Gennaro, G., Giampà, T., De Risi, M., Meldolesi, G. N., Mascia, A., . . . Picardi, A. (2009). Memory outcome 2 years after anterior temporal lobectomy in patients with drug-resistant epilepsy. *Seizure, 18*(2), 139-144. doi: 10.1016/j.seizure.2008.08.008

*Grammaldo, L. G., Giampa, T., Quarato, P. P., Picardi, A., Mascia, A., Sparano, A., . . . Di Gennaro, G. (2006). Lateralizing value of memory tests in drug-resistant temporal lobe epilepsy. *European Journal of Neurology, 13*(4), 371-376. doi: 10.1111/j.1468-1331.2006.01236.x

*Griffith, H. R., Perlman, S. B., Woodard, A. R., Rutecki, P. A., Jones, J. C., Ramirez, L. F., . . . Hermann, B. P. (2000). Preoperative FDG-PET temporal lobe hypometabolism and verbal memory after temporal lobectomy. *Neurology, 54*(5), 1161-1165.

Golby, A. J., Poldrack, R. A., Brewer, J. B., Spencer, D., Desmond, J. E., Aron, A. P., & Gabrieli, J. D. E. (2001). Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. *Brain, 124*, 1841-1854. doi:10.1093/brain/124.9.1841

Hampstead, B. M., Lacey, S., Ali, S., Phillips, P. A., Stringer, A. Y., & Sathian, K. (2010). Use of complex three-dimensional objects to assess visuospatial memory in healthy individuals and patients with unilateral amygdalohippocampectomy. *Epilepsy and Behavior, 18*(1-2), 54-60.

*Hanoğlu, L., Özkara, C., Keskinkilic, C., Altin, Ü., Uzan, M., Tuzgen, S., . . . Özyurt, E. (2004). Correlation between 1H MRS and memory before and after surgery in mesial temporal lobe epilepsy with hippocampal sclerosis. *Epilepsia, 45*(6), 632-640. doi: 10.1111/j.0013-9580.2004.54302.x

*Harvey, D. J., Naugle, R. I., Magleby, J., Chapin, J. S., Najm, I. M., Bingaman, W., & Busch, R. M. (2008). Relationship between presurgical memory performance on the Wechsler Memory Scale-III and memory change following temporal resection for treatment of

intractable epilepsy. *Epilepsy and Behavior, 13*(2), 372-375. doi:10.1016/j.yebeh.2008.04.024

Haxby, J. V., Ungerleider, L. G., Horwitz, B., Maisog, J. M., Rapoport, S. I., & Grady, C. L. (1996). Face encoding and recognition in the human brain. *Proceedings of the National Academy of Sciences of the United States of America, 93*(2), 922-927. doi:10.1073/pnas.93.2.922

*Helmstaedter, C., & Elger, C. E. (2000). Behavioral markers for self- and other-attribution of memory: a study in patients with temporal lobe epilepsy and healthy volunteers. *Epilepsy research, 41*(3), 235-243. doi: 10.1016/s0920-1211(00)00148-0

*Helmstaedter, C., Hufnagel, A., & Elger, C. E. (1992). Preoperative memory profiles in patients with temporal-lobe epilepsy are related to postoperative seizure outcome. *Journal of Epilepsy, 5*(1), 17-23. doi: 10.1016/s0896-6974(05)80016-7

*Helmstaedter, C., Petzold, I., & Bien, C. G. (2011). The cognitive consequence of resecting nonlesional tissues in epilepsy surgery-Results from MRI- and histopathology-negative patients with temporal lobe epilepsy. *Epilepsia, 52*(8), 1402-1408. doi: 10.1111/j.1528-1167.2011.03157.x

*Helmstaedter, C., Pohl, C., & Elger, C. E. (1995). Relations between verbal and nonverbal memory performance - evidence of confounding effects particularly in patients with right temporal-lobe epilepsy. *Cortex, 31*(2), 345-355.

*Helmstaedter, C., Richter, S., Röske, S., Oltmanns, F., Schramm, J., & Lehmann, T. N. (2008). Differential effects of temporal pole resection with amygdalohippocampectomy versus selective amygdalohippocampectomy on material-specific memory in patients with mesial temporal lobe epilepsy. *Epilepsia, 49*(1), 88-97. doi: 10.1111/j.1528-1167.2007.01386.x

*Helmstaedter, C., Roeske, S., Kaaden, S., Elger, C. E., & Schramm, J. (2011). Hippocampal resection length and memory outcome in selective epilepsy surgery. *Journal of*

Neurology Neurosurgery and Psychiatry, 82(12), 1375-1381. doi: 10.1136/jnnp.2010.240176

*Helmstaedter, C., Sonntag-Dillender, M., Hoppe, C., & Elger, C. E. (2004). Depressed mood and memory impairment in temporal lobe epilepsy as a function of focus lateralization and localization. *Epilepsy & Behavior, 5*(5), 696-701. doi: 10.1016/j.yebeh.2004.06.008

*Helmstaedter, C., Van Roost, D., Clusmann, H., Urbach, H., Elger, C. E., & Schramm, J. (2004). Collateral brain damage, a potential source of cognitive impairment after selective surgery for control of mesial temporal lobe epilepsy. *Journal of Neurology Neurosurgery and Psychiatry, 75*(2), 323-326.

*Hermann, B. P., Connell, B., Barr, W. B., & Wyler, A. R. (1995). The utility of the Warrington Recognition Memory Test for temporal-lobe epilepsy: Pre- and postoperative results. *Journal of Epilepsy, 8*(2), 139-145. doi: 10.1016/0896-6974(95)00022-6

*Hermann, B. P., Seidenberg, M., Schoenfeld, J., & Davies, K. (1997). Neuropsychological characteristics of the syndrome of mesial temporal lobe epilepsy. *Archives of Neurology, 54*(4), 369-376.

*Hill, S. W., Gale, S. D., Pearson, C., & Smith, K. (2012). Neuropsychological outcome following minimal access subtemporal selective amygdalohippocampectomy. *Seizure-European Journal of Epilepsy, 21*(5), 353-360. doi: 10.1016/j.seizure.2012.03.002

*Hocking, J., Thomas, H., Dzafic, I., Williams, R., Reutens, D., & Spooner, D. (2013). Disentangling the cognitive components supporting Austin Maze performance in left versus right temporal lobe epilepsy. *Epilepsy & Behavior, 29*(3), 485-491. doi: http://dx.doi.org/10.1016/j.yebeh.2013.08.020

Hunter, J. E., & Schmidt, F. L. (2000). Fixed effects vs. random effects meta-analysis models: Implications for cumulative research knowledge. *International Journal of Selection and Assessment, 8*(4), 275-292. doi:10.1111/1468-2389.00156

*Hurtado, B., Thompson, P., & Baxendale, S. (2009). The clinical utility of the Warrington Recognition Memory Test in people with a low IQ. *Journal of Clinical and Experimental Neuropsychology, 31*(8), 955-958. doi: 10.1080/13803390902766887

*Immonen, A., Jutila, L., Muraja-Murro, A., Mervaala, E., Äikiä, M., Lamusuo, S., . . . Kälviäinen, R. (2010). Long-term epilepsy surgery outcomes in patients with MRI-negative temporal lobe epilepsy. *Epilepsia, 51*(11), 2260-2269. doi: 10.1111/j.1528-1167.2010.02720.x

Janszky, J., Jokeit, H., Heinemann, D., Schulz, R., Woermann, F. G., & Ebner, A. (2003). Epileptic activity influences the speech organization in medial temporal lobe epilepsy. *Brain, 126*, 2043-2051. doi:10.1093/brain/awg193

Jones-Gotman, M., Smith, M. L., Frisk, V., & Routhier, N. (1996). Learning and retention of connected prose before and after surgical resection from a temporal lobe. *Epilepsia, 37*(S5), 120-120.

Jones-Gotman, M., Zatorre, R. J., Olivier, A., Andermann, F., Cendes, F., Staunton, H., . . . Wieser, H. G. (1997). Learning and retention of words and designs following excision from medial or lateral temporal-lobe structures. *Neuropsychologia, 35*(7), 963-973. doi:10.1016/s0028-3932(97)00024-9

Jones-Gotman, M., Harnadek, M. C. S., & Kubu, C. S. (2000). Neuropsychological assessment for temporal lobe epilepsy surgery. *Canadian Journal of Neurological Sciences, 27*, S39-S43. Retrieved from <Go to ISI>://WOS:000087067100010

Jones-Gotman, M., Smith, M. L., Risse, G. L., Westerveld, M., Swanson, S. J., Giovagnoli, A. R., . . . Piazzini, A. (2010). The contribution of neuropsychology to diagnostic assessment in epilepsy. *Epilepsy & Behavior, 18*(1-2), 3-12. doi: 10.1016/j.yebeh.2010.02.019

*Jutila, L., Aikia, M., Immonen, A., Mervaala, E., Alafuzoff, I., & Kalviainen, R. (2014). Long-term memory performance after surgical treatment of unilateral temporal lobe

epilepsy (TLE). *Epilepsy research, 108*(7), 1228-1237. doi: 10.1016/j.eplepsyres.2014.05.002

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17*(11), 4302-4311.

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., . . . Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron, 20*(5), 927-936. doi:10.1016/s0896-6273(00)80474-2

Kessels, R. P. C., de Haan, E. H. F., Kappelle, L. J., & Postma, A. (2001). Varieties of human spatial memory: a meta-analysis on the effects of hippocampal lesions. *Brain Research Reviews, 35*(3), 295-303.

*Kessels, R. P. C., Hendriks, M., Schouten, J., Van Asselen, M., & Postma, A. (2004). Spatial memory deficits in patients after unilateral selective amygdalohippocampectomy. *Journal of the International Neuropsychological Society: JINS, 10*(6), 907-912.

*Kikuchi, S., Kubota, F., Hattori, S., Oya, N., & Mikuni, M. (2001). A study of the relationship between metabolism using H-1-MRS and function using several neuropsychological tests in temporal lobe epilepsy. *Seizure-European Journal of Epilepsy, 10*(3), 188-193. doi: 10.1053/siez.2000.0498

*Kim, H., Yi, S., Son, E. I., & Kim, J. (2003). Material-specific memory in temporal lobe epilepsy: Effects of seizure laterality and language dominance. *Neuropsychology, 17*(1), 59-68. doi: 10.1037/0894-4105.17.1.59

*Kneebone, A. C., Lee, G. P., Wade, L. T., & Loring, D. W. (2007). Rey Complex Figure: Figural and spatial memory before and after temporal lobectomy for intractable epilepsy. *Journal of the International Neuropsychological Society, 13*(4), 664-671. doi:10.1017/s135617707070828

*Knopman, A. A., Wong, C. H., Stevenson, R. J., Homewood, J., Mohamed, A., Somerville, E., . . . Bleasel, A. F. (2015). The relationship between neuropsychological functioning and FDG-PET hypometabolism in intractable mesial temporal lobe epilepsy. *Epilepsy & Behavior, 44*, 136-142. doi:10.1016/j.yebeh.2015.01.023

*Kubu, C. S., Girvin, J. P., McLachlan, R. S., Pavol, M., & Harnadek, M. C. (2000). Does the intracarotid amobarbital procedure predict global amnesia after temporal lobectomy? *Epilepsia, 41*(10), 1321-1329.

Kühn, S., & Gallinat, J. (2014). Segregating cognitive functions within hippocampal formation: A quantitative meta-analysis on spatial navigation and episodic memory. *Human Brain Mapping, 35*(4), 1129-1142.

*La Cour, P., & Andersen, R. (2006). Neuropsychological assessment with the Visual Gestalt Test: Psychometric properties and differential diagnostic probabilities. *Scandinavian Journal of Psychology, 47*(1), 1-8. doi: 10.1111/j.1467-9450.2006.00487.x

*Lacritz, L. H., Barnard, H. D., Van Ness, P., Agostini, M., Diaz-Arrastia, R., & Cullum, C. M. (2004). Qualitative analysis of WMS-III Logical Memory and Visual Reproduction in temporal lobe epilepsy. *Journal of Clinical and Experimental Neuropsychology, 26*(4), 521-530. doi: 10.1080/13803390490496650

*Lah, S., Grayson, S., Lee, T., & Miller, L. (2004). Memory for the past after temporal lobectomy: impact of epilepsy and cognitive variables. *Neuropsychologia, 42*(12), 1666-1679. doi: 10.1016/j.neuropsychologia.2004.04.008

*Lah, S., Lee, T., Grayson, S., & Miller, L. (2006). Effects of temporal lobe epilepsy on retrograde memory. *Epilepsia, 47*(3), 615-625. doi: 10.1111/j.1528-1167.2006.00476.x

*Lah, S., Lee, T., Grayson, S., & Miller, L. (2008). Changes in retrograde memory following temporal lobectomy. *Epilepsy & Behavior, 13*(2), 391-396. doi: 10.1016/j.yebeh.2008.05.002

*Lambon Ralph, M. A., Cipolotti, L., Manes, F., & Patterson, K. (2010). Taking both sides: do unilateral anterior temporal lobe lesions disrupt semantic memory? *Brain, 133*, 3243-3255. doi: 10.1093/brain/awq264

*Lambon Ralph, M. A., Ehsan, S., Baker, G. A., & Rogers, T. T. (2012). Semantic memory is impaired in patients with unilateral anterior temporal lobe resection for temporal lobe epilepsy. *Brain, 135*(1), 242-258. doi: 10.1093/brain/awr325

Langner, R., & Eickhoff, S. B. (2013). Sustaining Attention to Simple Tasks: A Meta-Analytic Review of the Neural Mechanisms of Vigilant Attention. *Psychological Bulletin, 139*(4), 870-900. doi:10.1037/a0030694

Lee, T. M. C., Yip, J. T. H., & Jones-Gotman, M. (2002). Memory deficits after resection from left or right anterior temporal lobe in humans: A meta-analytic review. *Epilepsia, 43*(3), 283-291

*Leijten, F. S. S., Alpherts, W. C. J., Van Huffelen, A. C., Vermeulen, J., & Van Rijen, P. C. (2005). The effects on cognitive performance of tailored resection in surgery for nonlesional mesiotemporal lobe epilepsy. *Epilepsia, 46*(3), 431-439. doi: 10.1111/j.0013-9580.2005.33604.x

*Lespinet, V., Bresson, C., N'Kaoua, B., Rougier, A., & Claverie, B. (2002). Effect of age of onset of temporal lobe epilepsy on the severity and the nature of preoperative memory deficits. *Neuropsychologia, 40*(9), 1591-1600. doi: 10.1016/s0028-3932(02)00012-x

Lezak, M. D., Howieson, D., Bigler, E., & Tranel, D. (2012). Neuropsychological assessment (5th ed.). New York: Oxford University Press.

Lipsey, M.W. and Wilson, D.B. (2001) *Practical Meta-analysis*. Thousand Oaks, CA: Sage

*Loring, D. W., Hermann, B. P., Lee, G. P., Drane, D. L., & Meador, B. J. (2000). The Memory Assessment Scales and lateralized temporal lobe epilepsy. *Journal Of Clinical Psychology, 56*(4), 563-570. doi: 10.1002/(sici)1097-4679(200004)56:4<563::aid-jclp9>3.0.co;2-k

Loring, D. W., Lowenstein, D. H., Barbaro, N. M., Fureman, B. E., Odenkirchen, J., Jacobs, M. P., . . . Gaillard, W. D. (2011). Common data elements in epilepsy research: development and implementation of the NINDS epilepsy CDE project. *Epilepsia, 52*(6), 1186-1191.

*Lutz, M. T., Clusmann, H., Elger, C. E., Schramm, J., & Helmstaedter, C. (2004). Neuropsychological outcome after selective amygdalohippocampectomy with transsylvian versus transcortical approach: A randomized prospective clinical trial of surgery for temporal lobe epilepsy. *Epilepsia, 45*(7), 809-816. doi: 10.1111/j.0013-9580.2004.54003.x

Majdan, A., Sziklas, V., & JonesGotman, M. (1996). Performance of healthy subjects and patients with resection from the anterior temporal lobe on matched tests of verbal and visuoperceptual learning. *Journal of Clinical and Experimental Neuropsychology, 18*(3), 416-430. doi:10.1080/01688639608408998

*Malikova, H., Kramska, L., Liscak, R., Vojtech, Z., Prochazka, T., Mareckova, I., . . . Druga, R. (2012). Stereotactic radiofrequency amygdalohippocampectomy for the treatment of temporal lobe epilepsy: Do good neuropsychological and seizure outcomes correlate with hippocampal volume reduction? *Epilepsy Research, 102*(1-2), 34-44.

*Malikova, H., Kramska, L., Vojtech, Z., Liscak, R., Sroubek, J., Lukavsky, J., & Druga, R. (2014). Different Surgical Approaches for Mesial Temporal Epilepsy: Resection Extent, Seizure, and Neuropsychological Outcomes. *Stereotactic And Functional Neurosurgery, 92*(6), 372-380. doi: 10.1159/000366003

*Mantoan, M. A. S., Caboclo, L., Guilhoto, L., Lin, K., Noffs, M. H. D., Tudesco, I. D. S., . . . Yacubian, E. M. T. (2009). Correlation between memory, proton magnetic resonance spectroscopy, and interictal epileptiform discharges in temporal lobe epilepsy related to mesial temporal sclerosis. *Epilepsy & Behavior, 16*(3), 447-453. doi: 10.1016/j.yebeh.2009.08.032

*Marquez De La Plata, C., Lacritz, L. H., Mitschke, R., Van Ness, P., Agostini, M., Diaz-Arrastia, R., & Cullum, C. M. (2009). Detecting differential memory performance among Spanish-speaking patients with temporal lobe epilepsy. *NeuroRehabilitation, 24*(1), 87-93. doi: 10.3233/NRE-2009-0457

*Martin, P., Maestu, F., & Sola, R. G. (2002). Effects of surgical treatment on intellectual performance and memory in a Spanish sample of drug-resistant partial onset-temporal lobe epilepsy patients. *Seizure-European Journal of Epilepsy, 11*(3), 151-156. doi: 10.1053/seiz.2001.0618

*Martin, R. C., Hugg, J. W., Roth, D. L., Bilir, E., Gilliam, F. G., Faught, E., & Kuzniecky, R. I. (1999). MRI extrahippocampal volumes and visual memory: Correlations independent of MRI hippocampal volumes in temporal lobe epilepsy patients. *Journal of the International Neuropsychological Society, 5*(6), 540-548.

*Martin, R. C., Sawrie, S., Hugg, J., Gilliam, F., Faught, E., & Kuzniecky, R. (1999). Cognitive correlates of H-1 MRSI-detected hippocampal abnormalities in temporal lobe epilepsy. *Neurology, 53*(9), 2052-2058.

Martinez, A., Di Russo, F., Anllo-Vento, L., & Hillyard, S. A. (2001). Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clinical Neurophysiology, 112*(11), 1980-1998.

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

*McConley, R., Martin, R., Palmer, C. A., Kuznieck, R., Knowlton, R., & Faught, E. (2008). Rey Osterrieth complex figure test spatial and figural scoring: Relations to seizure focus and hippocampal pathology in patients with temporal lobe epilepsy. *Epilepsy & Behavior, 13*(1), 174-177. doi: 10.1016/j.yebeh.2008.03.003

*McCormick, C., Quraan, M., Cohn, M., Valiante, T. A., & McAndrews, M. P. (2013). Default mode network connectivity indicates episodic memory capacity in mesial temporal lobe epilepsy. *Epilepsia, 54*(5), 809-818.

*McDonald, C. R., Ahmadi, M. E., Hagler, D. J., Tecoma, E. S., Iragui, V. J., Gharapetian, L., . . . Halgren, E. (2008). Diffusion tensor imaging correlates of memory and language impairments in temporal lobe epilepsy. *Neurology, 71*(23), 1869-1876. doi: 10.1212/01.wnl.0000327824.05348.3b

*Moore, P. M., & Baker, G. A. (1996). Validation of the Wechsler memory scale-revised in a sample of people with intractable temporal lobe epilepsy. *Epilepsia, 37*(12), 1215-1220. doi: 10.1111/j.1528-1157.1996.tb00556.x

*Moran, M., Seidenberg, M., Sabsevitz, D., & Swanson, S. (2005). The acquisition of face and person identity information following anterior temporal lobectomy. *Journal of the International Neuropsychological Society, 11*(3), 237-248. doi: 10.1017/s1355617705050290

*Morino, M., Ichinose, T., Uda, T., Kondo, K., Ohfuji, S., & Ohata, K. (2009). Memory outcome following transsylvian selective amygdalohippocampectomy in 62 patients with hippocampal sclerosis: Clinical article. *Journal Of Neurosurgery, 110*(6), 1164-1169.

*Morino, M., Uda, T., Naito, K., Yoshimura, M., Ishibashi, K., Goto, T., . . . Hara, M. (2006). Comparison of neuropsychological outcomes after selective amygdalohippocampectomy versus anterior temporal lobectomy. *Epilepsy & Behavior, 9*(1), 95-100. doi: 10.1016/j.yebeh.2006.04.017

*Morris, R. G., Abrahams, S., Baddeley, A. D., & Polkey, C. E. (1995). Doors and People: Visual and verbal memory after unilateral temporal lobectomy. *Neuropsychology, 9*(4), 464-469.

*Morris, R. G., Abrahams, S., & Polkey, C. E. (1995). Recognition memory for words and faces following unilateral temporal lobectomy. *The British Journal Of Clinical Psychology / The British Psychological Society, 34 (Pt 4)*, 571-576.

*Moser, D. J., Bauer, R. M., Gilmore, R. L., Dede, D. E., Fennell, E. B., Algina, J. J., . . . Cohen, R. A. (2000). Electroencephalographic, volumetric, and neuropsychological

indicators of seizure focus lateralization in temporal lobe epilepsy. *Archives of Neurology, 57*(5), 707-712. doi: 10.1001/archneur.57.5.707

*Narayanan, J., Duncan, R., Greene, J., Leach, J. P., Razvi, S., McLean, J., & Evans, J. J. (2012). Accelerated long-term forgetting in temporal lobe epilepsy: Verbal, nonverbal and autobiographical memory. *Epilepsy & Behavior, 25*(4), 622-630. doi: 10.1016/j.yebeh.2012.06.038

*Naugle, R. I., Chelune, G. J., Cheek, R., Luders, H., & Awad, I. A. (1993). Detection of changes in material-specific memory following temporal lobectomy using the Wechsler Memory Scale-Revised. *Archives of Clinical Neuropsychology, 8*(5), 381-395. doi:10.1016/0887-6177(93)90002-i

*Naugle, R. I. (1994). Recognition Memory for Words and Faces Before and After Temporal Lobectomy (pp. 373-381).

*Neves, R. S. D., Tudesco, I. D. S., Jardim, A. P., Caboclo, L., Lancellotti, C., Ferrari-Marinho, T., . . . Yacubian, E. M. T. (2012). Granule cell dispersion is associated with memory impairment in right mesial temporal lobe epilepsy. *Seizure-European Journal of Epilepsy, 21*(9), 685-690. doi: 10.1016/j.seizure.2012.07.008

Novelly, R. A., Augustine, E. A., Mattson, R. H., Glaser, G. H., Williamson, P. D., Spencer, D. D., & Spencer, S. S. (1984). Selective memory improvement and impairment in temporal lobectomy for epilepsy. *Annals of Neurology, 15*(1), 64-67. doi:10.1002/ana.410150112

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map* (Vol. 3): Clarendon Press Oxford.

*Ogden-Epker, M., & Cullum, C. M. (2001). Quantitative and qualitative interpretation of neuropsychological data in the assessment of temporal lobectomy candidates. *Clinical Neuropsychologist, 15*(2), 183-195. doi: 10.1076/clin.15.2.183.1900

Orwin, R. G. (1983). A fail-safe N for effect size. *Journal of Educational Statistics, 8*, 157–159.

*Pacagnella, D., Lopes, T. M., Morita, M. E., Yasuda, C. L., Cappabianco, F. A. M., Bergo, F., . . . Cendes, F. (2014). Memory impairment is not necessarily related to seizure frequency in mesial temporal lobe epilepsy with hippocampal sclerosis. *Epilepsia, 55*(8), 1197-1204. doi: 10.1111/epi.12691

*Paradiso, S., Hermann, B. P., Blumer, D., Davies, K., & Robinson, R. G. (2001). Impact of depressed mood on neuropsychological status in temporal lobe epilepsy. *Journal of Neurology Neurosurgery and Psychiatry, 70*(2), 180-185. doi: 10.1136/jnnp.70.2.180

*Parente, A., Manfredi, V., Villani, F., Franceschetti, S., & Giovagnoli, A. R. (2013). Investigating higher-order cognitive functions in temporal lobe epilepsy: Cognitive estimation. *Epilepsy & Behavior, 29*(2), 330-336. doi: 10.1016/j.yebeh.2013.07.031

*Pauli, E., Eberhardt, K. W., Schäfer, I., Tomandl, B., Huk, W. J., & Stefan, H. (2000). Chemical shift imaging spectroscopy and memory function in temporal lobe epilepsy. *Epilepsia, 41*(3), 282-289.

*Pegna, A. J., Caldara-Schnetzer, A. S., Perrig, S. H., Lazeyras, F., Khateb, A., Landis, T., & Seeck, M. (2002). Is the right amygdala involved in visuospatial memory? Evidence from MRI volumetric measures. *European Neurology, 47*(3), 148-155. doi: 10.1159/000047973

*Pereira, F. R. S., Alessio, A., Sercheli, M. S., Pedro, T., Bilevicius, E., Rondina, J. M., . . . Cendes, F. (2010). Asymmetrical hippocampal connectivity in mesial temporal lobe epilepsy: evidence from resting state fMRI. *BMC Neuroscience, 11*. doi:10.1186/1471-2202-11-66

*Phillips, N. A., & McGlone, J. (1995). Grouped data do not tell the whole story: individual analysis of cognitive change after temporal lobectomy. *Journal of Clinical and Experimental Neuropsychology, 17*(5), 713-724.

Pigott, S., & Milner, B. (1993). Memory for different aspects of complex visual scenes after unilateral temporal- or frontal-lobe resection. *Neuropsychologia, 31*(1), 1-15.

*Piguet, O., Saling, M. M., Oshea, M. F., Berkovic, S. F., & Bladin, P. F. (1994). Rey figure distortions reflect nonverbal recall differences between right and left foci in unilateral temporal lobe epilepsy. *Archives of Clinical Neuropsychology, 9*(5), 451-460. doi: 10.1016/0887-6177(94)90007-8

Postma, A., Kessels, R. P., & van Asselen, M. (2008). How the brain remembers and forgets where things are: The neurocognition of object–location memory. *Neuroscience & Biobehavioral Reviews, 32*(8), 1339-1345.

*Powell, H., Richardson, M. P., Symms, M. R., Boulby, P. A., Thompson, P. J., Duncan, J. S., & Koepp, M. J. (2007). Reorganization of Verbal and Nonverbal Memory in Temporal Lobe Epilepsy Due to Unilateral Hippocampal Sclerosis. *Epilepsia, 48*(8), 1512-1525. doi: http://dx.doi.org/10.1111/j.1528-1167.2007.01053.x

*Powell, H. W. R., Richardson, M. P., Symms, M. R., Boulby, P. A., Thompson, P. J., Duncan, J. S., & Koepp, M. J. (2008). Preoperative fMRI predicts memory decline following anterior temporal lobe resection. *Journal of Neurology Neurosurgery and Psychiatry, 79*(6), 686-693. doi: 10.1136/jnnp.2007.115139

*Raspall, T., Doñate, M., Boget, T., Carreño, M., Donaire, A., Agudo, R., . . . Salamero, M. (2005). Neuropsychological tests with lateralizing value in patients with temporal lobe epilepsy: Reconsidering material-specific theory. *Seizure, 14*(8), 569-576. doi: 10.1016/j.seizure.2005.09.007

*Rausch, R., & Ary, C. M. (1990). Supraspan learning in patients with unilateral anterior temporal lobe resections. *Neuropsychologia, 28*(2), 111-120.

*Rausch, R., Boone, K., & Ary, C. M. (1991). Right-Hemisphere Language Dominance in Temporal Lobe Epilepsy: Clinical and Neuropsychological Correlates. *Journal of Clinical and Experimental Neuropsychology, 13*(2), 217-231.

*Rausch, R., & Babb, T. L. (1993). Hippocampal neuron loss and memory scores before and after temporal lobe surgery for epilepsy. *Archives of Neurology, 50*(8), 812-817.

Rausch, R., Kraemer, S., Pietras, C. J., Le, M., Vickrey, B. G., & Passaro, E. A. (2003). Early and late cognitive changes following temporal lobe surgery for epilepsy. *Neurology, 60*(6), 951-959. Retrieved from <Go to ISI>://WOS:000182948600013

Rey, A. (1941). L'examen psychologique dans les cas d'encéphalopathie traumatique. *Archives de Psychologie, 28*, 286-340.

Rey, A. (1964). *L'examen clinique in psychologie.* Paris: Press Universiraire de France; 1964.

Rey, A. (1968). *Epreuves mnesiques et d'apprentissage.* Neuchatel, Delachaux & Niestle.

Rey, A. (1999). *Teste de cópia e de reproducao de memória de figuras geométricas complexas: manual*. Casa do Psicólogo, Sao Paulo.

*Rougier, M. B., Guillem, F., Nkaoua, B., Rougier, A., Lerebeller, M. J., & Claverie, B. (1994). Memory-induced subcortical modulation of early visual evoked activity in temporal lobectomy patients. *Neuro-ophthalmology, 14*(2), 103-111. doi: 10.3109/01658109409024033

*Samson, S., & Zatorre, R. J. (1992). Learning and retention of melodic and verbal information after unilateral temporal lobectomy. *Neuropsychologia, 30*(9), 815-826.

*Sass, K. J., Sass, A., Westerveld, M., Lencz, T., Rosewater, K. M., Novelly, R. A., . . . Spencer, D. D. (1992). Russell's adaptation of the Wechsler Memory Scale as an index of hippocampal pathology. *Journal of Epilepsy, 5*(1), 24-30. doi: 10.1016/s0896-6974(05)80017-9

*Sawrie, S. M., Martin, R. C., Gilliam, F. G., Roth, D. L., Faught, E., & Kuzniecky, R. (1998). Contribution of neuropsychological data to the prediction of temporal lobe epilepsy surgery outcome. *Epilepsia, 39*(3), 319-325. doi: 10.1111/j.1528-1157.1998.tb01380.x

*Seidenberg, M., Hermann, B., Wyler, A. R., Davies, K., Dohan, F. C., & Leveroni, C. (1998). Neuropsychological outcome following anterior temporal lobectomy in patients with and without the syndrome of mesial temporal lobe epilepsy. *Neuropsychology, 12*(2), 303-316. doi: 10.1037/0894-4105.12.2.303

*Selwa, L. M., Berent, S., Giordani, B., Henry, T. R., Buchtel, H. A., & Ross, D. A. (1994). Serial cognitive testing in temporal lobe epilepsy: longitudinal changes with medical and surgical therapies. *Epilepsia, 35*(4), 743-749.

Sherman, E. M. S., Wiebe, S., Fay-McClymont, T. B., Tellez-Zenteno, J., Metcalfe, A., Hernandez-Ronquillo, L., . . . Jette, N. (2011). Neuropsychological outcomes after epilepsy surgery: Systematic review and pooled estimates. *Epilepsia, 52*(5), 857-869. doi:10.1111/j.1528-1167.2011.03022.x

*Shin, M. S., Lee, S., Seol, S. H., Lim, Y. J., Park, E. H., Sergeant, J. A., & Chung, C. (2009). Changes in neuropsychological functioning following temporal lobectomy in patients with temporal lobe epilepsy. *Neurological Research, 31*(7), 692-701. doi: 10.1179/174313209x389848

Shulman, G. L., Pope, D. L. W., Astafiev, S. V., McAvoy, M. P., Snyder, A. Z., & Corbetta, M. (2010). Right Hemisphere Dominance during Spatial Selective Attention and Target Detection Occurs Outside the Dorsal Frontoparietal Network. *Journal of Neuroscience, 30*(10), 3640-3651. doi:10.1523/jneurosci.4085-09.2010

*Sidhu, M. K., Stretton, J., Winston, G. P., Symms, M., Thompson, P. J., Koepp, M. J., & Duncan, J. S. (2015). Factors affecting reorganisation of memory encoding networks in temporal lobe epilepsy. *Epilepsy research, 110*, 1-9. doi: 10.1016/j.eplepsyres.2014.11.001

Smith, M. L., Bigel, M., & Miller, L. A. (2011). Visual paired-associate learning: In search of material-specific effects in adult patients who have undergone temporal lobectomy. *Epilepsy and Behavior, 20*(2), 326-330.

*Soble, J. R., Eichstaedt, K. E., Waseem, H., Mattingly, M. L., Benbadis, S. R., Bozorg, A. M., . . . Schoenberg, M. R. (2014). Clinical utility of the Wechsler Memory Scale-Fourth Edition (WMS-IV) in predicting laterality of temporal lobe epilepsy among surgical candidates. *Epilepsy & Behavior, 41*, 232-237. doi:10.1016/j.yebeh.2014.10.014

*Sperling, M. R., Oconnor, M. J., Saykin, A. J., & Plummer, C. (1996). Temporal lobectomy for refractory epilepsy. *Jama-Journal of the American Medical Association, 276*(6), 470-475. doi: 10.1001/jama.276.6.470

*Spiers, H. J., Burgess, N., Maguire, E. A., Baxendale, S. A., Hartley, T., Thompson, P. J., & O'Keefe, J. (2001). Unilateral temporal lobectomy patients show lateralized topographical and episodic memory deficits in a virtual town. *Brain, 124*, 2476-2489. doi: 10.1093/brain/124.12.2476

Springer, J. A., Binder, J. R., Hammeke, T. A., Swanson, S. J., Frost, J. A., Bellgowan, P. S. F., . . . Mueller, W. M. (1999). Language dominance in neurologically normal and epilepsy subjects - A functional MRI study. *Brain, 122*, 2033-2045. doi:10.1093/brain/122.11.2033

*St-Laurent, M., McCormick, C., Cohn, M., Misic, B., Giannoylis, I., & McAndrews, M. (2014). Using multivariate data reduction to predict postsurgery memory decline in patients with mesial temporal lobe epilepsy. *Epilepsy & Behavior, 31*, 220-227. doi: http://dx.doi.org/10.1016/j.yebeh.2013.09.043

Strauss, E., Sherman, E. M., & Spreen, O. (2006). *A compendium of neuropsychological tests: Administration, norms, and commentary*: Oxford University Press, USA.

Suthana, N. A., Ekstrom, A. D., Moshirvaziri, S., Knowlton, B., & Bookheimer, S. Y. (2009). Human Hippocampal CA1 Involvement during Allocentric Encoding of Spatial Information. *Journal of Neuroscience, 29*(34), 10512-10519. doi:10.1523/jneurosci.0621-09.2009

*Tanriverdi, T., Dudley, R. W. R., Hasan, A., Al Jishi, A., Al Hinai, Q., Poulin, N., . . . Olivier, A. (2010). Memory outcome after temporal lobe epilepsy surgery: corticoamygdalohippocampectomy versus selective amygdalohippocampectomy. *Journal Of Neurosurgery, 113*(6), 1164-1175. doi: 10.3171/2009.10.jns09677

*Testa, S. M., Schefft, B. K., Privatera, M. D., & Yeh, H. S. (2004). Warrington's recognition memory for faces: interpretive strategy and diagnostic utility in temporal lobe epilepsy. *Epilepsy & Behavior, 5*(2), 236-243. doi: 10.1016/j.yebeh.2003.12.011

*Trenerry, M. R., Jack, C. R., Ivnik, R. J., Sharbrough, F. W., Cascino, G. D., Hirschorn, K. A., . . . Meyer, F. B. (1993). MRI hippocampal volumes and memory function before and after temporal lobectomy. *Neurology, 43*(9), 1800-1805.

*Tudesco, I. D. S., Vaz, L. J., Mantoan, M. A. S., Belzunces, E., Noffs, M. H., Caboclo, L., . . . Bueno, O. F. A. (2010). Assessment of working memory in patients with mesial temporal lobe epilepsy associated with unilateral hippocampal sclerosis. *Epilepsy & Behavior, 18*(3), 223-228. doi: 10.1016/j.yebeh.2010.04.021

van der Ham, I. J. M., Postma, A., & Laeng, B. (2014). Lateralized perception: The role of attention in spatial relation processing. *Neuroscience and Biobehavioral Reviews, 45*, 142-148. doi:10.1016/j.neubiorev.2014.05.006

Vaz, S. A. M. (2004). Nonverbal memory functioning following right anterior temporal lobectomy: a meta-analytic review. *Seizure-European Journal of Epilepsy, 13*(7), 446-452. doi:10.1016/j.seizure.2003.12.004

Viechtbauer W (2005). Bias and Efficiency of Meta-Analytic Variance Estimators in the Random-Effects Model. *Journal of Educational and Behavioral Statistics, 30*(3), 261–293.

*Vingerhoets, G., Miatton, M., Vonck, K., Seurinck, R., & Boon, P. (2006). Memory performance during the intracarotid amobarbital procedure and neuropsychological assessment in medial temporal lobe epilepsy: The limits of material specificity. *Epilepsy & Behavior, 8*(2), 422-428. doi: 10.1016/j.yebeh.2005.11.013

*Wagner, K., Uherek, M., Horstmann, S., Kadish, N. E., Wisniewski, I., Mayer, H., . . . Schulze-Bonhage, A. (2013). Memory outcome after hippocampus sparing resections in the temporal lobe. *Journal of Neurology Neurosurgery and Psychiatry, 84*(6), 630-636. doi: 10.1136/jnnp-2012-304052

*Wang, W. H., Liou, H. H., Chen, C. C., Chiu, M. J., Chen, T. F., Cheng, T. W., & Hua, M. S. (2011). Neuropsychological performance and seizure-related risk factors in patients with temporal lobe epilepsy: A retrospective cross-sectional study. *Epilepsy & Behavior, 22*(4), 728-734. doi: 10.1016/j.yebeh.2011.08.038

*Wechsler, D. (1997). *Wechsler memory scale (WMS-III)*: Psychological Corporation.

*Wechsler, D. (2009). Wechsler Memory Scale-(WMS-IV). *New York: The Psychological Corporation*.

*Weniger, G., Ruhleder, M., Lange, C., & Irle, E. (2012). Impaired egocentric memory and reduced somatosensory cortex size in temporal lobe epilepsy with hippocampal sclerosis. *Behavioural Brain Research, 227*(1), 116-124. doi: 10.1016/j.bbr.2011.10.043

*Wilde, N., Strauss, E., Chelune, G. J., Loring, D. W., Martin, R. C., Hermann, B. P., . . . Hunter, M. (2001). WMS-III performance in patients with temporal lobe epilepsy: group differences and individual classification. *Journal of the International Neuropsychological Society, 7*(7), 881-891.

*Wilkinson, H., Holdstock, J. S., Baker, G., Herbert, A., Clague, F., & Downes, J. J. (2012). Long-term accelerated forgetting of verbal and non-verbal information in temporal lobe epilepsy. *Cortex, 48*(3), 317-332. doi: 10.1016/j.cortex.2011.01.002

Appendix

Glossary of terms for tables

Tests:

7/24_SLT:	7/24 Spatial Learning Test
AFLT:	Aggie Figure Learning Test
AustMaze:	Austin Maze
BFLT-E:	Biber Figure Learning Test - Extended
BLT:	Brown Location Test
BVMT-R:	Brief Visuospatial Memory Test - Revised
BVRT:	Benton Visual Retention Test
DCS-I:	Diagnostikum für Cerebralschädigung
DCS-M:	Diagnostikum für Cerebralschädigung (Modified)
DCS-R:	Diagnostikum für Cerebralschädigung (Revised)
Designs_WMS-IV:	Designs - WMS-IV
DL_AMIPB:	Design Learning - Adult Memory and Information Processing Battery
Doors_D&P:	Doors test - Doors & People test
Fac_ALSTER:	Alsterdorfer Faces Test
Fac_DADE:	Dade Face Learning Test
Fac_DENMAN:	Denman Facial Recognition Test
FacDsc_FAB:	Facial Discrimination subtest (adapted from subtest 1 of the Florida Affect Battery)
Faces_WMS-III:	Faces - WMS-III
FacRMT_WARR:	Warrington Recognition Memory Test for Faces
FamPic_WMS-III:	Family Pictures - WMS-III
FL_AMIPB:	Figure Learning - Adult Memory and Information Processing Battery
GHFMT:	Graduate Hospital Facial Memory Test
LGT-3:	Lern- und Gedächtnistest-3
NVM_FACT:	Nonverbal Memory Factor (VisPA_WMS-R: VR-II_WMS-III: Faces_WMS-III: FamPic_WMS-III)
NVSRT:	Nonverbal Selective Reminding Test
PMQ_WMS-I:	Performance Memory Quotient
RCF:	Rey Complex Figure test
RCF/AFLT_Dl_Composite:	Rey Complex Figure test and/or Aggie Figure Learning Test (Delayed Measures)
RCF/VRII_WMS-R:	average of Rey Complex Figure test (Delay) and VR-II
ReccFLT:	Recurring Figures Learning Test
Route_RBMT:	Remembering a new route - Rivermead Behavioural memory Test
RouteLT:	Route Learning Test
RULIT:	Ruff-Light Trail Learning Test
RVDLT:	Rey Visual Design Learning Test
RVDT:	Rey Visual Design Test
Shapes_D&P:	Shapes test - Doors & People test
TopogRMT_CAM:	Topographical Recognition Memory Test - Camden Memory Test battery
VDI_WMS-III:	Visual Delayed memory Index (Faces II: Family Pictures II)
VDI_WMS-III_SP:	Visual Delayed memory Index - Standardization Protocol: (Dot Location II: Visual Reproduction II: Faces II: Design Location II: Family Pictures II: Picture Naming II)
VDLT:	Visual Design Learning Test
VGT:	Visual Gestalt Test
VII_WMS-III:	Visual Immediate memory Index (Faces I: Family Pictures I)
VII_WMS-III_SP:	Visual Immediate memory Index - Standardization Protocol (Dot Location I: Visual Reproduction I: Faces I: Design Location: Family Pictures I: Picture Naming):
VisPA_WMS-R:	Visual Paired Associates - WMS-R
VM_FACT:	composite measure made up of Warrington Faces (total score), Rey Visual Design Learning Test (Sum of Learning Trials 1 to 5), and Spatial Conditional

	Associative Learning Task (total trials to criterion)
	VM_WMS-R: Visual Memory quotient (Figural Memory: Visual Paired Associates I: Visual Reproduction I)
VMI_MAS:	composite measure from VR_MAS and VRecog_MAS
VMI_WMS-IV:	Visual Memory Index - WMS-IV
VMI_WMS-IV:	Visual Memory Index (Designs I: Designs II: Visual Reproduction I: Visual Reproduction II)
VR_MAS:	Visual Reproduction - Memory Assessment Scale version
VR_WMS-I:	Visual Reproduction - WMS-I
VR_WMS-I_RUS:	Visual Reproduction - WMS-I (Russell Revision)
VR_WMS-III:	Visual Reproduction - WMS-III
VR_WMS-R:	Visual Reproduction - WMS-R
VRecog_MAS:	Visual Recognition test - Memory Assessment Scale
VSLT:	Visual Spatial Learning Test
VSRT:	Visual Selective Reminding Test (precursor test to version in TOMAL-2 battery).

Test measures:

Im:	Immediate
Dl:	Delayed
Pc:	Percent Retention
Lrn:	Learning
Cap:	Capacity
Rcg:	Recognition
Cor:	Correct
Er:	Error
CLTR:	Continuous Long Term Retrieval
Rep:	Reproduction
Lt:	Long Term
Tr6:	Trial 6
Dscr:	Discrimination

TOTAL: meta-analysis of entire category.

Statistics:

k:	number of studies
N:	number of patients
d:	pooled estimate of effect size (Cohen's *d*)
CI_lo:	lower bound of 95% confidence interval
CI_up:	upper bound of 95% confidence interval
z:	*z*-test for significance of effect size
p	*p*-value for *z*-test
Nfs:	fail-safe N
Q:	test for heterogeneity
Q_p:	significance of test for heterogeneity
I^2:	percent of total variability explained by heterogeneity.

Supplementary Table 1. Details of studies included in the meta-analysis

First author	Year	*N*-pre L \ R	*N*-post L \ R	Age L \ R	Epilepsy onset L \ R	Surgery	Tests
Abrahams	1999	25 \ 22		30.6 \ 32.0	5.9 \ 7.8		RCF
Adda	2008	22 \ 26		37.2 \ 38.2	10.5 \ 11.5		RCF
Akanuma	2003	51 \ 47		29.2 \ 32.4	8.2 \ 11.7		RCF
Alessio	2006	20 \ 19					VM_WMS-R
Alessio	2013	8 \ 8		37.6 \ 40.3	5.4 \ 6.5		VM_WMS-R
Araujo	2009	32 \ 20		39.1 \ 40.1			VR_WMS-III; RULIT
Baker	2003	63 \ 36		34.5 \ 32.6	14.4 \ 17.6		Faces_WMS-III; FamPic_WMS-III; VII_WMS-III; VDI_WMS-III
Bandt	2013	6 \ 13	6 \ 13	48.5 \ 39.6	13.5 \ 12.8	tmtg-SAH	VR_WMS-III
Barnett	2015	12 \ 14		35.9 \ 36.2	19 \ 20.9		VM_FACT
Barr	1997a~	57 \ 48		31.3 \ 33	13.2 \ 15.8		Fac_DENMAN; VM_WMS-R
Barr	1997a~	33 \ 32					7/24_SLT
Barr	1997b	47 \ 35		32.1 \ 34.4	13.2 \ 15.7		VR_WMS-R; VisPA_WMS-R; VM_WMS-R
Barr	1997c~	187 \ 168		32.3 \ 32.4	11.8 \ 13.5		RCF
Barr	1997c~	84 \ 82		31.8 \ 32.4	13.2 \ 14.5		VR_WMS-I_RUS
Barr	1997c~	277 \ 256		31.6 \ 32.2	12.4 \ 13.6		VR_WMS-R
Barr	2004	25 \ 22		35.4 \ 34.7	26.5 \ 18.4		BVMT-R
Baxendale	1998	42 \ 27		29.1 \ 29.7	12.1 \ 9.8		DL_AMIPB; FL_AMIPB
Baxendale	2000	9 \ 8	9 \ 8	31.1 \ 28.7	14.1 \ 14.2	ATL	FL_AMIPB
Baxendale	2008	132 \ 105	132 \ 105	31.1 \ 32.7	9.4 \ 9.7	ATL	DL_AMIPB
Baxendale	2012	33 \ 37	33 \ 37	33.1 \ 34.5	9.6 \ 14.6	ATL	DL_AMIPB
Baxendale	1997	28 \ 24	28 \ 24			ATL	FacRMT_WARR
Bell	2005	22 \ 20		34 \ 40	13.9 \ 13.1		VSRT
Bengner	2006	19 \ 30		41 \ 40	23 \ 23^		Fac_ALSTER
Bianchin	2013	105 \ 93	105 \ 93			ATL	VR_WMS-R; RCF; RVDLT
Bigras	2013	25 \ 19		35.9 \ 42.3	17.7 \ 25.47		FacRMT_WARR
Binder	2008~	58 \ 59	58 \ 59	34.4 \ 40.3#	15.1 \ 14.9#	ATL	7/24_SLT
Binder	2008~	59 \ 62	59 \ 62	34.4 \ 40.3#	15.1 \ 14.9#	ATL	VR_WMS-I

Bjornaes	2005	41 \ 50	41 \ 50	33.4 \ 31.2	14.7 \ 11.4	ATL-H+ or ATL-H-	BVRT
Blake	2000	9 \ 5		36.7 \ 32.3	14.3 \ 9.8		VR_WMS-R; TopogRMT_CAM
Bonelli	2010	41 \ 31					DL_AMIPB
Breier	1996	24 \ 30		32.8 \ 34.6	12.1 \ 13.5		RCF
Breier	1997	22 \ 28		36.6 \ 34.3	16.9 \ 13.6		VR_WMS-R
Brown	2010		9 \ 9			ATL	BLT
Busch	2011	110 \ 101	110 \ 101	34.9 \ 35.8	15.4 \ 16.1	ATL	VDI_WMS-III
Carvajal	2009		20 \ 23	35.4 \ 35	17 \ 18.1	ATL	VR_WMS-R; FacDsc_FAB
Castro	2013	43 \ 44		37.6 \ 37.5	9.4 \ 9.5		RCF; RVDLT
Chelune	1991	23 \ 19	23 \ 19	30.3 \ 28.3	12.1 \ 12.2	ATL	VR_WMS-R; VM_WMS-R
Chelune	1993	47 \ 49	47 \ 49	29.4 \ 29.5	12.5 \ 13.8	ATL	VM_WMS-R
Chiaravalloti	2004	10 \ 16	10 \ 16	36.3 \ 38.9	5.5 \ 9.13	ATL	Faces_WMS-III; GHFMT
da Costa Neves	2012	27 \ 27		36.7 \ 38.5	13.2 \ 17.2		VR_WMS-R; RCF
Dade	2001		19 \ 17	33.5 \ 35.9		SAH or CAH	FacLT_DADE
Dige	2001	12 \ 12		29.4 \ 38.1	9.6 \ 18.3		DCS-M
Dodrill	2007	79 \ 47					RCF
Doss	2000~		11 \ 19	34.6 \ 35.5	16.1 \ 11.8	ATL	VII_WMS-III; VDI_WMS-III
Doss	2000~		22 \ 11	32.3 \ 31.2	14.6 \ 7.3^	ATL	VII_WMS-III_SP; VDI_WMS-III_SP
Doss	2004		56 \ 51	32.7 \ 34.3	13.8 \ 13.9	ATL	Faces_WMS-III; FamPic_WMS-III; VII_WMS-III; VDI_WMS-III
Doucet	2013	8 \ 8					Faces_WMS-III
Doucet	2015	16 \ 16	16 \ 16	43 \ 43	25 \ 21	ATL w partial AH+	Faces_WMS-III
Dulay	2009~	24 \ 37	24 \ 37	28.8 \ 31.3#	13.5 \ 14.8#	ATL	BVRT
Dulay	2009~	15 \ 15	15 \ 15	28.8 \ 31.3#	13.5 \ 14.8#	ATL	FacRMT_WARR
Dulay	2009~	34 \ 44	34 \ 44	28.8 \ 31.3#	13.5 \ 14.8#	ATL	NVSRT
Dulay	2009~	17 \ 18	17 \ 18	28.8 \ 31.3#	13.5 \ 14.8#	ATL	RCF
Dulay	2002	36 \ 21		38 \ 37	22.5 \ 20.9		BVRT; FacRMT_WARR; FamPic_WMS-III
Dupont	2010~	10 \ 12		40.0 \ 37.4#	11.2 \ 16.1#		AFLT
Dupont	2010~	10 \ 14		40.0 \ 37.4#	11.2 \ 16.1#		RCF
Dupont	2010~	10 \ 15	9 \ 15	40.0 \ 37.4#	11.2 \ 16.1#	ATL	RCF/AFLT_Composite

Focke	2008~	40 \ 28					DL_AMIPB
Focke	2008~	37 \ 35					FacRMT_WARR
Focke	2008~	39 \ 32					FL_AMIPB
Frank	2003		20 \ 19	33.2 \ 35.7	5.2 \ 8.8	SAH or anteromedial ATL	RCF
Gargaro	2013	203 \ 191	203 \ 191	36.9 \ 37.0	9.1 \ 9.3	ATL+AH	VR_WMS-R; RCF; RVDLT
Giovagnoli	2007	12 \ 12	12 \ 12	34.3 \ 31.7	27.9 \ 21.4	Tailored lesionectomy	RCF; VSRT
Gleissner	2002	66 \ 74	66 \ 74	32.8 \ 31.7	11.1 \ 11.2	SAH	DCS-R
Glogau	2004	15 \ 18		33.7 \ 39.9	15.0 \ 15.7^		DCS-R
Glosser	2002	25 \ 46		32.8 \ 35.2	12.3 \ 14.7		BFLT-E
Goldstein	1992		29 \ 17	25.0 \ 26.9	7.0 \ 11.4	ATL or SAH	RCF
Goldstein	1993	22 \ 20	22 \ 20	26.9 \ 30.6	6.7 \ 12.3	ATL or SAH	RCF; BVRT
Grammaldo	2006	36 \ 37		35.9 \ 36.1	14 \ 16.1		RCF
Grammaldo	2009	35 \ 47	35 \ 47			ATL	RCF
Griffith	2000	27 \ 33	27 \ 33	34 \ 31.3	13.23 \ 13.72	ATL	VR_WMS-I
Hanoglu	2004	11 \ 11	11 \ 11	26.2 \ 28.6	8.0 \ 13.9	SAH	VR_WMS-I
Harvey	2008	80 \ 81	80 \ 81	33.9 \ 36.1	13.3 \ 14.5	ATL	VII_WMS-III; VDI_WMS-III
Helmstaedter	1992	26 \ 26		11.6 \ 14.9	27 \ 29.5		DCS-R
Helmstaedter	1995	30 \ 30		27 \ 30.7	12.4 \ 14.6		BVRT
Helmstaedter	2000	24 \ 21			13 \ 13		BVRT; DCS-R
Helmstaedter	2004a	14 \ 20	14 \ 20			ATL	DCS-R
Helmstaedter	2004b	42 \ 37		33.95 \ 36.11	13.2 \ 13.1		DCS-R
Helmstaedter	2008	51 \ 46	51 \ 46			TPR w ts-SAH or SAH	DCS-R
Helmstaedter	2011a	20 \ 10	20 \ 10	38 \ 36.5	14.4 \ 13.6	ATL or SAH or ATL-AH+ or ATL-AH-	DCS-R
Helmstaedter	2011b	20 \ 10	33 \ 31			ts-SAH	DCS-R
Hermann	1995	48 \ 29	48 \ 29	30.6 \ 34.2	11.1 \ 12.5	ATL	FacRMT_WARR
Hermann	1997	62 \ 45		31.3 \ 31.9	12.4 \ 11.1		VR_WMS-I
Hill	2012	25 \ 22	25 \ 22	39.9 \ 34.6	15.3 \ 14.4	SAH	BVMT-R
Hocking	2013	16 \ 18		35.3 \ 36.2	19.3 \ 16.3		AustMaze
Hurtado	2009	46 \ 48		32.1 \ 32.9	9.9 \ 8.9		FacRMT_WARR
Immonen	2010	23 \ 15	23 \ 15			ATL+AH or SAH	VR_WMS-I

Jutila	2014	44 \ 54	44 \ 54	34 \ 34	14.0 \ 12.0	ATL or tmtg-SAH	VR_WMS-I; RCF
Kessels	2004		16 \ 9	40.2 \ 39.7	11.3 \ 19.0	SAH	VM_WMS-R
Kikuchi	2001	15 \ 9					VR_WMS-R; BVRT; FacRMT_WARR
Kim	2003	24 \ 40		30.8 \ 28.6	16.2 \ 14.0		RCF*
Kneebone	2007	42 \ 38	42 \ 38			ATL	RCF
Knopman	2015		14 \ 18	29.6 \ 37.7	8.0 \ 13.3	ATL	NVM_FACT
Kubu	2000	5 \ 2	5 \ 2			ATL	VR_WMS-I
La Cour	2006~	12 \ 12		43.1 \ 37			VGT
La Cour	2006~		26 \ 34	31.7 \ 31.8		ATL	VGT
Lacritz	2004	25 \ 25		34 \ 36.7			VR_WMS-III
Lah	2004		15 \ 15	33.5 \ 33.9	9.8 \ 12.7	ATL	FamPic_WMS-III
Lah	2006	15 \ 14		37.8 \ 42.7	18.1 \ 26.6		FamPic_WMS-III
Lah	2008	7 \ 8	7 \ 8	40.4 \ 43.7	16.3 \ 24.7	ATL	RCF; FamPic_WMS-III
Lambon Ralph	2010		3 \ 2	40 \ 39	37 \ 36	ATL	FacRMT_WARR
Lambon Ralph	2012		9 \ 11	33.8 \ 35.6	16.9 \ 9.6	ATL	RCF*
Leijten	2005	34 \ 46	34 \ 36	34.41 \ 36	11 \ 9.0	ATL	RCF*
Lespinet	2002	24 \ 32		30.8 \ 29.2	9.9 \ 11.0		VR_WMS-R; RCF; VisPA_WMS-R
Loring	2000	51 \ 50		31.2 \ 31.8	11.2 \ 12.7		VR_MAS; VRecog_MAS; VMI_MAS
Lutz	2004	40 \ 40	40 \ 40	35.2 \ 38.3	10.6 \ 11.8	ts-SAH or tc-SAH	DCS-I
Malikova	2012	26 \ 11					VM_WMS-R
Malikova	2014	43 \ 32	43 \ 32			ATL or SRF-SAH	VM_WMS-R
Mantoan	2009	15 \ 14		38.9 \ 36.4	14.3 \ 12.6		VR_WMS-R; RCF
Marquez de la Plata	2009	23 \ 15		40.4 \ 32.9	17.0 \ 9.0		RCF
Martin	2002	25 \ 30	25 \ 30			ATL	VR_WMS-R
Martin	1999a	22 \ 25		31.5 \ 32.6	15.7 \ 11.5		VR_WMS-I
Martin	1999b	32 \ 14		35.7 \ 33	11.8 \ 18.7		VR_WMS-I
McConley	2008	55 \ 44		33.2 \ 33.6	11.1 \ 14.3		RCF
McCormick	2013	18 \ 20	9 \ 10	36.2 \ 37.3	15.8 \ 19.3	ATL	FacRMT_WARR
McDonald	2008	9 \ 8					Faces_WMS-III
Moore & Baker	2002	77 \ 61		30.7 \ 31.4	12.9 \ 13.1		VR_WMS-R; VisPA_WMS-R; VM

							_WMS-R
Moran	2005		15 \ 15	38.1 \ 35.9	9.9 \ 12.3^	ATL	VR_WMS-I
Morino	2006	26 \ 23	26 \ 23			ATL or ts-SAH	BVRT
Morino	2009	31 \ 31	31 \ 31	34.4 \ 34.4	13.2 \ 17.5	ts-SAH	BVRT; VM_WMS-R
Morris	1995a		24 \ 23	33.5 \ 34.8		ATL	RCF; FacRMT_WARR
Morris	1995b		24 \ 23	33.5 \ 34.8		ATL	Doors_D&P; Shapes_D&P
Moser	2000	26 \ 18		33.7 \ 34.8	11.9 \ 10.2		RCF/VRII_WMS-R
Narayanan	2012	8 \ 6		32.9 \ 34.5			RCF*
Naugle	1993	30 \ 30	30 \ 30	28.3 \ 30.6	11.9 \ 15.9	ATL	VR_WMS-R; VM_WMS-R
Naugle	1994	27 \ 36	27 \ 36	31.0 \ 31	10.8 \ 15.0	ATL	FacRMT_WARR
Neves	2012	27 \ 27		36.7 \ 38.5	13.2 \ 17.2		VR_WMS-R; RCF
Ogden-Epker	2001	27 \ 29		36.9 \ 33.1	13.1 \ 10.3		VR_WMS-R; RCF; FacRMT_WARR
Pacagnella	2004	4 \ 18					VM_WMS-R
Paradiso	2001	47 \ 23					VR_WMS-I; FacRMT_WARR
Parente	2013	67 \ 41		38.9 \ 37.6	23.5 \ 17.8		RCF
Pauli	2000	4 \ 4					VM_WMS-R
Pegna	2002	16 \ 13		32.3 \ 34.7	12.3 \ 15.7		RVDT*
Pereira	2010~	8 \ 8					VM_WMS-R
Pereira	2010~	20 \ 20		36 \ 38.5	20.9 \ 19.5		RouteLT
Phillips	1995	13 \ 25	13 \ 25	32.9 \ 28.4	11.9 \ 8.5	ATL	VR_WMS-I; RCF; FacRMT_WARR; ReccFLT
Piguet	1994	26 \ 44	26 \ 44	31.7 \ 29.9	10.2 \ 11.6	ATL	RCF
Powell	2007	7 \ 7		32.3 \ 36.3	11.9 \ 11.9		DL_AMIPB
Powell	2008	7 \ 7	7 \ 7	32.6\ 37.1	7.3 \ 13.8	ATL	DL_AMIPB
Raspall	2005	12 \ 17		38.2 \ 39.1	13.5 \ 17.7		VR_WMS-III; Faces_WMS-III
Rausch	1990		27 \ 36	30.8 \ 31		ATL	VR_WMS-I
Rausch	1991	19 \ 32		25.5 \ 25.8	10.2 \ 12.2		VR_WMS-I; RCF
Rausch	1993	12 \ 13	12 \ 13			ATL (1 w SAH)	VR_WMS-I; RCF
Rougier	1994		6 \ 6	37 \ 36	17 \ 23	ATL	PMQ_WMS-I
Samson	1992		20 \ 20	30.3 \ 30		ATL	VR_WMS-I; RCF
Sass	1992		28 \ 31	29.8 \ 32	10.8 \ 10.5	ATL w radical H+	VR_WMS-I
Sawrie	1998		79 \ 62			ATL	VR_WMS-I; RCF

Seidenberg	1998	31 \ 21	31 \ 21	30.2 \ 33.8	6.7 \ 5.6	ATL	VR_WMS-I
Selwa	1994	17 \ 14	17 \ 14	29 \ 31.4	11.2 \ 14.2	ATL	VR_WMS-I
Shin	2009	30 \ 24	30 \ 24	30.1 \ 30.1	15.2 \ 16.2	ATL	RCF; VII_WMS-III; VDI_WMS-III
Sidhu	2015	29 \ 24		40 \ 42.5	14.6 \ 13.2		DL_AMIPB
Soble	2014	28 \ 29		38.4 \ 41.3	20.0 \ 24.4		VMI_WMS-IV
Sperling	1996	33 \ 34	33 \ 34			ATL	VR_WMS-I; GHFMT
Spiers	2001		13 \ 17	34.8 \ 37.5	8.5 \ 10.9	ATL	RCF; FacRMT_WARR
St-Laurent	2014	28 \ 28	28 \ 28	37.5 \ 38.4	12.3 \ 17	ATL or SAH	FacRMT_WARR; RVDLT
Tanriverdi	2010	132 \ 124	132 \ 124	29.7 \ 36.1	8.5 \ 11.5	SAH or CAH	VR_WMS-I; RCF
Testa	2004	26 \ 27		36.6 \ 35.6	19.6 \ 17.8		FacRMT_WARR
Trennery	1993~	42 \ 30	42 \ 30	33.8 \ 33.8#	11.1 \ 13.8#	ATL	VR_WMS-R
Trennery	1993~	36 \ 32		33.8 \ 33.8#	11.1 \ 13.8#		VSLT
Tudesco	2010	20 \ 19		33.9 \ 36.5	14.4 \ 14		VR_WMS-R; RCF
Vingerhoets	2006	39 \ 50		31.9 \ 31.9			RCF; VDLT
Wagner	2013	30 \ 24	30 \ 24			ATL	DCS-R
Wang	2011~	24 \ 25					BVRT
Wang	2011~	21 \ 21					VR_WMS-III
Wechsler	1997		15 \ 12			ATL	VII_WMS-III; VDI_WMS-III
Wechsler	2009		8 \ 15			ATL	VR_WMS-IV; Designs_WMS-IV; VMI_WMS-IV
Weniger	2012	24 \ 20		38.5 \ 41.5	17.5 \ 21.5		Route_RBMT; LGT-3; VM_WMS-R
Wilde	2001~	55 \ 47		34.2 \ 34.0#	15.9 \ 15.2#		Faces_WMS-III
Wilde	2001~	53 \ 47		34.2 \ 34.0#	15.9 \ 15.2#		FamPic_WMS-III
Wilde	2001~	55 \ 46		34.2 \ 34.0#	15.9 \ 15.2#		VDI_WMS-III
Wilde	2001~	53 \ 47		34.2 \ 34.0#	15.9 \ 15.2#		VII_WMS-III
Wilkinson	2012	15 \ 12		34.8 \ 38.7	11.5 \ 17.3		RCF

Data for age and epilepsy onset are mean years. * modification or adaptation of the standard test. ^ age of epilepsy onset calculated from participant age minus duration of epilepsy. # age/onset provided is from total sample which con tains additional participants. ˜ non-equivalent samples within same paper

Surgery: +, including; -, sparing; w, with; AH, amygdalohippocampetcomy; ATL, standard 2/3 anterior temporal lobectomy or a tailored variant of this procedure; H, hippocampus; CAH, selective cortico-AH; SAH, selective-AH; SR F-SAH, stereotactic radiofrequency-SAH; tc-SAH: trans-cortical SAH; ts-SAH, trans-Sylvian SAH; tmtg-SAH: trans-middle temporal gyrus SAH; TPR+, additional temporal pole resection

Tests: 7/24_SLT, 7/24 Spatial Learning Test; AFLT, Aggie Figure Learning Test; AustMaze, Austin Maze; BFLT-E, Biber Figure Learning Test - Extended; BLT, Brown Location Test; BVMT-R, Brief Visuospatial Memory Test - Revi sed; BVRT, Benton Visual Retention Test; DCS-I, Diagnostikum für Cerebralschädigung; DCS-M, Diagnostikum für Cerebralschädigung (Modified); DCS-R, Diagnostikum für Cerebralschädigung (Revised); Designs_WMS-IV, Des igns - WMS-IV; DL_AMIPB, Design Learning - Adult Memory and Information Processing Battery; Doors_D&P, Doors test - Doors & People test; Fac_ALSTER, Alsterdorfer Faces Test; Fac_DADE, Dade Face Learning Test; Fac_ DENMAN, Denman Facial Recognition Test; FacDsc_FAB, Facial Discrimination subtest (adapated from subtest 1 of the Florida Affect Battery); Faces_WMS-III, Faces - WMS-III; FacRMT_WARR, Warrington Recognition Memo ry Test for Faces; FamPic_WMS-III, Family Pictures - WMS-III; FL_AMIPB, Figure Learning - Adult Memory and Information Processing Battery; GHFMT, Graduate Hospital Facial Memory Test; LGT-3, Lern- und Gedächtnistes t-3 ; NVM_FACT, Nonverbal Memory Factor (VisPA_WMS-R, VR-II_WMS-III, Faces_WMS-III, FamPic_WMS-III); NVSRT, Nonverbal Selective Reminding Test; PMQ_WMS-I, Performance Memory Quotient; RCF, Rey Compl ex Figure test; RCF/AFLT_Composite, Rey Complex Figure test and/or Aggie Figure Learning Test; RCF/VRII_WMS-R, average of Rey Complex Figure test (Delay) and VR-II; ReccFLT, Recurring Figures Learning Test; Route_R BMT, Remembering a new route - Rivermead Behavioural memory Test ; RouteLT, Route Learning Test; RULIT, Ruff-Light Trail Learning Test; RVDLT, Rey Visual Design Learning Test; RVDT, Rey Visual Design Test; Shapes_D &P, Shapes test - Doors & People test; TopogRMT_CAM, Topographical Recognition Memory Test - Camden Memory Test battery; VDI_WMS-III, Visual Delayed memory Index (Faces II, Family Pictures II); VDLT, Visual Design Learning Test; VGT, Visual Gestalt Test; VII_WMS-III, Visual Immediate memory Index (Faces I, Family Pictures I); VII_WMS-III_SP, Visual Immediate memory Index - Standardization Protocol; VisPA_WMS-R, Visual Paired As sociates - WMS-R; VM_FACT, composite measure made up of Warrington Faces (total score), Rey Visual Design Learning Test (Sum of Learning Trials 1 to 5), and Spatial Conditional Associative Learning Task (total trials to criteri on); VM_WMS-R, Visual Memory quotient (Figural Memory, Visual Paired Associates I, Visual Reproduction I); VMI_MAS, composite measure from VR_MAS and VRecog_MAS; VMI_WMS-IV, Visual Memory Index - WMS-IV ; VMI_WMS-IV, Visual Memory Index (Designs I, Designs II, Visual Reproduction I, Visual Reproduction II); VR_MAS, Visual Reproduction - Memory Assessment Scale version; VR_WMS-I, Visual Reproduction - WMS-I; VR_ WMS-I_RUS, Visual Reproduction - WMS-I (Russell Revision); VR_WMS-III, Visual Reproduction - WMS-III; VR_WMS-R, Visual Reproduction - WMS-R; VRecog_MAS, Visual Recognition test - Memory Assessment Scale; V SLT, Visual Spatial Learning Test; VSRT, Visual Selective Reminding Test (precursor test to version in TOMAL-2 battery)

Supplementary Table 2. Meta-analytic results of the performance on visual memory tests in left versus right presurgical patients, by material and test type.

Material: trial type	**Test type**	**Test measures**	***k***	***N_Left***	***N_Right***	***d***	***CI_lo***	***CI_up***	***z***	***p***	***Nfs***	***Q***	***Q_p***	***I²***
Designs: Single Trial	Immediate	VR_I	35	1358	1247	-0.05	-0.14	0.04	-1.16	.24	-	52.53	.02	11%
		RCF_Im	15	475	455	-0.12	-0.25	0.01	-1.74	.08	-	13.64	.48	14%
		BVRT_Cor	10	273	267	0.25	-0.52	1.03	0.64	.53	-	127.71	<.001	94%
		VRecog_MAS	1	51	50	-0.27	-0.66	0.12	-1.34	.18	-	0	1	0%
		TOTAL	61	2157	2019	-0.04	-0.18	0.10	-0.50	.62	-	203.56	<.001	78%
	Delayed	VR_II	34	1595	1512	-0.08	-0.18	0.02	-1.43	.14	-	58.02	<.01	39%
		RCF_Dl	34	1487	1459	-0.20	-0.34	-0.05	-2.66	<.01	636	165.23	<.001	70%
		TOTAL	68	3082	2971	-0.14	-0.23	-0.04	-2.88	<.01	870	239.44	<.001	65%
	% Retention	VR_Pc	13	672	563	-0.02	-0.19	0.14	-0.30	.77	-	17.07	.15	35%
		RCF_Pc	5	309	287	-0.81	-2.12	0.50	-1.22	.22	-	60.64	<.001	98%
		TOTAL	18	981	850	-0.23	-0.57	0.11	-1.32	.19	-	83.76	<.001	91%
Designs: Repeated Trials	Learning	DL_AMIPB_Lrn	8	331	266	-0.49	-0.67	-0.30	-5.16	<.0001	382	7.42	.39	13%
		DCS_Lrn	7	222	210	-0.16	-0.37	0.06	-1.42	.16	-	8.60	.20	19%
		DCS_LrnCap	4	136	131	-0.24	-0.98	0.50	-0.64	.52	-	19.35	<.001	86%
		AFLT_Tr6	1	10	12	-0.28	-1.12	0.57	-0.64	.52	-	0	1	0%
		BFLT_Lrn	1	25	46	-0.45	-0.95	0.04	-1.81	.07	-	0	1	0%
		BVMT_Lrn	1	25	22	-0.13	-0.71	0.44	-0.45	.65	-	0	1	0%
		FL_AMIPB_Im	1	9	8	-1.40	-2.46	-0.34	-2.58	<.01	139	0	1	0%
		ReccFLT_LrnRcg	1	13	25	0.37	-0.31	1.04	1.07	.28	-	0	1	0%
		RVDLT_Im	1	43	44	-0.22	-1.01	0.22	-0.64	.20	-	0	1	0%
		RVDLT_Lrn	1	28	28	-0.07	-0.59	0.46	-0.26	.80	-	0	1	0%
		RVDT_Im	1	16	13	-0.55	-1.29	0.20	-1.44	.15	-	0	1	0%
		VDLT_Lrn	1	39	50	0.18	-0.24	0.60	0.85	.39	-	0	1	0%
		VGT_LrnEr	1	12	12	-0.02	-0.82	0.78	-0.06	.95	-	0	1	0%
		VSRT_CLTR	1	12	12	-0.10	-0.90	0.70	-0.25	.80	-	0	1	0%

		VSRT_Lrn	1	22	20	0.00	-0.61	0.61	0.00	1.00	-	0	1	0%
		TOTAL	31	943	899	-0.26	-0.40	-0.12	-3.67	<.001	783	58.95	<.01	50%
	Delayed Recall	RVDLT_Dl	3	351	328	0.13	-0.16	0.42	0.88	.38	-	5.11	.08	28%
		FL_AMIPB_Dl	3	90	67	-0.74	-1.15	-0.33	-3.55	<.001	220	3.21	.20	
		BVMT_Dl	2	50	44	-0.32	-0.96	0.33	-0.96	.34	-	2.47	.12	60%
		DL_AMIPB_Dl	2	71	51	-0.47	-0.88	-0.07	-2.28	.02	93	1.22	.27	18%
		BFLT_Dl	1	25	46	-0.44	-0.93	0.05	-1.75	.08	-	0	1	0%
		DCS_Dl	1	12	12	-0.86	-1.70	-0.03	-2.02	.04	85	0	1	0%
		RVDT_Dl	1	16	13	-0.86	-1.62	-0.09	-2.19	.03	85	0	1	0%
		VDLT_Dl	1	39	50	0.06	-0.36	0.47	0.26	.79	-	0	1	0%
		VGT_RepEr	1	12	12	0.43	-0.38	1.24	1.04	.30	-	0	1	0%
		VSRT_Dl	1	22	20	0.52	-0.09	1.14	1.67	.10	-	0	1	0%
		TOTAL	16	688	643	-0.27	-0.51	-0.03	-2.17	0.03	410	58.15	<.001	75%
	Delayed Recognition	DCS_RcgCor	2	52	52	-0.04	-0.42	0.35	-0.20	.84	-	0.33	.57	0%
		DCS_RcgEr	2	83	77	-0.20	-0.51	0.11	-1.28	.20	-	0.02	.88	0%
		RVDLT_Rcg	2	148	137	-0.04	-0.27	0.19	-0.32	.75	-	0.50	.48	0%
		AFLT_DlRcg	1	10	12	-0.44	-1.28	0.41	-1.01	.31	-	0	1	
		BFLT_RcgDscr	1	25	46	-0.40	-0.89	0.10	-1.58	.11	-	0	1	
		BVMT_Hit	1	25	22	-0.36	-0.94	0.21	-1.24	.22	-	0	1	
		VDLT_Rcg	1	39	50	0.23	-0.19	0.65	1.07	.28	-	0	1	0%
		TOTAL	10	382	396	-0.10	-0.24	0.04	-1.42	.16	-	6.81	.66	0%
Faces	Immediate	FacRMT_WARR	15	436	388	-0.17	-0.34	0.01	-1.90	.06	-	19.71	.14	33%
		Faces_I_WMS-III	6	164	140	-0.17	-0.43	0.10	-1.23	.22	-	7.33	.20	18%
		GHFMT	2	43	50	-0.32	-1.30	0.66	-0.64	.52	-	4.27	.04	77%
		Fac_ALSTER	1	19	30	-0.25	-0.82	0.33	-0.84	.40	-	0	1	0%
		FacLT_DADE	1	19	17	-1.05	-1.75	-0.35	-2.95	<.01	104	0	1	0%
		Fac_DENMAN	1	57	48	-0.50	-0.89	-0.11	-2.51	.01	49	0	1	0%
		TOTAL	26	738	673	-0.22	-0.36	-0.08	-3.11	<.01	544	39.98	.03	37%

	Delayed	Faces_II_WMS-III	7	173	148	-0.09	-0.31	0.14	-0.76	.45	-	3.93	.69	0%
		GHFMT	2	43	50	-0.15	-0.74	0.44	-0.49	.62	-	1.73	.19	42%
		Fac_ALSTER	1	19	30	-0.58	-1.17	0.00	-1.94	.05	-	0	1	0%
		FacLT_DADE	1	19	17	-0.30	-0.96	0.35	-0.91	.37	-	0	1	0%
		TOTAL	11	254	245	-0.15	-0.33	0.03	-1.63	.10	-	8.35	.59	0%
Spatial	Learning	7/24_SLT	2	91	91	0.01	-0.29	0.30	0.04	.97	-	0.05	.83	0%
		AustMaze	1	16	18	-0.86	-1.56	-0.15	-2.39	.02	85	0	1	0%
		BLT_Lrn	1	9	9	-1.56	-2.61	-0.50	-2.89	<.01	155	0	1	0%
		LGT-3	1	24	20	-0.51	-1.12	0.09	-1.67	.09	-	0	1	0%
		Route_RBMT	1	24	20	-0.08	-0.67	0.51	-0.27	.79	-	0	1	0%
		RouteLT	1	20	20	-2.65	-3.50	-1.80	-6.12	<.0001	264	0	1	0%
		RULIT	1	32	20	0.43	-0.13	1.00	1.50	.13	-	0	1	0%
		TOTAL	8	216	198	-0.60	-1.27	0.08	-1.72	.09	-	49.08	<.001	90%
	Delayed	7/24_SLT	2	91	91	-0.27	-0.56	0.02	-1.79	.07	-	0.01	.91	0%
		BLT_Dl	1	9	9	-1.04	-2.02	-0.05	-2.07	.04	103	0	1	0%
		NVSRT	1	34	44	0.25	-0.20	0.70	1.08	.28	-	0	1	0%
		RULIT	1	32	20	0.45	-0.12	1.01	1.55	.12	-	0	1	0%
		TOTAL	5	166	164	-0.09	-0.47	0.29	-0.46	.64	-	10.60	.03	63%

Supplementary Table 3. Meta-analytic results of the performance on visual memory tests in left versus right postsurgical patients, by material and test type.

Material: trial type	**Test type**	**Test_measure**	***k***	***N_Left***	***N_Right***	***d***	***CI_lo***	***CI_up***	***z***	***p***	***Nfs***	***Q***	***Q_p***	***I²***
Designs: Single Trial	Immediate	VR_I	23	742	741	-0.18	-0.29	-0.07	-3.28	<.001	398	24.99	.30	6%
		BVRT_Cor	5	144	161	0.24	-0.59	1.06	0.56	.57	-	51.46	<.001	92%
		RCF_Im	4	87	99	0.00	-0.29	0.29	-0.02	.99	-	1.12	.77	0%
		ShapesDP	1	24	23	-0.45	-1.03	0.13	-1.51	.13	-	0	1	0%
		Designs_I_Content_WMS-IV	1	8	15	-0.56	-1.44	0.31	-1.26	.21	-	0	1	0%

		TOTAL	34	1005	1039	-0.12	-0.29	0.04	-1.46	.14	-	94.33	<.001	67%
	Delayed	VR_II	22	983	952	-0.16	-0.27	-0.06	-3.16	<.001	58	20.81	.47	13%
		RCF_Dl	19	859	870	-0.27	-0.53	-0.02	-2.12	.03	71	166.23	<.001	82%
		Designs_II_Content_WMS-IV	1	8	15	0.15	-0.71	1.01	0.33	.74	-	0	1	0%
		TOTAL	42	1850	1837	-0.21	-0.34	-0.07	-3.04	<.001	130	209.54	<.001	72%
	% Retention	VR_Pc	4	110	90	-0.02	-0.30	0.26	-0.12	.90	-	1.49	.69	0%
		RCF_Pc	3	3568	2822	-0.50	-0.85	-0.15	-2.80	<.01	18	1.98	.37	1%
		TOTAL	7	185	150	-0.21	-0.47	0.04	-1.66	.10	-	7.92	.24	23%
Designs: Repeated Trials	Learning	DCS_Lrn	5	168	161	-0.31	-0.68	0.06	-1.64	.10	-	9.88	.04	63%
		DL_AMIPB_Lrn	3	172	149	-0.48	-0.71	-0.26	-4.25	<.0001	18	1.42	.49	0%
		DCS_LrnCap	2	86	84	-0.37	-1.01	0.28	-1.11	.27	-	2.50	.11	60%
		FL_AMIPB_Im	1	9	8	-0.45	-1.42	0.51	-0.92	.36	-	0	1	0%
		ReccFLT_LrnRcg	1	13	25	-0.03	-0.70	0.64	-0.07	.94	-	0	1	0%
		RVDLT_Lrn	1	28	28	-0.03	-0.55	0.50	-0.10	.92	-	0	1	0%
		VGT_LrnEr	1	26	34	0.40	-0.11	0.92	1.54	.12	-	0	1	0%
		VSRT_CLTR	1	12	12	-0.69	-1.51	0.13	-1.64	.10	-	0	1	0%
		TOTAL	16	554	533	-0.26	-0.44	-0.08	-2.77	<.01	58	29.47	.01	49%
	Delayed Recall	RVDLT_Dl	2	308	284	-0.05	-0.36	0.26	-0.32	.75	-	3.39	.07	70%
		BVMT_Dl	1	25	22	-0.51	-1.09	0.07	-1.71	.09	-	0	1	0%
		FL_AMIPB_Dl	1	9	8	-0.81	-1.80	0.18	-1.61	.11	-	0	1	0%
		VGT_RepEr	1	26	34	-0.33	-0.85	0.18	-1.27	.21	-	0	1	0%
		VSLT_LtPc	1	40	32	-0.29	-0.76	0.18	-1.22	.22	-	0	1	0%
		TOTAL	6	408	380	-0.20	-0.42	0.01	-1.86	.06	-	7.91	.16	40%
	Delayed Recognition	DCS_RcgEr	2	83	77	0.19	-0.12	0.51	1.23	.22	-	0.05	.83	0%
		DCS_RcgCor	1	40	40	-0.09	-0.53	0.35	-0.41	.68	-	0	1	0%
		RVDLT_Rcg	1	105	93	-0.29	-0.57	-0.01	-2.02	.04	4	0	1	0%
		TOTAL	4	228	210	-0.04	-0.30	0.23	-0.26	.79	-	5.17	.16	43%

Faces	Immediate	FacRMT_WARR	11	223	224	-0.59	-0.83	-0.35	-4.78	<.0001	75	17.07	.07	31%
		Faces_I_WMS-III	3	82	83	-0.56	-1.05	-0.06	-2.19	.03	20	3.96	.14	49%
		GHFMT	2	43	50	-0.49	-0.90	-0.07	-2.29	.02	12	0.91	.34	0%
		FacDsc_FAB	1	20	23	0.07	-0.53	0.67	0.22	.83	-	0	1	0%
		TOTAL	17	368	380	-0.53	-0.71	-0.35	-5.64	<.0001	107	26.20	.05	30%
	Delayed	Faces_II_WMS-III	3	82	83	-0.37	-0.68	-0.06	-2.36	.02	14	0.51	.78	49%
		GHFMT	2	43	50	-0.41	-0.82	0.01	-1.92	.05	10	0.82	.36	0%
		TOTAL	5	125	133	-0.38	-0.63	-0.14	-3.04	<.001	24	1.34	.85	0%
Spatial	Learning	7/24_SLT_Lrn	1	58	59	-0.04	-0.40	0.33	-0.19	.85	-	0	1	0%
		Designs_I_Spatial_WMS-IV	1	8	15	-0.74	-1.62	0.14	-1.64	.10	-	0	1	0%
		TOTAL	2	66	74	-0.27	-0.92	0.38	-0.81	.42	-	2.09	.15	52%
	Delayed	7/24_SLT_LoDl	1	58	59	-0.36	-0.73	0.00	-1.94	.05	-	0	1	0%
		NVSRT_Dl	1	34	44	-0.37	-0.82	0.08	-1.62	.11	-	0	1	0%
		Designs_II_Spatial_WMS-IV	1	8	15	-0.38	-1.25	0.48	-0.86	.39	-	0	1	0%
		TOTAL	3	100	118	-0.37	-0.64	-0.10	-2.67	<.01	14	0.00	1	0%

Supplementary Table 4. Meta-analytic results of the presurgical minus postsurgical difference in performance on visual memory tests in left- and right-sided patients, by material and test type.

Material: trial type	**Test type**	**Test_measure**	***k***	***Hem***	***N***	***d***	***CI_lo***	***CI_up***	***z***	***p***	***Nfs***	***Q***	***Q_p***	***I²***
Designs: Single Trial	Immediate	VR_I	16	L	548	0.07	-0.05	0.19	1.09	.27	-	3.92	1	0%
				R	540	-0.02	-0.14	0.10	-0.40	.69	-	7.63	.94	0%
		BVRT_Cor	5	L	144	0.18	-0.27	0.64	0.79	.43	-	15.04	.00	73%
				R	161	-0.31	-0.57	-0.05	-2.36	.02	150	4.83	.30	24%
		RCF_Im	2	L	65	0.18	-0.28	0.64	0.77	.44	-	1.74	.19	42%
				R	71	0.17	-0.16	0.50	0.99	.32	-	0.68	.41	0%
		TOTAL	23	L	757	0.11	0.01	0.21	2.10	.04	226	22.59	.43	0%
				R	772	-0.07	-0.17	0.04	-1.27	.20	129	20.63	.54	2%

Designs: Single Trial	Delayed	VR_II	16	L	806	0.04	-0.08	0.16	0.66	.51	-	16.53	.35	22%
				R	773	-0.04	-0.14	0.06	-0.79	.43	-	17.57	.29	0%
		RCF_Dl	14	L	712	0.23	0.09	0.37	3.24	<.01	312	15.60	.27	31%
				R	737	0.17	0.07	0.27	3.29	<.01	227	15.95	.25	29%
		TOTAL	30	L	1518	0.13	0.03	0.23	2.58	<.01	365	44.13	.04	37%
				R	1510	0.07	-0.02	0.16	1.45	.15	-	41.97	.06	29%
Designs: Single Trial	% Retention	VR_Pc	3	L	82	0.01	-0.30	0.32	0.05	.96	-	0.65	.72	0%
				R	59	-0.17	-0.53	0.19	-0.93	.35	-	0.85	.65	0%
		RCF_Pc	1	L	22	0.12	-0.47	0.71	0.39	.70	-	0	1	0%
				R	20	-0.04	-0.66	0.58	-0.14	.89	-	0	1	0%
		TOTAL	4	L	104	0.03	-0.24	0.30	0.23	.82	-	0.75	.86	0%
				R	79	-0.14	-0.45	0.17	-0.87	.38	-	0.97	.81	0%
Designs: Repeated Trials	Learning	DCS_Lrn	5	L	222	-0.16	-0.38	0.06	-1.45	.15	-	13.91	.01	73%
				R	210	-0.49	-0.87	-0.10	-2.49	.01	240	11.29	.02	65%
		DL_AMIPB_Lrn	3	L	172	-0.03	-0.24	0.18	-0.26	.80	-	0.36	.83	0%
				R	149	-0.04	-0.27	0.19	-0.36	.72	-	1.20	.55	0%
		DCS_LrnCap	2	L	86	0.04	-0.26	0.33	0.23	.82	-	0.01	.91	0%
				R	84	-0.11	-0.41	0.19	-0.71	.48	-	0.23	.63	0%
		FL_AMIPB_Im	1	L	9	-0.43	-1.37	0.50	-0.91	.36	-	0	1	0%
				R	8	0.39	-0.60	1.38	0.777	.44	-	0	1	0%
		ReccFLT_LrnRcg	1	L	13	-0.02	-0.79	0.75	-0.05	.96	-	0	1	0%
				R	25	-0.35	-0.91	0.21	-1.22	.22	-	0	1	0%
		RVDLT_Lrn	1	L	28	-0.28	-0.80	0.25	-1.03	.30	-	0	1	0%
				R	28	-0.23	-0.76	0.30	-0.86	.39	-	0	1	0%
		VSRT_CLTR	1	L	12	0.35	-0.46	1.15	0.84	.40	-	0	1	0%
				R	12	-0.18	-0.99	0.62	-0.45	.65	-	0	1	0%
		TOTAL	15	L	578	-0.05	-0.21	0.10	-0.70	.49	-	19.25	.16	27%
				R	545	-0.20	-0.39	-0.01	-2.06	.04	287	26.35	.02	50%
	Delayed Recall	RVDLT_Dl	2	L	28	0.32	0.09	0.55	2.71	<.01	62	1.95	.16	49%

				R	28	0.02	-0.14	0.19	0.2788	.78	-	0.05	.82	0%
		BVMT_Dl	1	L	25	-0.19	-0.74	0.37	-0.67	.51	-	0	1	0%
				R	22	-0.08	-0.67	0.51	-0.26	.80	-	0	1	0%
		FL_AMIPB_Dl	1	L	9	-0.60	-1.55	0.34	-1.25	.21	-	0	1	0%
				R	8	0.17	-0.81	1.15	0.34	.73	-	0	1	0%
		TOTAL	5	L	378	0.13	-0.14	0.39	0.95	.34	-	9.40	.05	57%
				R	346	0.02	-0.13	0.17	0.25	.80	-	0.25	.99	0%
	Delayed Recognition	DCS_RcgEr	2	L	83	0.08	-0.23	0.38	0.48	.63	-	0.57	.45	0%
				R	77	0.47	0.15	0.79	2.87	<.01	92	0.60	.44	0%
		DCS_RcgCor	1	L	40	0.18	-0.26	0.62	0.79	.43	-	0	1	0%
				R	40	0.08	-0.35	0.52	0.38	.70	-	0	1	0%
		RVDLT_Rcg	1	L	105	0.49	0.21	0.76	3.47	<.001	48	0	1	0%
				R	93	0.18	-0.11	0.46	1.20	.23	-	0	1	0%
		TOTAL	4	L	228	0.25	0.00	0.50	1.95	.05	-	4.68	.20	40%
				R	210	0.26	0.07	0.46	2.6928	<.01	102	3.16	.37	0%
Faces	Immediate	FacRMT_WARR	7	L	177	0.23	0.02	0.44	2.12	.03	154	2.01	.92	0%
				R	177	-0.30	-0.51	-0.08	-2.72	<.01	201	4.98	.55	0%
		Faces_I_WMS-III	2	L	26	0.36	-0.19	0.91	1.28	.20	-	0.00	.98	0%
				R	32	0.15	-0.34	0.64	0.59	.55	-	0.36	.55	0%
		GHFMT	2	L	43	0.50	0.07	0.93	2.263	.02	97	0.60	.44	0%
				R	50	0.13	-0.26	0.53	0.67	.50	-	0.11	.73	0%
		TOTAL	11	L	246	0.29	0.11	0.47	3.16	<.01	309	3.86	.95	0%
				R	259	-0.15	-0.33	0.02	-1.72	.09	-	10.70	.38	0%
	Delayed	Faces_II_WMS-III	2	L	26	0.39	-0.16	0.94	1.38	.17	-	0.40	.53	0%
				R	32	-0.02	-0.51	0.47	-0.07	.95	-	0.21	.64	0%
		GHFMT	2	L	43	0.41	-0.02	0.84	1.89	.06	-	0.41	.52	0%
				R	50	0.04	-0.35	0.43	0.19	.85	-	0.26	.61	0%
		TOTAL	4	L	69	0.40	0.07	0.74	2.3388	.02	157	0.81	.85	0%
				R	82	0.02	-0.29	0.32	0.11	.91	-	0.50	.92	0%

Spatial	Learning	7/24_SLT_Lrn	1	L	58	0.00	-0.36	0.36	0.00	1.00	-	0	1	0%
				R	59	-0.02	-0.38	0.34	-0.09	.93	-	0	1	0%
	Delayed	7/24_SLT_LoDl	1	L	58	-0.05	-0.42	0.31	-0.2856	.78	-	0	1	0%
				R	59	-0.12	-0.48	0.24	-0.65	.52	-	0	1	0%
		NVSRT_Dl	1	L	34	0.18	-0.30	0.66	0.7393	.46	-	0	1	0%
				R	44	-0.44	-0.86	-0.01	-2.0275	.04	43	0	1	0%
		TOTAL	2	L	92	0.03	-0.26	0.32	0.222	.82	-	0.58	.45	0%
				R	103	-0.26	-0.57	0.05	-1.6426	.10	-	1.25	.26	20%

Supplementary Table 5. Meta-analytic results of the presurgical minus postsurgical difference in performance on uncategorised visual memory tests in left- and right-sided patients.

Material	**Test type**	**Test_measure**	***k***	***Hem***	***N_Left***	***N_Right***	***d***	***CI_lo***	***CI_up***	***z***	***p***	***Nfs***	***Q***	***Q_p***	***I^2***
Presurgical															
Scene	Immediate	FamPic_WMS-III	4		159	112	-0.15	-0.40	0.11	-1.10	0.27	-	2.94	.40	8%
		TopogRMT_CAM	1		9	5	0.08	-1.01	1.17	0.14	0.89	-	0.00	1.00	0%
		DoorsDP_pos_out	1		24	23	-2.00	-2.70	-1.30	-5.59	<.0001	199	0.00	1.00	0%
	Delayed	FamPic_WMS-III	5		176	124	-0.04	-0.27	0.19	-0.32	0.75	-	1.30	.86	0%
Associative (design/colour)	Immediate	VisPA_WMS-R	3		148	128	0.30	-0.24	0.83	1.08	0.28	-	7.68	.02	78%
	Delayed	VisPA_WMS-R	3		148	128	0.16	-0.08	0.40	1.32	0.19	-	2.12	.35	0%
Associative (design/position)	Learning	VSLT_Lrn	1		36	29	0.04	-0.45	0.53	0.17	0.87	-	0.00	1	0%

	Delayed	VSLT_LtPc	1		36	32	-0.10	-0.57	0.38	-0.39	0.70	-	0.00	1	0%
Postsurgical															
Scene	Immediate	FamPic_WMS-III	3		78	74	-0.14	-0.63	0.35	-0.57	0.57	-	3.58	.17	39%
	Delayed	FamPic_WMS-III	3		78	74	-0.07	-0.45	0.30	-0.38	0.70	-	2.25	.32	14%
Associative (design/location)	Immediate	Designs_WMS-IV_Total	1		8	15	-1.00	-1.91	-0.10	-2.17	0.03	99	0.00	1.00	0%
	Delayed	Designs_WMS-IV_Total	1		8	15	-0.35	-1.21	0.51	-0.79	0.43	-	0.00	1.00	0%
Associative (design/position)	Learning	VSLT_Lrn	1		40	32	0.15	-0.32	0.61	0.62	0.54	-	0.00	1.00	0%
	Delayed	VSLT_LtPc	1		40	32	-0.29	-0.76	0.18	-1.22	0.22	-	0.00	1.00	0%
Postsurgical change															
Scene	Immediate	FamPic_WMS-III	1	L	7		-0.54	-1.61	0.53	-0.99	0.32	-	0.00	1.00	0%
			1	R		8	-0.05	-1.03	0.93	-0.11	0.92	-	0.00	1.00	0%
	Delayed	FamPic_WMS-III	1	L	7		-0.57	-1.64	0.50	-1.04	0.30	-	0.00	1.00	0%
			1	R		8	-0.07	-1.05	0.91	-0.14	0.89	-	0.00	1.00	0%
Associative (design/position)	Learning	VSLT_Lrn	1	L	36		0.22	-0.24	0.67	0.93	0.35	-	0.00	1.00	0%
				R		29	0.38	-0.13	0.88	1.46	0.15	-	0.00	1.00	0%
	Delayed	VSLT_LtPc	1	L	36		0.04	-0.41	0.49	0.19	0.85	-	0.00	1.00	0%
				R		32	0.01	-0.48	0.50	0.04	0.97	-	0.00	1.00	0%

Supplementary Table 6. Meta-analytic results of the presurgical minus postsurgical difference in performance on composite visual memory measures in left- and right-sided patients.

Surgery status	Composite measure	*k*	*Hem*	*N_Left*	*N_Right*	*d*	*CI_lo*	*CI_up*	*z*	*p*	*Nfs*	*Q*	*Q_p*	I^2
Presurgical														
	VM_WMS-R	15		423	382	-0.03	-0.17	0.11	-0.40	0.69	-	15.62	.34	1%
	VII_WMS-III	4		226	188	-0.26	-0.45	-0.06	-2.59	<.01	99	0.45	.93	0%
	VDI_WMS-III	4		258	207	-0.24	-0.42	-0.05	-2.51	0.01	90	0.73	.87	0%
	VMI_WMS-IV	1		28	29	-0.26	-0.78	0.26	-0.98	0.33	-	0.00	1.00	0%
	RCF/AFLT_Dl_Composite	1		10	15	-0.37	-1.18	0.43	-0.91	0.36	-	0.00	1.00	0%
	RCF/VRII_WMS-R	1		26	18	-0.27	-0.87	0.34	-0.86	0.39	-	0.00	1.00	0%
	VM_FACT	1		12	14	-0.78	-1.58	0.02	-1.92	0.05	-	0.00	1.00	0%
	VMI_MAS	1		51	50	-0.40	-0.80	-0.09	-2.00	0.05	-	0.00	1.00	0%
Postsurgical														
	VM_WMS-R	6		190	170	0.06	0.26	0.11	-0.15	0.60	-	3.00	.70	0%
	VII_WMS-III	5		192	187	-0.45	-0.24	0.10	-0.65	<.0001	219	1.33	.86	0%
	VDI_WMS-III	5		222	207	-0.32	-0.13	0.10	-0.51	<.01	154	2.69	.61	0%
	VII_WMS-III_Im_SP	1		22	11	-0.54	-1.28	0.19	-1.44	0.15	-	0.00	1.00	0%
	VII_WMS-III_Dl_SP	1		22	11	-0.36	-1.09	0.37	-0.98	0.33	-	0.00	1.00	0%
	VMI_WMS-IV	1		8	15	-0.85	0.05	0.46	-1.74	0.06	-	0.00	1.00	0%
	RCF/AFLT_Dl_Composite	1		9	15	-0.55	-1.39	0.29	-1.29	0.20	-	0.00	1.00	0%
	NVM_FACT	1		14	18	-0.87	-1.57	-0.17	-2.44	0.01	86	0.00	1.00	0%
	PMQ_WMS-I	1		6	6	-0.55	-1.39	0.29	-1.29	0.20	-	0.00	1.00	0%
Posturgical change														
	VM_WMS-R	5	L	174		0.11	0.32	0.11	-0.10	0.32	-	0.49	.97	0%

		R		161	0.10	0.32	0.11	-0.12	0.38	-	1.61	.81	0%
VII_WMS-III	2	L	110		0.23	0.50	0.14	-0.04	0.09	-	0.85	.36	0%
		R		105	0.04	0.31	0.14	-0.23	0.76	-	0.17	.68	0%
VDI_WMS-III	2	L	140		0.12	0.35	0.12	-0.12	0.32	-	0.20	.66	0%
		R		125	0.07	0.53	0.23	-0.38	0.75	-	2.23	.14	55%
RCF/AFLT_Dl_Composite	1	L	10		0.43	1.34	0.46	-0.48	0.35	-	0.00	1.00	0%
		R		15	0.16	0.88	0.37	-0.55	0.66	-	0.00	1.00	0%

Segue to Chapter 3

The meta-analysis in Chapter 2 provided evidence that different types of nonverbal materials had an effect on the prediction of right versus left temporal lobe pathology, such that tests of facial and spatial memory showed larger effect sizes than did design memory tests. By contrast, differences in the type of learning format (single trial versus multiple trials) and the time of memory testing following learning trials (immediate or delayed) had little effect.

Chapter 2 provided insights into the validity of clinical tests for assessing right temporal lobe pathology. The results also highlight that clear gaps remain between clinical and experimental findings, with promising experimental findings (as reviewed in Chapter 1) not necessarily translating into tests with high clinical utility. Bridging this gap requires a more in-depth understanding of the underlying cognitive and brain processes related to lateralisation in healthy individuals. While the temporal lobes of persons with lateralised pathology are of critical importance for understanding memory function, the temporal lobes are not the only brain region important for memory, nor does the pattern of lateralisation in persons with pathology necessarily reflect the patterns in persons without pathology. As reviewed in Chapter 1, the parietal regions have been closely associated with differential patterns of lateralisation for different kinds of spatial tasks, and the frontal regions have shown differing sensitivity to the type of memory process involved (encoding or retrieval).

Another important consideration is that the meta-analytic method involves comparing broad groups of varieties of clinical tests in a necessarily post-hoc fashion. By contrast, experiments which actively manipulate and precisely control the variables of interest in Chapter 2 (material and processing) could more clearly reveal the underlying causes of lateralisation. The results of experimental findings would usefully complement and inform those of the meta-analysis, and potentially provide clues into how clinical tests could be developed to maximise their lateralising potential. While the meta-analytic and experimental methods each have their advantages and disadvantages, the complementary use of both techniques may yield a more nuanced and complete picture of the factors associated with

lateralisation than would a uniform focus on the temporal lobe alone. Insights taken from experimental studies could be potentially used to improve the development of appropriate tools for persons with lateralised brain pathology.

More specifically, previous ERP/EEG research findings had found memory effects (e.g., "old/new" effects in which previously learned items produced larger ERPs than never-learned items) primarily at frontal and parietal electrode locations (see Chapters 3 and 4 for full details). Yet there has been little investigation of material or processing effects on lateralisation within these studies. The aim of the empirical Chapters 3 and 4 was to meaningfully build upon these findings in the context of potentially superimposed lateralisation effects, by measuring from scalp locations that were at least roughly comparable to the underlying brain regions measured in previous research. A focus only on electrodes directly over the temporal lobes would have resulted in a missed opportunity in this regard. Furthermore, temporal electrodes, while highly lateralised, are known to be produce a much noisier, less reliable signal than frontal and parietal electrodes. Recording from electrodes (F7, F8, P7, P8) that were lateralised and adjacent to temporal electrodes, along with more mildly lateralised sites (F3, F4, P3, P4) that have been frequently associated with memory effects, was considered an acceptable compromise between the needs to detect both "memory effects" and patterns of lateralisation. Furthermore, while it is true that the frontal and parietal scalp locations are most sensitive to neural activity from these respective brain regions, the EEG signal in these regions is also sensitive (though not exclusively) to activity in the medial temporal region such as the hippocampus (see Chapters 3 and 4 for more detail).

In this vein, Chapters 3 and 4 further investigated the relative effects of material (verbal versus nonverbal) and task demands (encoding versus retrieval) on hemispheric lateralisation measured by electroencephalographic recordings from the frontal and parietal brain regions.

In the following empirical Chapters 3 to 6, spatial rather than facial materials were used for the experimental nonverbal memory tasks, for a number of reasons. Chapters 1 and 2

revealed great promise regarding particular kinds of spatial memory tests, albeit these required further investigation, while in contrast there had been a much larger number of studies dedicated to facial memory. Hence there was considered to be a larger gap in the research literature for investigating lateralisation associated with spatial memory. A potential limitation of facial memory tests is their vulnerability to cultural bias, for example, the faces subtest of the Warrington Face Recognition Memory test presents only male Caucasian stimuli, and may therefore have reduced predictive value in non-Caucasian patients. By contrast, tests of spatial memory tap into functions that are less likely to have intrinsic cultural bias, such as navigation of a route or identifying the spatial relation between locations on a map. Moreover, spatial stimuli are easier to manipulate than facial stimuli, allowing for precise control over perceptual attributes such as spatial frequency, which were explored in Chapters 5 and 6. In sum, while Chapters 3 to 6 were experimental in nature, the experimental tasks were designed to maximise their potential clinical value in the future, should the results suggest they were an effective method of eliciting right-lateralised brain activity.

Chapter 3: Material type and task demands interactively affect hemispheric lateralisation of early ERP measures during a memory task

Adam Bentvelzen[1,2], Genevieve McArthur[1,3], Nicholas A. Badcock[1,3], Blake Johnson[1,3], Megan Willis[1,4], Stuart Lee[5], & Greg Savage[1,2]

[1] ARC Centre of Excellence in Cognition and its Disorders, Macquarie University, NSW, 2109, Australia;

[2] Department of Psychology, Macquarie University, NSW, 2109, Australia;

[3] Department of Cognitive Science, Macquarie University, NSW, 2109, Australia;

[4] School of Psychology, Australian Catholic University, 25a Barker Road, Strathfield, 2135.

[5] Monash Alfred Psychiatry Research Centre, Melbourne, Victoria, 3004, Australia;

Keywords: material specificity; nonverbal memory; lateralisation; ERP; HERA.

Running title: Effects of material type and task factors on ERP lateralisation

Corresponding author: Adam Bentvelzen. ARC Centre of Excellence in Cognition and its Disorders, Department of Psychology, Macquarie University, NSW, 2109, Australia. Email: adam.bentvelzen@students.mq.edu.au

Acknowledgements: This work was funded by an Australian Postgraduate Award (APA) to Adam Bentvelzen and a Macquarie University Research Development Grant to Greg Savage, and supported by the Australian Research Council Centre of Excellence for Cognition and its Disorders (CE110001021) http://www.ccd.edu.au

Abstract

Verbal memory impairment is consistently associated with left temporal lobe pathology, but nonverbal memory impairment does not reliably predict right temporal lobe pathology, undermining the traditional material specificity model. An alternative model – hemispheric encoding retrieval asymmetry (HERA) - predicts that, regardless of material type, the left prefrontal cortex is more involved in memory encoding than in retrieval, while the right prefrontal cortex shows the opposite pattern. While research into material and processing effects has centred on the medial temporal and prefrontal cortices respectively, recent research suggests that these lateralising influences may interact within and across both of these regions. Therefore, considering the lateralising effects of both material and processing may guide improvements in the clinical assessment of right medial temporal pathology. The precise timing of lateralisation related to material and processing, however, remains poorly understood. In order to examine the interaction between the effects of material type (verbal, nonverbal) and processing type (encoding, retrieval) on lateralisation in the temporal domain, we measured event-related potentials (ERPs) in 22 healthy adults during encoding and retrieval of verbal (printed pseudoword) and nonverbal (dot pattern) material at frontal and parietal sites. The nonverbal memory task was associated with right-lateralisation that was particularly strong during encoding for early peaks (N170) over the parietal cortex, while verbal material did not show expected left-lateralisation. Processing-related lateralisation was related to brain region and timing, with stronger support for the HERA model at frontal sites, while results from parietal sites either opposed or were neutral with regards to HERA. Overall, these findings suggest an important spatiotemporal relationship for material- and processing-related lateralisation and their interaction in early neural responses.

1. Introduction

Early observations of memory deficits after unilateral temporal lobe resection led to the idea of material specificity: the medial temporal lobe (MTL) in the left hemisphere mediates memory for verbal material and its right hemisphere counterpart mediates memory for nonverbal material, assuming left hemisphere language dominance (Blakemore & Falconer, 1967; Kimura, 1963; Milner, 1970). Subsequent studies of unilateral temporal lobe epilepsy patients have reliably shown effects of left-sided damage on verbal memory (e.g., Alpherts et al., 2006; Ojemann & Dodrill, 1985), but not of right-sided damage on nonverbal memory (Barr, 1997; Bell & Davies, 1998; Lee, Yip, & Jones-Gotman, 2002; Vaz, 2004). Most clinical tests of nonverbal memory involve memory for abstract designs (Vaz, 2004). In contrast, meta-analyses suggest that clinical tests of facial memory and experimental tests of spatial memory are better than design memory tests in detecting right MTL pathology (Kessels, de Haan, Kappelle, & Postma, 2001; Sherman et al., 2011; Vaz, 2004).

The reason for these differences may be due to the lower verbalisability of the facial and spatial stimuli, and hence the reduced involvement of left-lateralised verbal processing (Barr, 1997). This suggestion has been supported in neuroimaging studies with healthy participants which showed that the level of verbalisability, as measured by a dual-task verbal interference paradigm, differed between types of nonverbal stimuli (i.e., scenes > faces > abstract patterns), with the degree of verbalisability correlating negatively with the extent of right-lateralised MTL activity (Golby et al., 2001). In addition, spatial processing appears to play an important role, with a meta-analysis of indicating the right-MTL has a greater role in memory for spatial information compared with non-spatial information (Kuhn & Gallinat, 2014). Taken together, the use of stimuli that are difficult to verbalise and place heavy demands on spatial processing, may form the conditions to engage the right-MTL.

In comparison with the effects of material, the impact of differences in processing on hemispheric lateralisation has attracted less consideration. A large collection of imaging evidence (i.e., positron emission tomography, PET; functional magnetic resonance imaging,

fMRI) supports the hemispheric encoding retrieval asymmetry (HERA) model (e.g., Babiloni et al., 2006; Blanchet et al., 2001; Cabeza & Nyberg, 2000; Desgranges, Baron, & Eustache, 1998; Nyberg, Cabeza, & Tulving, 1996; Rossi et al., 2001; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). The most recent instantiation of HERA predicts that, independent of material type, the left prefrontal cortex is more involved with memory encoding than later retrieval, while the right prefrontal cortex shows a greater involvement in retrieval than in encoding (Habib, Nyberg, & Tulving, 2003). HERA is supported for many types of verbal and nonverbal materials and across a variety of encoding and retrieval conditions (see review by Nyberg, Cabeza, & Tulving, 1996).

While HERA explicitly involves the prefrontal cortex and the material specificity model primarily applies to lateralisation within the MTL, HERA is sufficiently influential to be compared experimentally with material specificity accounts of lateralisation. However, the prefrontal and MTL regions are closely interconnected both anatomically and functionally, suggesting cross-region or within-region interactions between lateralisation effects due to material and processing (Anderson, Rajagovindan, Ghacibeh, Meador, & Ding, 2010; Fernandez & Tendolkar, 2001; Schacter & Wagner, 1999). Within the prefrontal cortex, some findings provide support for both proposals (e.g., Johnson, Raye, Mitchell, Greene, & Anderson, 2003; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999; Nyberg et al., 2000), while others suggest material specificity over HERA (e.g., Golby et al., 2001; Kelley et al., 1998; Lee, Robbins, Pickard, & Owen, 2000; Opitz, Mecklinger, & Friederici, 2000; Wagner et al., 1998). Within the MTL, one fMRI study suggests both processing and material specific lateralisation effects, with the left entorhinal cortex involved during encoding, right hippocampal activation for nonverbal material, and left entorhinal and perirhinal regions involved for verbal material (Kennepohl, Sziklas, Garver, Wagner, & Jones-Gotman, 2007). Further investigation of processing relative to material are required to disambiguate the relative strength of each effect and how they interact across brain regions.

Taken together, it is possible that the material specificity and HERA models could be

integrated to ascertain the type of memory task that elicits the strongest right-lateralisation. These possibilities will be explored here using electroencephalography (EEG) with a four-way design: material (verbal, nonverbal) by processing (encoding, retrieval) by region (frontal, parietal) by hemisphere (left, right). Event-related potentials (ERPs) add a novel and informative temporal dimension in addressing the effects of material and processing on lateralisation due to the millisecond resolution of the electrophysiological response to neural activity, in contrast with the 5 to 10 second resolution of haemodynamic or neurometabolic measures. ERP evidence suggests material and processing effects may dissociate in the temporal domain, since material specific hemispheric lateralisation appears to be strongest during higher-order perceptual processing which occurs up to 250 ms after stimulus presentation while semantic, decisional and retrieval processes occur from 250 to 800 ms post-stimulus (Friedman & Johnson, 2000; Rugg & Curran, 2007) and show less material-related lateralisation (Friedman, Cycowicz, & Gaeta, 2001; Maillard et al., 2011). In addition, hemispheric differences due to material type are more strongly associated with parietal brain regions while conscious, voluntary aspects of retrieval have been related to frontal regions (Friedman & Johnson, 2000). Therefore, the ERP technique could help determine the relative lateralisation effects of material and processing type.

The current study involved healthy adults learning two types of visual stimuli: printed pseudowords (verbal) and spatial dot patterns (nonverbal). The effects of stimulus familiarity were minimised as neither contained semantic information, and the memory task, which involved an encoding phase followed by yes/no recognition judgments, was matched. The recognition format is more appropriate than recall for comparing verbal and nonverbal tasks as it avoids confounding the modality of the response (spoken for verbal recall and drawn for nonverbal recall) with the learned material type. We used a recognition task and considered this an appropriate format to test the predictions of HERA. The HERA model has been supported across a variety of different types of retrieval conditions, including recall, in which retrieving the memory involves a deliberate search of memory, and recognition, in which

memory retrieval does not require an explicit search since the original stimulus is re-presented (see review by Nyberg, Cabeza, & Tulving, 1996).

We measured lateralisation of brain activity by measuring ERPs during each memory task. ERPs were measured at frontal and parietal brain regions (known to be involved in memory, e.g., Friedman & Johnson, 2000) to test whether the relative effects of material and processing may differ between posterior and anterior regions of the brain. This was done as the majority of studies supporting HERA have shown the relevant effects occur in the prefrontal cortex or other frontal regions. We measured ERP peaks during three time windows of theoretical interest: 140 to 220, 220 to 340, and 340 to 800 ms following stimulus onset. The first time window, includes the N170, a negative-going ERP peak occurring from 140 to 220 ms following stimulus presentation/onset, maximal at occipitotemporal sites, that shows material specific hemispheric lateralisation for visual stimuli (left: words; right: pictures, faces, and spatial locations; Baker & Holroyd, 2013; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Cohen et al., 2000; Maillard et al., 2011; Martinez, Di Russo, Anllo-Vento, & Hillyard, 2001). For visual stimuli, the N170 likely reflects higher-order perceptual processing (Barbeau et al., 2008; Henson et al., 2003; Maillard et al., 2011). We measured the N170 at lateral parietal sites and also measured the vertex positive potential (VPP), a polarity reversed (i.e., positive-going) functionally equivalent frontal counterpart to the N170 (Joyce & Roisson, 2005).

The second time window includes the N270 and P300 peaks that occur between approximately 220 and 340 ms. The N270 is maximal at fronto-central sites, and has shown both material specific lateralisation and retrieval-related processing, including the "old/new effect" whereby retrieval testing of previously seen "old" stimuli produces greater positive amplitude than "new" foil stimuli (Barbeau et al., 2008; Maillard et al., 2011). The P300 is a positive peak (also termed 'P3b') which occurs from 300 to 500 ms, is maximal at parietal sites and is involved with attentional processes related to memory encoding and also to novelty-related changes, both of which are thought to involve hippocampal processing

(Azizian & Polich, 2007; Brazdil, Roman, Daniel, & Rektor, 2003; Friedman et al., 2001; Knight & Nakada, 1998; Polich, 2007; Shucard, Tekok-Kilic, Shiels, & Shucard, 2009).

During memory tasks, the ERP peaks within a third time window from 340 to 800 ms includes the N400 which has been linked to semantic access, the FN400 which has been associated with item familiarity, and the P600 which has been considered an index of successful episodic recollection (Duzel, Yonelinas, Mangun, Heinze, & Tulving, 1997; Fernandez et al., 1999; Kutas & Federmeier, 2011; Rugg & Curran, 2007). To anticipate the results, we did not see large peaks within this time window and therefore no analysis was conducted; in later discussion possible reasons for their absence are considered.

In summary, ERP peaks were measured in the frontal and parietal regions to investigate the separate and interacting effects of material and process type on lateralisation during memory retrieval. We predicted that 1) material would influence lateralisation, with left-lateralisation for verbal materials and right-lateralisation for nonverbal materials; and 2) the type of memory-related process would influence hemispheric lateralisation, with left-lateralisation for encoding and right-lateralisation for retrieval.

2. Materials and Methods

2.1 Participants

Twenty-two adults (mean age = 22.23 years, *SD* = 5.00, range 18 to 37; 17 females) were paid $30 to participate in the experiment. Data from two additional participants were excluded due to significant EEG artefacts (i.e., more than 30% of epochs rejected). All participants reported normal or corrected-to-normal vision and that they were right-handed for writing. The experimental methods were approved by the Macquarie University Human Research Ethics Committee (Ref# 5201100342) in accordance with the Declaration of Helsinki. Informed consent was obtained from all participants.

2.2 Apparatus

Testing occurred in a dimly lit room, with participants at a viewing distance 60 cm

from an 18” Sony Trinitron CRT monitor (resolution 1024 x 768 pixels, 32 bit, 96 dpi, 100 Hz refresh rate) showing a light grey background. Task instructions for both conditions were displayed onscreen. Stimuli were controlled using Presentation (Neurobehavioral Systems Inc, Version 10.3) and EEG was recorded with NeuroScan Synamps2. Participants responded with a Cedrus® RB830 button box, pressing one of two buttons that were positioned to the immediate left and right of the box’s midline.

2.3 Stimuli

2.3.1 Verbal (printed pseudowords)

Target stimuli for the verbal condition were six, disyllabic, eight-letter pseudowords (*boltrens*, *morphalt*, *prealent*, *breatish*, *calthern*, *slempern*). Foils always differed from the target stimuli by one letter, which could be any of the eight letters regardless of position in the word or whether a consonant or vowel (e.g. *boltrons, morthalt, crealent,* etc.) as long as the syllabic structure of the word was not altered. The resulting target-foil visual similarity was designed to require careful analysis of the entire pseudoword. These pseudowords were presented on the computer screen in Courier New font, subtending a maximum of 6.5 x 1.1^0 visual angle. There were 48 foils, 96 in total, and eight different foils per target stimulus.

2.3.2 Nonverbal (dot patterns)

Target stimuli for the nonverbal condition were six spatial arrays of three dark grey dots each with a diameter subtending a 0.63^0 visual angle, as shown in Figure 1(a). Pilot experiments indicated that these three-dot arrays were both difficult to verbalise in healthy participants and difficult to remember for people with right temporal lobe damage, suggesting their potential value in activating the right hemisphere (Lee, Gonzalez, & Savage, 2007). Each three-dot array was freely positioned, without a grid or outer boundary, within a maximum two-dimensional range of 9.12^0 by 6.30^0 visual angle centred on the screen.

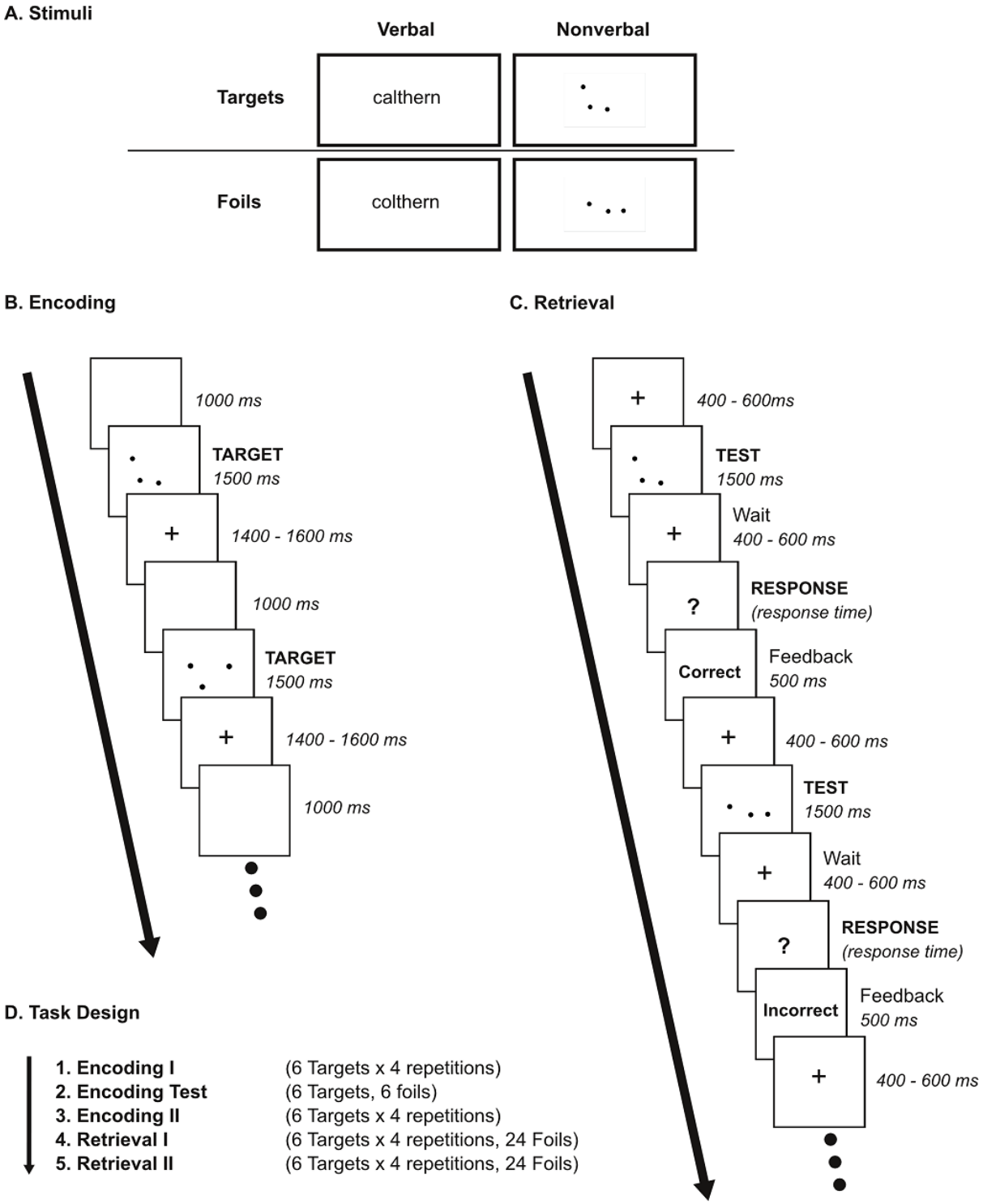

Fig 1. Experimental design. (a) Experimental stimuli - examples of targets and related foils for both material types. (b) Encoding phase - target presentation followed by interval of randomised duration; (c) Retrieval phase - test stimulus presentation (intermixed sequence of targets and foils) followed by interval of randomised duration, response screen and feedback. (d) Task Design – list of task phases including number of targets and foils per phase.

Arrays could take any combination of positions within the specified range with five

restrictions: 1) no pair of dots was completely aligned along the horizontal or vertical axis; 2) dots could not be aligned to form a straight line along any angle or point directly towards a corner of the screen as these may be verbalised (e.g., as “line”, “top left corner”); 3) no array configuration (i.e., the specific combination of angles between dots) could be repeated, transposed or rotated; 4) there was a minimum of a 0.81^0 visual angle between the nearest outer edges of adjacent dots; and 5) dots were separated from each other by at least this minimum distance. These restrictions encouraged encoding of exact dot locations and also their spatial inter-relation. The foils corresponding with each target stimulus were produced by rearrangement of target dot positions such that there was one to three with a changed position, and the average positional change in any direction was 1.11^0 visual angle per dot (*SD* = 0.13, maximum 5.37). Otherwise, foil arrays had the same restrictions as target stimuli.

2.4 Procedure

2.4.1 Task design

The format of the memory task, depicted in Figure 1(b,c), was equivalent for both material types, and involved five phases: Encoding I; Encoding Test; Encoding II; Retrieval I; Retrieval II. In Encoding I, participants were instructed to remember the target stimuli, with no instructions to categorise or label the stimuli. The six stimuli were presented sequentially in pseudorandom order, then repeated four times with the restriction that immediate repetitions were avoided. This was followed by an Encoding Test (six target items and six foils with no repetitions, intermixed in pseudorandom order) in order to ensure that participants were learning and understood the task. Encoding I was then repeated with a re-randomised stimulus order (Encoding II). Note that memory performance and ERP data were analysed from Encoding I and II phases but not the Encoding Test.

The Encoding phases were followed by two consecutive Retrieval phases in which the six target items were repeated four times (48 total target trials), intermixed with 24 different foils, shown once each (with 24 foil trials over 2 phases, eight unique foils per target stimulus,

and no foil repeated). Each target was repeated 8 times and foils were refreshed with each repetition to ensure that memory for multiple aspects of the target stimuli were being tested. For example, for different pseudoword foils, different letters within the words were changed in order to ensure that memory for the target word as a whole was tested rather than only the initial letter cluster, thereby requiring encoding, and subsequent recognition, of all associated word features.

Across all phases the stimuli were presented for 1500 ms, and, to enhance sustained attention to the task, the duration of pre- and post-stimulus intervals, during which participants were instructed to fixate a cross, was jittered randomly (Encoding: between 1400 and 1600 ms; Retrieval: 400 to 600 ms) as shown in Figure 1(b,c). During the Encoding Test and Retrieval I and II phases, participants fixated the cross before either a target or foil stimulus was presented and pressed one button to indicate a match to a target stimulus ("yes—seen before") or a second button to indicate a new item ("no—unseen"). On-screen feedback was provided in both the Encoding Test and Retrieval I and II phases ("correct" or "incorrect"). Participants were encouraged to respond quickly and accurately. To account for potential response-hand-related hemispheric lateralisation in ERP peaks, response-hand was counterbalanced between participants: half used the right button for "yes" and the left for "no" for both types of task, with the assignment reversed for the other half.

2.5 EEG recording and offline analysis

EEG data were recorded during all five task phases using sintered Ag-AgCl electrodes mounted in an Easy-Cap according to the 10-20 system (FP1, FP2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz, and O2). The ground electrode was positioned between FPz and Fz. Activity from both mastoids was recorded and the left mastoid served as the online reference. Vertical eye movements (VEOG; vertical electrooculogram) were measured with electrodes placed above and below the left eye. Horizontal eye movements were measured with electrodes on the outer canthi of each eye. Electrode impedance was kept below 5 kΩ. The signal was amplified

20,000 times (SynAmps2 amplifier, Compumedics Limited), sampled at 500 Hz, low-pass filtered at 100 Hz online and saved to a hard disk.

Offline analysis was conducted using NeuroScan Edit software (Compumedics Limited). First, portions of EEG data containing large movement-related artefacts were rejected manually. The data were then re-referenced to the average activity of the left and right mastoids. The influence of VEOG activity was reduced using an ocular artefact rejection algorithm that was calculated from at least 40 x 400 ms epochs containing a clear blink (as subjectively judged by visualisation), and an amplitude increase of 10% of the maximum activity recorded at the VEOG channel. Data were band-pass filtered between 0.1 to 30 Hz (FIR, 12 dB roll-off). The EEG was divided into 1600 ms epochs with a -100 ms pre-stimulus interval relative to the onset of each stimulus (target or foil) in the Encoding (I and II) phases (ERPs were not calculated during the Encoding Test) and Retrieval (I and II) phases. Epochs were baseline corrected between -100 and 0 ms, and epochs with amplitude variations above 100 μV were removed from the analysis. The mean number of epochs rejected out of a possible 144 (48 for Encoding, 96 for Retrieval) was negligible (verbal: 3.37%; nonverbal: 2.46%). Epochs associated with incorrect responses were also excluded from further analysis: verbal M = 94.31% accepted, SD = 6.11; nonverbal M = 84.54% accepted, SD = 8.67.

2.6 ERPs

Accepted epochs were used to create 32 ERPs per participant: eight lateralised sites (left: F3, F7, P3, P7; right: F44, F8, P4, P8) by two material types (verbal, nonverbal) by two processes (encoding, retrieval). Visual inspection of the grand average and individual average waveforms showed a large positive-going peak (P100) at parietal sites and a smaller negative-going peak at frontal sites (N100) from 80 to 120ms, a large parietal negative-going peak (N170) and a large frontal positive-going peak (vertex positive potential, VPP) from 140 to 220 ms, and a large positive-going peak at parietal sites (P300) and a large negative-going peak at frontal sites (N270) from 220 to 340 ms. From 340 ms to 1500 ms there were no clear peaks and amplitudes deviated little from zero, therefore no peaks were calculated in this

period.

Mean amplitudes were calculated for each peak then corrected for the mean amplitude of the previous peak (e.g., corrected N170 = N170 minus P100; corrected N270 = N270 minus VPP). These corrections an extra precaution to ensure that any hemispheric differences measured occurred uniquely in the time window of interest, rather than as an artefact of earlier hemispheric differences or an increase in background noise (for more on the general effects of the baseline on mean amplitude measures see e.g., Clayson, Baldwin, & Larson, 2012). The corrected mean amplitudes are henceforth referred to as N170, VPP, P300, and N270. Region-wide measures were obtained by averaging the corrected mean amplitudes of P7 and P3 (left parietal), P8 and P4 (right parietal), F7 and F3 (left frontal), and F8 and F4 (right frontal), resulting in 32 measures for analysis (2 material types x 2 processes x 2 regions x 2 hemispheres x 2 time windows).

2.7 Statistical analyses

2.7.1 Memory performance

Mean percentage correct target and foil responses were calculated during the Retrieval Phase, from which mean percentage correct and sensitivity (*d'*) values for target/foil discrimination were calculated to ensure that each material type was learned adequately. *d'* is based on z-score transformations and takes into account both hits and false alarms, controlling for response biases (McNicol, 1972). Response times (RTs) were calculated by subtracting the time of response from the onset time of the response screen (see Figure 1), and median RTs were calculated for each participant. For analysis, RTs were inverse-transformed (i.e., 1/RT) to reduce the impact of outliers.

In order to determine whether task performance had a significant impact on EEG measures, correlations were calculated between: 1) the difference in retrieval accuracy (*d'*) between the materials (i.e., $d'_{\text{verbal}} - d'_{\text{nonverbal}}$), and 2) the difference in ERP measures between the materials (i.e., $ERP_{\text{verbal}} - ERP_{\text{nonverbal}}$), for each of the 8 ERP peak measures (all

combinations of Peak [VPP/N170, N270/P300] x Processing [encoding, retrieval], Region [Parietal, Frontal] x Hemisphere [left, right]). Equivalent correlations were calculated between (inverse-transformed) RTs and ERP measures. To calculate 95% confidence intervals for each correlation, a bootstrap method was conducted with 1000 samples (IBM SPSS Statistics version 22).

2.7.2 ERP hemispheric lateralisation and memory (old/new) effects

The key predictions of material and process effects on hemispheric differences were tested by comparing mean amplitudes using four-way repeated measures ANOVA with: material (verbal, nonverbal) x process (encoding, retrieval) x region (frontal, parietal) x hemisphere (left, right). Separate ANOVAs were run for peaks in each time window (i.e., 1. N170 and VPP; 2. N270 and P300). We analysed main effects and interactions between these factors as well as planned contrasts to compare material and process effects. As we used an experimental procedure with multiple repeated items and trials, in order to maximise the proportion of correct responses, we did not compare ERPs to correct and incorrect stimuli due to the low proportion, and hence poor reliability, of the incorrect ERPs. Instead, to assess memory for the Retrieval Phase, we compared repeated (old) with foil (new) stimuli using separate Material x Repetition (repeated, non-repeated) x Region x Hemisphere ANOVAs and contrast tests for each time window.

As each pair of peaks within each time window strongly resembled inverted versions of each other (negative N170 and positive VPP within 140 to 220 ms; positive P300 and negative N270 within 220 to 340 ms), the absolute values of the negative-going peaks (i.e., |N170| and |N270|) were calculated to standardise all measures as positive amplitudes. Therefore, positive means, *t*, and *d* values always corresponded to differences in the following directions: verbal > nonverbal (material), encoding > retrieval (process), parietal > frontal (region), and left > right (hemisphere), with negative values indicating the respective opposite effects (e.g., nonverbal > verbal for material). In-text reporting of contrasts is restricted to comparisons of direct theoretical relevance; for brevity, only p_p values are shown. Complete

inferential statistics for material/process ANOVAs are reported in Supplementary Tables 2 and 3, respectively, for VPP/N170 and N270/P300.

2.7.3 Data treatment, effect sizes and accounting for multiple comparisons

To ensure that analyses of accuracy, RT, and ERP measures were robust to the effect of outliers, extreme values were subjected to a Winsorisation procedure whereby values greater than the 95th or less than the 5th percentiles were adjusted to these cut-off values. Extreme values accounted for less than 5% of the data across variables. Effect size for all ANOVAs is reported as partial eta-squared (η_p^2), the proportion of variance explained controlling for other effects (interpreted as small: .01 to .09; medium: .09 to .25; or large: > 0.25; Kenny, 1987). For interaction contrast tests, the effect size (*d*) is reported, adjusted for repeated measures using Morris and DeShon's (2002) method and appraised according to Lipsey and Wilson (2001; i.e., small: < 0.3; medium: 0.3 to 0.7; large: > 0.7). For contrast tests, *p*-values were adjusted for multiple comparisons (reported as p_p) using a permutation testing procedure designed for repeated measures (10000 permutations, MATLAB function "mult_comp_perm_t1" by Groppe, Urbach, & Kutas, 2011). Like Bonferroni correction, this method adjusts *p*-values to control the family-wise error rate. However, for ERP data, the permutation method is more powerful than Bonferroni due to high within-subject correlations between sites and conditions (Blair & Karniski, 1993; Burgess & Gruzelier, 2000; Good, 1994; Manly, 1997).

3. Results

3.1 Behavioural performance

Retrieval accuracy (*d'*) was significantly higher for verbal stimuli, $M = 3.53$ [CI_{95}: 3.14 3.93] (94% correct), than nonverbal stimuli, $M = 2.22$ [1.90 2.54] (84%), $t(21) = 5.49$, $p < .001$. RTs did not significantly differ between verbal stimuli, $M = 324$ ms [291 365], and nonverbal stimuli, $M = 326$ ms [294 366], $F(1,21) = 0.01$, $p = .91$. There was minimal impact of performance variables on lateralisation of ERP measures, as differences in ERP measures

between the materials (i.e., verbal – nonverbal; averaged across process type, region, and hemisphere) did not significantly correlate with differences in *d*' between the materials, $r(20) = -.03$, $p = .91$, or with differences in RT between the materials, $r(20) = .09$, $p = .68$. Correlations between performance variables and ERP measures were also not significant when ERP measures were separated by region, and hemisphere (see Supplementary Tables 1 to 3 for complete statistics for *d'* and RT). In sum, the impact of differences in retrieval accuracy or response speed on ERP measures is minimal.

3.2 ERP hemispheric lateralisation: material and processing

Figure 2 shows grand average ERPs for both material types at frontal and parietal regions separated by task phase (encoding, retrieval) and hemisphere (left, right). As mentioned in the methods, negative amplitudes were reversed to standardise measures as positive, and therefore positive means, *t*, and *d* values always corresponded to differences in the following directions: verbal > nonverbal (material), encoding > retrieval (process), parietal > frontal (region), and left > right (hemisphere).

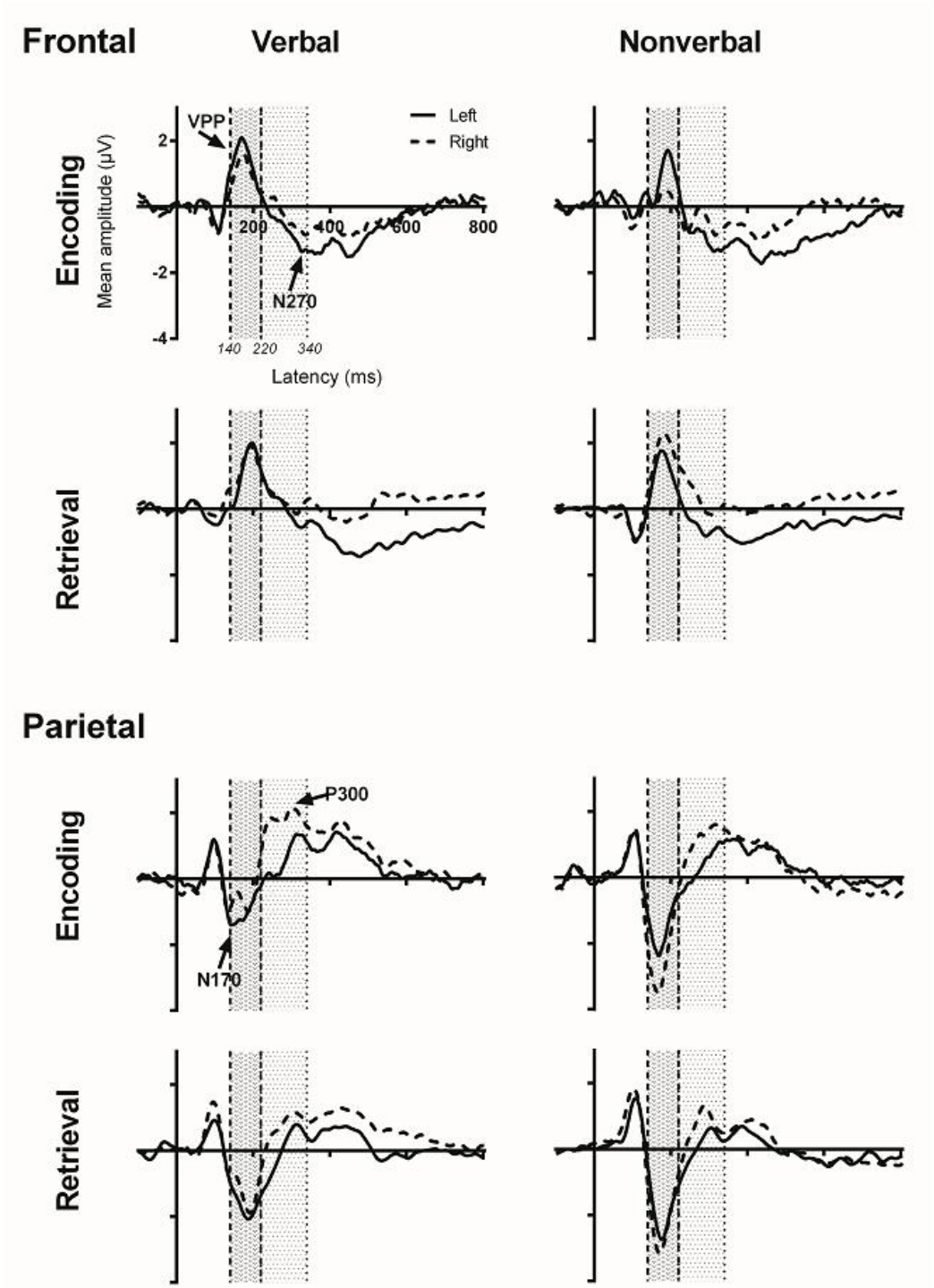

Fig. 2. Grand average ERP waveforms for verbal and nonverbal materials during encoding and retrieval with left and right hemisphere electrodes at frontal and parietal sites. Shaded areas indicate time intervals over which mean amplitude was calculated for VPP and N170 (140 to 220 ms) and N270 and P300 (220 to 340 ms).

3.2.1 VPP and N170 mean amplitude

The ANOVA revealed a significant main effect of material (nonverbal > verbal), $p < .001$, process (retrieval > encoding), $p = .002$, and region (parietal > frontal), $p < .001$, but

the effect of hemisphere was not significant, $p = .41$. The following interactions were significant: Material x Region, $p < .001$; Material x Hemisphere, $p < .001$; Process x Hemisphere, $p = .02$, and Material x Process x Region x Hemisphere, $p = .01$.

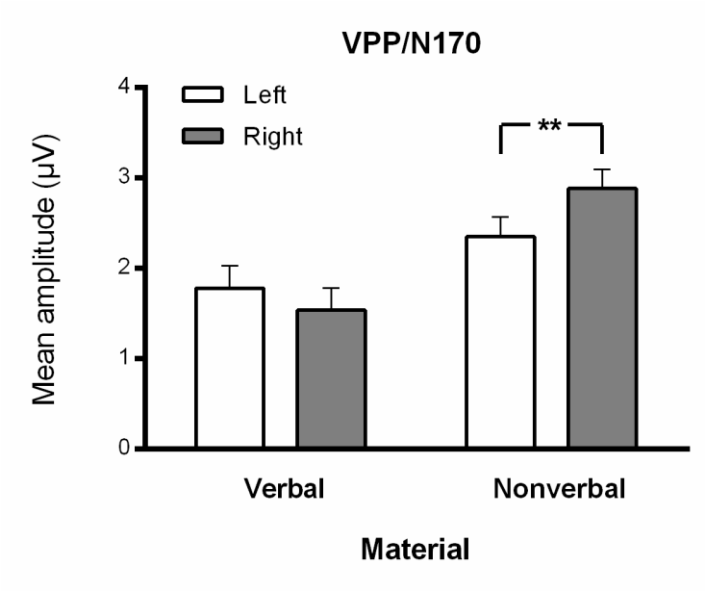

Fig. 3. Mean peak amplitude (corrected and standardised, with standard error bars) for combined early peak data (VPP/N170) in the left and right hemisphere for verbal and nonverbal material. Asterisks refer to significant simple contrasts for hemispheric lateralisation (left – right, located by x-axis labels) and for material (verbal – nonverbal, by legend labels) within each hemisphere for the Material x Hemisphere interaction. ** $p < .01$.

Further analysis showed right-lateralisation of mean amplitude of the early peaks for nonverbal compared with verbal material, $p_p < .001$, and for nonverbal materials in isolation, the right-lateralisation was significant, $p_p = .009$ (verbal, $p_p = .66$; see Figure 3), supporting the material hypothesis. Indicating the consistency of the nonverbal-right hemisphere relationship, nonverbal material produced significantly larger peaks in the right hemisphere than the left during both encoding and retrieval, all p_ps < .001, in the frontal and parietal regions, p_ps < .001, and for each combination of process and region in the four-way interaction, p_ps < .04.

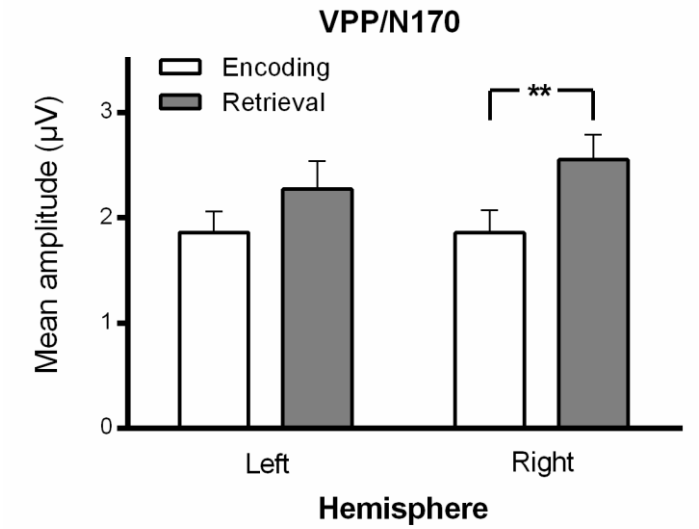

Fig. 4. Mean peak amplitude (corrected and standardised, with standard error bars) for combined early peak data (VPP/N170) in the left and right hemisphere during encoding and retrieval. Asterisks refer to significant contrasts for process (encoding – retrieval, located by x-axis labels) within each hemisphere for the Process x Hemisphere interaction. ** $p < .01$.

The right hemisphere peaks were significantly larger during retrieval than encoding, supporting the process hypothesis, $p_p = .005$ (left, $p_p = .07$; see Figure 4). The four-way interaction was explained by a larger process effect (retrieval > encoding) in the right than left frontal VPP for both material types, p_ps = .003, supporting the process hypothesis. In contrast for the parietal N170, this effect was only significant for verbal material, $p_p = .04$, indicating that the process hypothesis was supported for verbal material but not for nonverbal material. In addition the relative right-lateralisation of nonverbal versus verbal materials was only significant for the parietal N170 during encoding, $p_p = .004$ (retrieval, $p_p = .99$). Figure 5 shows the pattern of hemispheric lateralisation for early peaks across all combinations of material and process, with region separated by panel: frontal in the upper, parietal in the lower. All contrasts for hemispheric lateralisation (left – right) were not significant (p_ps > .05) for the Material x Process x Region x Hemisphere interaction.

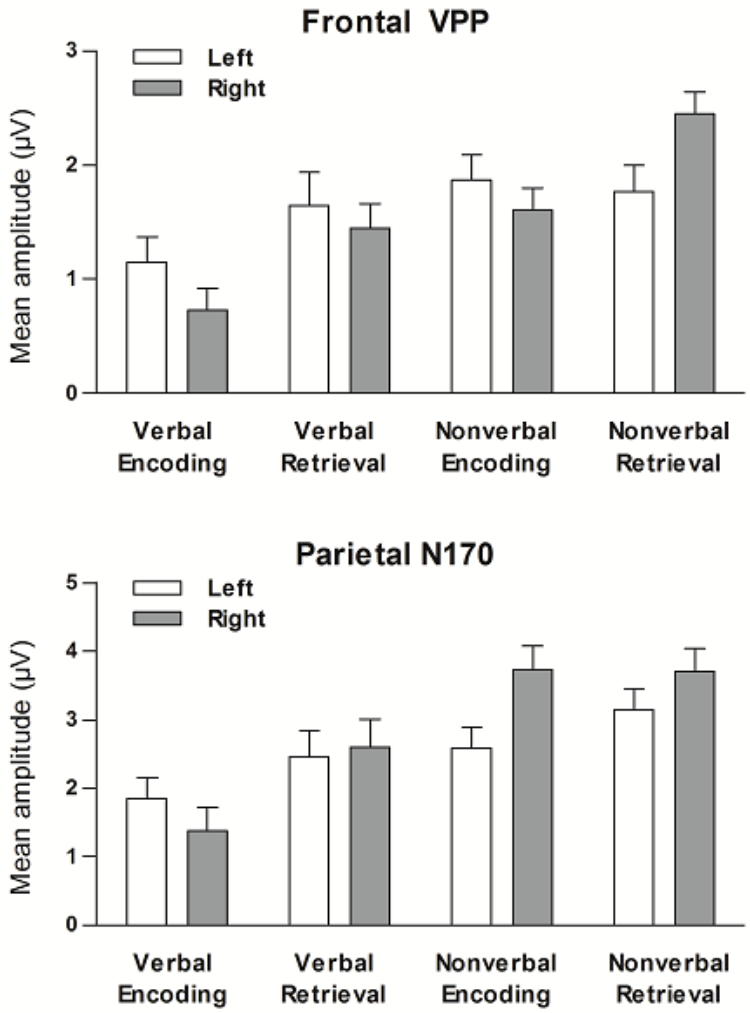

Fig. 5. Mean peak amplitude (corrected and standardised, with standard error bars) for early peaks in the left and right hemisphere for all combinations of material and process. Top: frontal VPP. Bottom: parietal N170.

3.2.2 N270 and P300 mean amplitude

The ANOVA revealed a significant main effect of material (nonverbal > verbal), $p = .002$, and region (parietal > frontal), $p < .001$, while effects of hemisphere, $p = .07$, and process, $p = .30$, were not significant. The following interactions were significant: Material x Region, $p = .045$; Material x Hemisphere, $p = .02$; Region x Hemisphere, $p < .001$; Material x Process x Region, $p = .03$; and Process x Region x Hemisphere, $p < .001$.

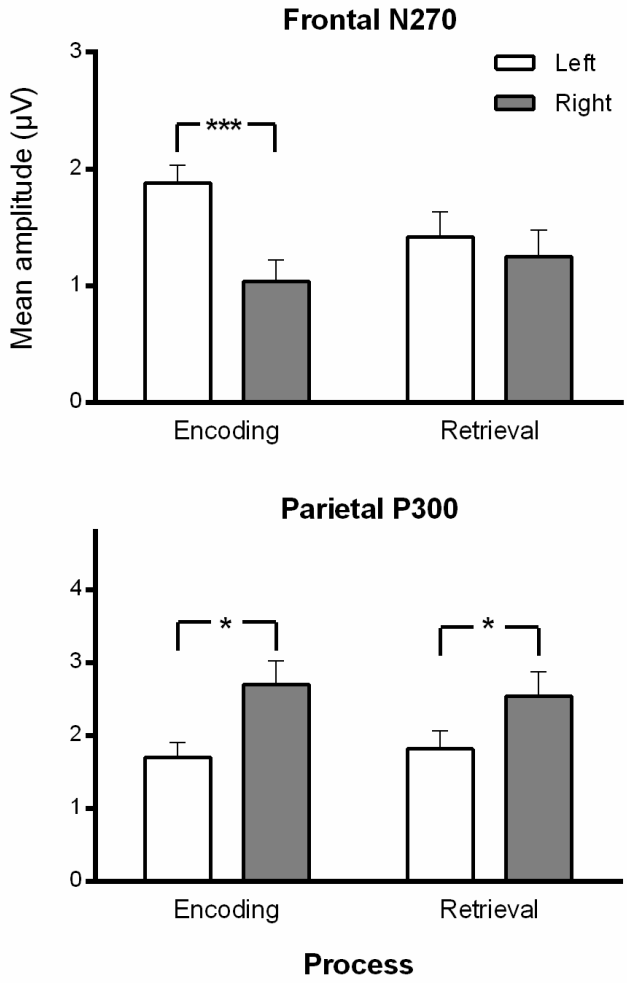

Fig. 6. Mean peak amplitude (corrected and standardised, with standard error bars) for combined late peak data (N270/P300) in the left and right hemisphere for encoding and retrieval. Asterisks refer to significant contrasts for hemispheric lateralisation (left - right, by legend labels) within each process for the Process x Region x Hemisphere interaction. * $p < .05$, *** $p < .001$.

Further analysis showed nonverbal material produced larger peaks than verbal material in the right hemisphere, $p_p = .004$, supporting the material hypothesis. In the frontal region there was significant left-lateralisation during encoding, $p_p < .001$, but not during retrieval, $p_p = .77$ (encoding > retrieval, $p_p = .003$; see Figure 6), consistent with the process hypothesis. In contrast, in the parietal region there was significant right-lateralisation during both encoding, $p_p < .001$, and retrieval, $p_p = .03$ (encoding > retrieval, $p_p = .02$), challenging the process hypothesis. The above effects occurred in the context of overall right-lateralisation of the parietal P300, $p_p < .001$, versus left-lateralisation of the frontal N270, $p_p = .003$. Figure 7 shows the pattern of hemispheric lateralisation for late peaks across all combinations of

material and process.

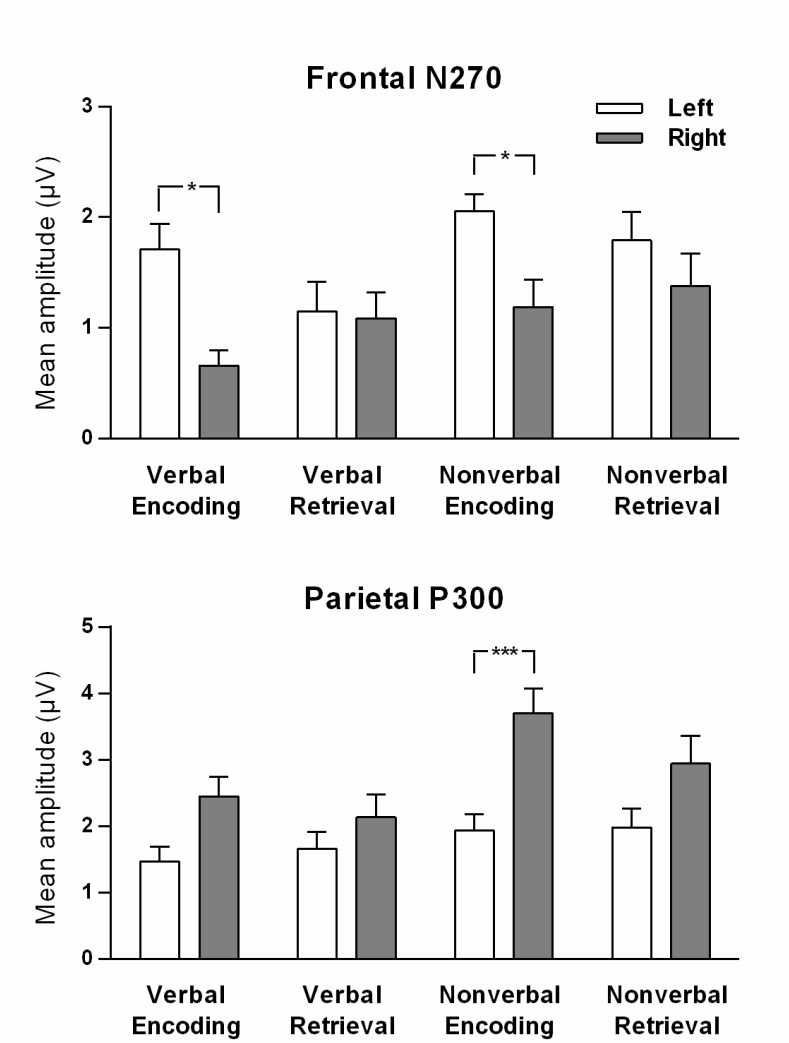

Fig. 7. Mean peak amplitude (corrected and standardised, with standard error bars) for late peaks in the left and right hemisphere for all combinations of material and process. Top: frontal N270. Bottom: parietal P300. Asterisks refer to significant contrasts for hemispheric lateralisation (left – right) within the Material x Process x Region x Hemisphere interaction. * $p < .05$, *** $p < .001$.

3.3 Mean amplitude effects due to item repetition (old/new effect)

For both VPP/N170 and N270/P300 all main effects, interactions, and contrasts associated with Repetition were non-significant, p_ps > .053 (i.e., there were no old/new memory effects for early or late peaks; complete inferential statistics for repetition (old versus new) analyses for VPP/N170 and N270/P300 respectively can be found in Supplementary Tables 4 and 5).

4. Discussion

The aim of this study was to investigate the separate and interacting effects of material and processing on hemispheric lateralisation of memory processing. The first prediction was that material would have an effect on lateralisation, with relative left-lateralisation for verbal material and relative right-lateralisation for nonverbal material. The second prediction was that the type of memory processing would also have an effect on hemispheric lateralisation, with relative left-lateralisation for encoding and relative right-lateralisation for retrieval. We also explored the mediating effects of brain region by measuring event-related potentials (ERPs) in frontal and parietal regions, and whether the effects would occur relatively early or late following stimulus onset. To our knowledge, this study is the first to use ERPs to directly compare material and processing accounts of hemispheric lateralisation.

The results showed a consistent effect of material on lateralisation. Compared with verbal material, nonverbal material produced larger peak amplitudes over the right-hemisphere during encoding and retrieval, in early peaks (140 to 220 ms, frontal VPP and parietal N170) and late peaks (220 to 340 ms, frontal N270 and parietal P300, albeit weaker in strength). However, there was a partial material specific hemispheric dissociation; when considered in isolation, verbal material was not associated with left-lateralisation.

The effect of process on lateralisation depended on the brain region and whether early or late ERP peaks were involved. In general, the results supported the process hypothesis in frontal regions for both early and late peaks: regardless of material type, the frontal VPP was right-lateralised during retrieval relative to encoding, and the frontal N270 was more left-lateralised for encoding compared with retrieval. In contrast, the results for the parietal N170 for nonverbal material contradicted the processing hypothesis, with right-lateralisation during encoding compared with retrieval, and for the parietal P300 there was right-lateralisation regardless of the process type.

In summary, the data support an account in which nonverbal material affects right-lateralisation in a consistent manner, while the effects of processing are consistent with HERA

predictions at frontal sites, but are affected by interactions with material type at parietal sites. Therefore, the effects of material and process on lateralisation interact in a manner that depended on the timing of the brain response by brain region. The finding that process affected lateralisation in the manner predicted by HERA at frontal sites but only for verbal materials at parietal sites, is broadly consistent with evidence of process-related lateralisation in the prefrontal cortex (e.g., Cabeza & Nyberg, 2000) and with interactions between brain regions by processing by material (e.g., McDermott et al., 1999; Nyberg et al., 2000). In this study, while nonverbal materials did not adhere to the predictions of HERA for parietal peaks, supporting previous assertions that the HERA model may not be valid for nonverbal material (Wagner et al., 1998), the pattern of lateralisation for nonverbal material at frontal sites did support HERA.

It has been suggested that attempts to verbalise nonverbal materials may explain left frontal activations during encoding (e.g., Wagner et al., 1998). However, the findings of the current study suggest that the left frontal N270 involved during encoding is not related to the verbalisability of the material, as left-lateralisation occurred for both verbal and nonverbal stimuli (see Figure 7, top). In addition, neither stimulus type contained semantic information, and participants were not instructed to categorise or label the stimuli, likely reducing the chance that verbalisation confounded the results of our study compared to previous studies. Therefore, the findings for the frontal N270 peak are interpreted as more likely to reflect a left frontal neural substrate for encoding, consistent with previous findings supporting HERA. Future investigations with quantification of the level of verbalisability may cast further light on the effect of verbalisation on lateralisation in frontal regions.

Our findings of an association between nonverbal material and right-lateralisation is consistent with previous neuropsychological, neuroimaging, and ERP evidence of right-lateralisation during memory processing of nonverbal materials such as abstract geometric figures or spatial positions (Bellgowan, Buffalo, Bodurka, & Martin, 2009; Bohbot et al., 1998; Diaz-Asper, Dopkins, Potolicchio, & Caputy, 2006; Kessels, Postma, de Haan, &

Kappelle, 2002). The strength of this nonverbal material effect was greater for the early peaks than for late peaks, consistent with previous ERP findings (Baker & Holroyd, 2013; Beisteiner et al., 1996; Maillard et al., 2011). In addition, the finding that processing of nonverbal stimuli was more right-lateralised during encoding than during retrieval supports previous neuropsychological findings that right MTL damage has a greater effect on initial learning of material than on its subsequent retrieval after a delay (Jones-Gotman, Smith, Frisk, & Routhier, 1996; Majdan, Sziklas, & Jones-Gotman, 1996).

The absence of left-lateralised processing of verbal material stands in contrast with studies showing left hemisphere dominance for pseudoword processing (e.g., Bentin et al., 1999; Falk, Cole, & Glosser, 2002; Kotz, Cappa, von Cramon, & Friederici, 2002; Moser, Baker, Sanchez, Rorden, & Fridriksson, 2009). Our findings are indirectly supported, however, by some findings of relative right-lateralisation for processing pseudowords compared with real words (Doyle, Rugg, & Wells, 1996; Evans & Federmeier, 2007; Marsolek, Kosslyn, & Squire, 1992; Sekiguchi, Koyama, & Kakigi, 2001; Swick & Knight, 1997). Pseudowords lack meaning, and have novel orthographic and phonological forms. In the case of our stimuli, as foils only differed from targets by one letter in any position, detailed visual analysis was required to successfully perform the memory task, and both foils and targets lacked orthographic or phonological neighbours from which existing networks could be drawn to aid memory. Therefore, relative to real words, remembering pseudowords is likely to require a greater dependence on processes that have been associated with right-lateralised brain activity, such as letter-by-letter reading and spatial localisation and ordering of the letters (e.g., Bouma, 1987; Ellis et al., 2004; Gross, 1972; Pirozzolo & Rayner, 1977). Nevertheless, we observed greater involvement of the right hemisphere in memory for the dot arrays than the pseudowords, suggesting that the added requirement for spatial memory increased right-lateralisation above and beyond the influences of novelty and spatial attention per se.

4.1 Limitations and future research

One limitation of this study relates to the absence of large ERP peaks from 340 to 800 ms (e.g., FN400 and a late positive component/P600) that have been associated with memory encoding and retrieval tasks (e.g., Friedman & Johnson, 2000; Rugg & Curran, 2007). It is not clear why these later components did not emerge and drive commonly reported "old/new" memory effects. The absence of the memory effects may suggest that the observed material- and process-related hemispheric differences exclusively reflect non-memory processing such as perceptual priming. This account of the data seems unlikely, however: If repetition was sufficiently suppressive as to obscure old/new memory effects, it is unclear why other effects remained large in size (e.g., of material, processing, and hemisphere, with complex interactions). The main effects of processing type are particularly hard to explain since these occurred regardless of the type of stimulus, therefore obviating a perceptual priming explanation. Furthermore, this explanation would include a novelty effect (new > old) during retrieval as targets were repeated while foils were not, but this was not evident. Old/new memory effects were likely to be smaller than other effects (e.g., main effects of material) and hence were obscured while the latter were sufficiently large to remain statistically reliable. Given this account, and the lack of significant differences in ERPs due to accuracy, we interpret our findings as not confounded by repetition or priming effects.

Another important factor is the non-semantic nature of the materials used. Memory tasks using highly novel abstract items have often failed to produce an old/new effect (Beisteiner et al., 1996; Mecklinger & Müller, 1996; van Petten & Senkfor, 1996; Voss & Paller, 2009). Both our nonverbal and verbal materials may have failed to elicit the old/new effect due to their low level of meaningfulness (e.g., Voss & Paller, 2007; Yovel & Paller, 2004). Replication with the level of meaningfulness systematically manipulated could confirm the importance of this factor for demonstrating old/new effects.

An important issue relating to interpretation of the material effects is the potential role of low-level stimulus characteristics such as size and spatial frequency, since ERPs are

sensitive to differences in both (e.g., Luck, 2005; Sergent, 1982). The dot arrays were larger in size and lower in spatial frequency than the pseudowords, and there is evidence that both of these attributes are associated with increased right-lateralised attentional processes and hence confound the effects of spatial memory observed in the current study (e.g., van der Ham, Postma, & Laeng, 2014). To some extent, this is an intrinsic confound: spatial processing and memory usually pertain to lower spatial frequencies and larger stimulus sizes than word stimuli, and therefore the stimuli we used were ecologically valid and accurately represented each material type as they typically appear. However, to completely exclude these factors, this study should be replicated controlling for spatial frequency and size between the verbal and nonverbal stimuli (as carried out in Chapters 5 and 6).

Regarding the HERA model, our findings must be interpreted with caution. We acknowledge that aspects of our methodology, including multiple repetitions of stimuli across encoding trials (versus a simple study-test design) and the use of ERPs (versus PET or fMRI), do not directly conform with previous studies. Due to the low spatial resolution of ERPs and only four electrode sites, we cannot definitively attribute our results to hemispheric differences specifically between the temporal or prefrontal regions (e.g., Golby et al., 2001). Nor can we equate our findings with those from unilateral temporal lobe (or prefrontal cortex) patients (e.g., Redoblado, Grayson, & Miller, 2003). In addition, we did not observe the old/new effects for N400 and P600 peaks that have been connected with rhinal and hippocampal functioning (e.g., Fernandez et al., 1999; Smith, 1993). However, an MEG study investigating retrieval for words and kaleidoscope pictures found greater left activation for words and right activation for pictures in both temporoparietal regions (underlying the P7, P8 electrode sites we used) and the medial temporal lobe (Papanicolaou et al., 2002). Therefore, our observed right parietal lateralisation for nonverbal material may also be associated with similar medial temporal lobe asymmetries. Replication of our findings using techniques high spatial resolution and patients with lateralised lesions would clarify the role of both brain regions in the hemispheric asymmetries we observed.

4.2 Conclusion

The results of this ERP study confirm and expand upon previous research, showing that lateralising influences of material and process interact across early stages of neural processing (within 300 ms of stimulus onset). Importantly, lateralisation due to the type of memory processing may affect the degree of right-lateralisation elicited by nonverbal memory tasks. These findings suggest that considering both material specific and processing specific lateralisation effects has relevance in the clinical assessment of right hemispheric pathology.

References

Alpherts, W. C. J., Vermeulen, J., van Rijen, P. C., da Silva, F. H. L., van Veelen, C. W. M., & Dutch Collaborative Epilepsy, S. (2006). Verbal memory decline after temporal epilepsy surgery? A 6-year multiple assessments follow-up study. *Neurology, 67*(4), 626-631. doi: 10.1212/01.wnl.0000220139.45304.eb

Anderson, K. L., Rajagovindan, R., Ghacibeh, G. A., Meador, K. J., & Ding, M. Z. (2010). Theta oscillations mediate interaction between prefrontal cortex and medial temporal lobe in human memory. *Cerebral Cortex, 20*(7), 1604-1612. doi: 10.1093/cercor/bhp223

Azizian, A., & Polich, J. (2007). Evidence for attentional gradient in the serial position memory curve from event-related potentials. *Journal of Cognitive Neuroscience, 19*(12), 2071-2081. doi: 10.1162/jocn.2007.19.12.2071

Babiloni, C., Vecchio, F., Cappa, S., Pasqualetti, P., Rossi, S., Miniussi, C., & Rossini, P. M. (2006). Functional frontoparietal connectivity during encoding and retrieval processes follows HERA model - A high-resolution study. *Brain Research Bulletin, 68*(4), 203-212. doi: 10.1016/j.brainresbull.2005.04.019

Baker, T. E., & Holroyd, C. B. (2013). The topographical N170: Electrophysiological evidence of a neural mechanism for human spatial navigation. *Biological Psychology, 94*(1), 90-105.

Barbeau, E. J., Taylor, M. J., Regis, J., Marquis, P., Chauvel, P., & Liégeois-Chauvel, C. (2008). Spatio temporal dynamics of face recognition. *Cerebral Cortex, 18*(5), 997-1009. doi: 10.1093/cercor/bhm140

Barr, W. B. (1997). Examining the right temporal lobe's role in nonverbal memory. *Brain and Cognition, 35*(1), 26-41.

Beisteiner, R., Huter, D., Edward, V., Koch, G., Franzen, P., Egkher, A., . . . Lang, W. (1996). Brain potentials with old/new distinction of non-words and geometric figures. *Electroencephalography and Clinical Neurophysiology, 99*(6), 517-526.

Bell, B. D., & Davies, K. G. (1998). Anterior temporal lobectomy, hippocampal sclerosis, and memory: Recent neuropsychological findings. *Neuropsychology Review, 8*(1), 25-41. doi: 10.1023/a:1025679122911

Bellgowan, P. S. F., Buffalo, E. A., Bodurka, J., & Martin, A. (2009). Lateralized spatial and object memory encoding in entorhinal and perirhinal cortices. *Learning & Memory, 16*(7), 433-438. doi: 10.1101/lm.1357309

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience, 11*(3), 235-260.

Blair, R. C., & Karniski, W. (1993). An alternative method for significance testing of waveform difference potentials. *Psychophysiology, 30*(5), 518-524.

Blakemore, C. B., & Falconer, M. A. (1967). Long-term effects of anterior temporal lobectomy on certain cognitive functions. *Journal of Neurology, Neurosurgery, and Psychiatry, 30*(4), 364-367.

Blanchet, S., Desgranges, B., Denise, P., Lechevalier, B., Eustache, F., & Faure, S. (2001). New questions on the hemispheric encoding/retrieval asymmetry (HERA) model assessed by divided visual-field tachistoscopy in normal subjects. *Neuropsychologia, 39*(5), 502-509. doi: 10.1016/s0028-3932(00)00119-6

Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia, 36*(11), 1217-1238. doi: 10.1016/s0028-3932(97)00161-9

Bouma, A. (1987). Effects of concurrent spatial and verbal memory loads on serial position-functions of laterally presented letter strings. *Brain and Cognition, 6*(3), 295-320. doi:10.1016/0278-2626(87)90128-x

Brazdil, M., Roman, R., Daniel, P., & Rektor, I. (2003). Intracerebral somatosensory event-related potentials: effect of response type (button pressing versus mental counting) on

P3-like potentials within the human brain. *Clinical Neurophysiology, 114*(8), 1489-1496. doi: 10.1016/s1388-2457(03)00135-4

Burgess, A. P., & Gruzelier, J. H. (2000). Short duration power changes in the EEG during recognition memory for words and faces. *Psychophysiology, 37*(5), 596-606.

Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience, 12*(1), 1-47.

Clayson, P. E., Baldwin, S. A., & Larson, M. J. (2013). How does noise affect amplitude and latency measurement of event-related potentials (ERPs)? A methodological critique and simulation study. *Psychophysiology, 50*(2), 174-186.

Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, 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*, 291-307.

Desgranges, B., Baron, J. C., & Eustache, F. (1998). The functional neuroanatomy of episodic memory: The role of the frontal lobes, the hippocampal formation, and other areas. *Neuroimage, 8*(2), 198-213. doi: 10.1006/nimg.1998.0359

Diaz-Asper, C. M., Dopkins, S., Potolicchio, S. J., & Caputy, A. (2006). Spatial memory following temporal lobe resection. *Journal of Clinical and Experimental Neuropsychology, 28*(8), 1462-1481. doi: 10.1080/13803390500434359

Doyle, M. C., Rugg, M. D., & Wells, T. (1996). A comparison of the electrophysiological effects of formal and repetition priming. *Psychophysiology, 33*(2), 132-147. doi: 10.1111/j.1469-8986.1996.tb02117.x

Duzel, E., Yonelinas, A. P., Mangun, G. R., Heinze, H. J., & Tulving, E. (1997). Event-related brain potential correlates of two states of conscious awareness in memory. *Proceedings of the National Academy of Sciences of the United States of America, 94*(11), 5973-5978. doi: 10.1073/pnas.94.11.5973

Ellis, N. C., Natsume, M., Stavropoulou, K., Hoxhallari, L., Daal, V. H., Polyzoe, N., . . . Petalas, M. (2004). The effects of orthographic depth on learning to read alphabetic, syllabic, and logographic scripts. *Reading Research Quarterly, 39*(4), 438-468.

Evans, K. M., & Federmeier, K. D. (2007). The memory that's right and the memory that's left: Event-related potentials reveal hemispheric asymmetries in the encoding and retention of verbal information. *Neuropsychologia, 45*(8), 1777-1790. doi: 10.1016/j.neuropsychologia.2006.12.014

Falk, M. C., Cole, L. C., & Glosser, G. (2002). Pseudoword and real word memory in unilateral temporal lobe epilepsy. *Journal of Clinical and Experimental Neuropsychology, 24*(3), 327-334. doi: 10.1076/jcen.24.3.327.979

Fernandez, G., Effern, A., Grunwald, T., Pezer, N., Lehnertz, K., Dumpelmann, M., . . . Elger, C. E. (1999). Real-time tracking of memory formation in the human rhinal cortex and hippocampus. *Science, 285*(5433), 1582-1585. doi: 10.1126/science.285.5433.1582

Fernandez, G., & Tendolkar, I. (2001). Integrated brain activity in medial temporal and prefrontal areas predicts subsequent memory performance: Human declarative memory formation at the system level. *Brain Research Bulletin, 55*(1), 1-9. doi: 10.1016/s0361-9220(01)00494-4

Friedman, D., Cycowicz, Y. M., & Gaeta, H. (2001). The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience and Biobehavioral Reviews, 25*(4), 355-373. doi: 10.1016/S0149-7634(01)00019-7

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. doi: 10.1002/1097-0029(20001001)51:1<6::aid-jemt2>3.0.co;2-r

Golby, A. J., Poldrack, R. A., Brewer, J. B., Spencer, D., Desmond, J. E., Aron, A. P., & Gabrieli, J. D. E. (2001). Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. *Brain, 124*, 1841-1854. doi: 10.1093/brain/124.9.1841

Good, P. (1994). *Permutation Tests: A Practical Guide to Resampling Methods for Testing Hypotheses.* New York: Springer-Verlag.

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

Gross, M. M. (1972). Hemispheric specialization for processing of visually presented verbal and spatial stimuli. *Perception and Psychophysics, 12*(4), 357-363. doi:10.3758/bf03207222

Habib, R., Nyberg, L., & Tulving, E. (2003). Hemispheric asymmetries of memory: the HERA model revisited. *Trends in Cognitive Sciences, 7*(6), 241-245. doi: 10.1016/s1364-6613(03)00110-4

Henson, R. N., Goshen-Gottstein, Y., Ganel, T., Otten, L. J., Quayle, A., & Rugg, M. D. (2003). Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cerebral Cortex, 13*(7), 793-805.

Johnson, M. K., Raye, C. L., Mitchell, K. J., Greene, E. J., & Anderson, A. W. (2003). fMRI evidence for an organization of prefrontal cortex by both type of process and type of information. *Cerebral Cortex, 13*(3), 265-273. doi: 10.1093/cercor/13.3.265

Jones-Gotman, M., Smith, M. L., Frisk, V., & Routhier, N. (1996). Learning and retention of connected prose before and after surgical resection from a temporal lobe. *Epilepsia, 37*(S5), 120-120.

Joyce, C., & Rossion, B. (2005). The face-sensitive N170 and VPP components manifest the same brain processes: The effect of reference electrode site. *Clinical Neurophysiology, 116*(11), 2613-2631.

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., . . . Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron, 20*(5), 927-936. doi: 10.1016/s0896-6273(00)80474-2

Kennepohl, S., Sziklas, V., Garver, K. E., Wagner, D. D., & Jones-Gotman, M. (2007). Memory and the medial temporal lobe: Hemispheric specialization reconsidered. *Neuroimage, 36*(3), 969-978. doi: 10.1016/j.neuroimage.2007.03.049

Kenny, D. A. (1987). *Statistics for the social and behavioral sciences.* Boston: Little, Brown.

Kessels, R. P. C., de Haan, E. H. F., Kappelle, L. J., & Postma, A. (2001). Varieties of human spatial memory: a meta-analysis on the effects of hippocampal lesions. *Brain Research Reviews, 35*(3), 295-303.

Kessels, R. P. C., Kappelle, L. J., de Haan, E. H. F., & Postma, A. (2002). Lateralization of spatial-memory processes: evidence on spatial span, maze learning, and memory for object locations. *Neuropsychologia, 40*(8), 1465-1473.

Kimura, D. (1963). Right temporal-lobe damage. *Archives of Neurology, 8*, 264-271.

Knight, R. T., & Nakada, T. (1998). Cortico-limbic circuits and novelty: A review of EEG and blood flow data. *Reviews in the Neurosciences, 9*(1), 57-70.

Kotz, S. A., Cappa, S. F., von Cramon, D. Y., & Friederici, A. D. (2002). Modulation of the lexical-semantic network by auditory semantic priming: An event-related functional MRI study. *Neuroimage, 17*(4), 1761-1772. doi: 10.1006/nimg.2002.1316

Kühn, S., & Gallinat, J. (2014). Segregating cognitive functions within hippocampal formation: A quantitative meta-analysis on spatial navigation and episodic memory. *Human Brain Mapping, 35*(4), 1129-1142.

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*, 621-647. doi:10.1146/annurev.psych.093008.131123

Lee, S., Gonzalez, L., & Savage, G. (2007). Eye-tunes: Memory for spatial and melodic form. *Australian Journal of Psychology, 59*(S1), 222.

Lee, A. C. H., Robbins, T. W., Pickard, J. D., & Owen, A. M. (2000). Asymmetric frontal activation during episodic memory: the effects of stimulus type on encoding and retrieval. *Neuropsychologia, 38*(5), 677-692. doi: 10.1016/s0028-3932(99)00094-9

Lee, T. M. C., Yip, J. T. H., & Jones-Gotman, M. (2002). Memory deficits after resection from left or right anterior temporal lobe in humans: A meta-analytic review. *Epilepsia, 43*(3), 283-291.

Lipsey, M. W., & Wilson, D. B. (2001). *Practical meta-analysis* (Vol. 49): Sage publications Thousand Oaks, CA.

Luck, S. (2005). *An Introduction To The Event-Related Potential Technique*. Cambridge, Massachusetts: The MIT Press.

Maillard, L., Barbeau, E. J., Baumann, C., Koessler, L., Benar, C., Chauvel, P., & Liegeois-Chauvel, C. (2011). From Perception to Recognition Memory: Time Course and Lateralization of Neural Substrates of Word and Abstract Picture Processing. *Journal of Cognitive Neuroscience, 23*(4), 782-800. doi: 10.1162/jocn.2010.21434

Majdan, A., Sziklas, V., & Jones-Gotman, M. (1996). Performance of healthy subjects and patients with resection from the anterior temporal lobe on matched tests of verbal and visuoperceptual learning. *Journal of Clinical and Experimental Neuropsychology, 18*(3), 416-430. doi:10.1080/01688639608408998

Manly, B. F. J. (1997). *Randomization, Bootstrap, and Monte Carlo Methods in Biology* (2nd ed.). London: Chapman and Hall.

Marsolek, C. J., Kosslyn, S. M., & Squire, L. R. (1992). Form-specific visual priming in the right cerebral hemisphere. *Journal of Experimental Psychology-Learning Memory and Cognition, 18*(3), 492-508. doi: 10.1037//0278-7393.18.3.492

Martinez, A., Di Russo, F., Anllo-Vento, L., & Hillyard, S. A. (2001). Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clinical Neurophysiology, 112*(11), 1980-1998.

McDermott, K. B., Buckner, R. L., Petersen, S. E., Kelley, W. M., & Sanders, A. L. (1999). Set- and code-specific activation in the frontal cortex: An fMRI study of encoding and retrieval of faces and words. *Journal of Cognitive Neuroscience, 11*(6), 631-640. doi: 10.1162/089892999563698

McNicol, D. (1972). *A primer of signal detection theory*. Sydney: Australasian Publishing Company.

Mecklinger, A., & Muller, N. (1996). Dissociations in the processing of "what" and "where" information in working memory: An event-related potential analysis. *Journal of Cognitive Neuroscience, 8*(5), 453-473. doi: 10.1162/jocn.1996.8.5.453

Milner, B. (1970). Memory and the medial temporal regions of the brain. In B. Pribram K.H., D.E. (Ed.), *Biology of Memory*. New York: Academic Press.

Morris, S. B., & DeShon, R. P. (2002). Combining effect size estimates in meta-analysis with repeated measures and independent-groups designs. *Psychological Methods, 7*, 105-125.

Moser, D., Baker, J. M., Sanchez, C. E., Rorden, C., & Fridriksson, J. (2009). Temporal Order Processing of Syllables in the Left Parietal Lobe. *Journal of Neuroscience, 29*(40), 12568-12573. doi: 10.1523/jneurosci.5934-08.2009

Nyberg, L., Cabeza, R., & Tulving, E. (1996). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin & Review, 3*(2), 135-148. doi: 10.3758/bf03212412

Nyberg, L., Persson, J., Habib, R., Tulving, E., McIntosh, A. R., Cabeza, R., & Houle, S. (2000). Large scale neurocognitive networks underlying episodic memory. *Journal of Cognitive Neuroscience, 12*(1), 163-173.

Ojemann, G. A., & Dodrill, C. B. (1985). Verbal memory deficits after left temporal lobectomy for epilepsy. Mechanism and intraoperative prediction. *Journal of Neurosurgery, 62*(1), 101-107.

Opitz, B., Mecklinger, A., & Friederici, A. D. (2000). Functional asymmetry of human prefrontal cortex: Encoding and retrieval of verbally and nonverbally coded information. *Learning & Memory, 7*(2), 85-96. doi: 10.1101/lm.7.2.85

Papanicolaou, A. C., Simos, P. G., Castillo, E. M., Breier, J. I., Katz, J. S., & Wright, A. A. (2002). The hippocampus and memory of verbal and pictorial material. *Learning & Memory, 9*(3), 99-104. doi: 10.1101/lm.44302

Pirozzolo, F. J., & Rayner, K. (1977). Hemispheric specialization in reading and word recognition. *Brain and Language, 4*(2), 248-261. doi:10.1016/0093-934x(77)90021-9

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology, 118*(10), 2128-2148.

Redoblado, M. A., Grayson, S. J., & Miller, L. A. (2003). Lateralized-temporal-lobe-lesion effects on learning and memory: Examining the contributions of stimulus novelty and presentation mode. *Journal of Clinical and Experimental Neuropsychology, 25*(1), 36-48. doi: 10.1076/jcen.25.1.36.13625

Rossi, S., Cappa, S. F., Babiloni, C., Pasqualetti, P., Miniussi, C., Carducci, F., . . . Rossini, P. M. (2001). Prefontal cortex in long-term memory: An "interference" approach using magnetic stimulation. *Nature Neuroscience, 4*(9), 948-952. doi: 10.1038/nn0901-948

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

Schacter, D. L., & Wagner, A. D. (1999). Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus, 9*(1), 7-24. doi: 10.1002/(sici)1098-1063(1999)9:1<7::aid-hipo2>3.0.co;2-k

Sekiguchi, T., Koyama, S., & Kakigi, R. (2001). The Effect of Stimulus Repetition on Cortical Magnetic Responses Evoked by Words and Nonwords. *Neuroimage, 14*(1), 118-128. doi: http://dx.doi.org/10.1006/nimg.2001.0774

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation. *Journal of Experimental Psychology-Human Perception and Performance, 8*(2), 253-272. doi:10.1037/0096-1523.8.2.253

Sherman, E. M. S., Wiebe, S., Fay-McClymont, T. B., Tellez-Zenteno, J., Metcalfe, A., Hernandez-Ronquillo, L., . . . Jette, N. (2011). Neuropsychological outcomes after

epilepsy surgery: Systematic review and pooled estimates. *Epilepsia, 52*(5), 857-869. doi:10.1111/j.1528-1167.2011.03022.x

Shucard, J. L., Tekok-Kilic, A., Shiels, K., & Shucard, D. W. (2009). Stage and load effects on ERP topography during verbal and spatial working memory. *Brain Research, 1254*, 49-62. doi: 10.1016/j.brainres.2008.11.063

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

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.

Tulving, E., Kapur, S., Craik, F. I. M., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding / retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences of the United States of America, 91*(6), 2016-2020. doi: 10.1073/pnas.91.6.2016

Vaz, S. A. M. (2004). Nonverbal memory functioning following right anterior temporal lobectomy: a meta-analytic review. *Seizure-European Journal of Epilepsy, 13*(7), 446-452. doi: 10.1016/j.seizure.2003.12.004

van der Ham, I. J. M., Postma, A., & Laeng, B. (2014). Lateralized perception: The role of attention in spatial relation processing. *Neuroscience and Biobehavioral Reviews, 45*, 142-148. doi:10.1016/j.neubiorev.2014.05.006

van Petten, C., & Senkfor, A. J. (1996). Memory for words and novel visual patterns: Repetition, recognition, and encoding effects in the event-related brain potential. *Psychophysiology, 33*(5), 491-506.

Voss, J. L., & Paller, K. A. (2007). Neural correlates of conceptual implicit memory and their contamination of putative neural correlates of explicit memory. *Learning and Memory, 14*(4), 259-267.

Voss, J. L., & Paller, K. A. (2009). An electrophysiological signature of unconscious recognition memory. *Nature Neuroscience, 12*(3), 349-355. doi: 10.1038/nn.2260

Wagner, A. D., Poldrack, R. A., Eldridge, L. L., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. *Neuroreport, 9*(16), 3711-3717.

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. doi: 10.1016/j.neuroimage.2003.09.034

Supplementary Table 1

Correlations between $d'_{Ver} - d'_{Non}$ and $ERP_{Ver} - ERP_{Non}$

ERP measure	*r*	[CI_{95}]	*p*
N170 – Enc – L	-.23	[-.25 .57]	.31
N170 – Enc – R	.18	[-.25 .57]	.43
VPP – Enc – L	.22	[-.16 .64]	.33
VPP – Enc – R	-.17	[-.53 .27]	.46
P300 – Enc – L	.01	[-.56 .45]	.98
P300 – Enc – R	.25	[-.30 .66]	.26
N270 – Enc – L	.34	[-.14 .68]	.12
N270 – Enc – R	-.12	[-.50 .32]	.59
N170 – Rtv – L	-.06	[-.45 .37]	.80
N170 – Rtv – R	.19	[-.27 .52]	.41
VPP – Rtv – L	-.04	[-.43 .37]	.85
VPP – Rtv – R	.01	[-.35 .39]	.97
P300 – Rtv – L	-.33	[-.61 -.06]	.13
P300 – Rtv – R	-.33	[-.58 -.05]	.13
N270 – Rtv – L	-.23	[-.50 .08]	.31
N270 – Rtv – R	-.15	[-.45 .24]	.51
Average – Enc	.14	[-.30 .53]	.53
Average – Rtv	-.19	[-.49 .11]	.41
Average – Total	-.03	[-.37 .29]	.91

Ver = Verbal; Non = Nonverbal; Enc = Encoding; Rtv = Retrieval; L = Left; R = Right;

r = correlation coefficient;

[CI_{95}] = lower and upper bounds of 95% confidence interval (1000x bootstrapped);

p = significance test.

Supplementary Table 2

Correlations between $RT_{Ver} - RT_{Non}$ and $ERP_{Ver} - ERP_{Non}$

ERP measure	*r*	[CI_{95}]	*p*
N170 – Enc – L	-.28	[-.64 .21]	.22
N170 – Enc – R	-.16	[-.50 .31]	.48
VPP – Enc – L	.26	[-.19 .59]	.25
VPP – Enc – R	.19	[-.31 .54]	.40
P300 – Enc – L	-.05	[-.51 .40]	.83
P300 – Enc – R	-.11	[-.56 .43]	.63
N270 – Enc – L	.18	[-.34 .63]	.43
N270 – Enc – R	.28	[-.07 .63]	.20
N170 – Rtv – L	-.02	[-.45 .37]	.93
N170 – Rtv – R	.07	[-.47 .63]	.80
VPP – Rtv – L	.30	[-.26 .65]	.22
VPP – Rtv – R	-.04	[-.43 .48]	.86
P300 – Rtv – L	.14	[-.33 .52]	.58
P300 – Rtv – R	-.33	[-.42 .73]	.17
N270 – Rtv – L	-.38	[-.73 .16]	.11
N270 – Rtv – R	-.14	[-.58 .53]	.57

Average – Enc	.08	[-.34 .50]	.72
Average – Rtv	-.01	[-.49 .57]	.98
Average – Total	.09	[-.35 .46]	.68

Ver = Verbal; Non = Nonverbal; Enc = Encoding; Rtv = Retrieval; L = Left; R = Right;

r = correlation coefficient;

[CI_{95}] = lower and upper bounds of 95% confidence interval (1000x bootstrapped);

p = significance test.

Supplementary Table 3

Correlations between $RT_{Enc} - RT_{Rtv}$ and $ERP_{Enc} - ERP_{Rtv}$

ERP measure	*r*	[CI_{95}]	*p*
N170 – Ver – L	-.18	[-.53 .20]	.43
N170 – Ver – R	-.07	[-.42 .29]	.75
VPP – Ver – L	.20	[-.29 .53]	.39
VPP – Ver – R	.02	[-.43 .48]	.92
P300 – Ver – L	-.13	[-.48 .31]	.57
P300 – Ver – R	-.13	[-.44 .21]	.59
N270 – Ver – L	.13	[-.15 .41]	.59
N270 – Ver – R	.09	[-.41 .65]	.70
N170 – Non – L	-.51	[-.83 .12]	.03
N170 – Non – R	-.31	[-.65 .10]	.19
VPP – Non – L	.33	[-.16 .69]	.17
VPP – Non – R	.06	[-.49 .52]	.81
P300 – Non – L	-.16	[-.46 -.14]	.52
P300 – Non – R	-.12	[-.44 -.27]	.63
N270 – Non – L	.05	[-.28 .35]	.85
N270 – Non – R	.15	[-.31 .48]	.55
Average – Ver	-.15	[-.53 .17]	.50
Average – Non	-.26	[-.76 .12]	.25
Average – Total	-.36	[-.69 -.04]	.10

Ver = Verbal; Non = Nonverbal; Enc = Encoding; Rtv = Retrieval; L = Left; R = Right;

r = correlation coefficient;

[CI_{95}] = lower and upper bounds of 95% confidence interval (1000x bootstrapped);

p = significance test.

Supplementary Table 4a.

Descriptive and test statistics for VPP/N170 mean amplitude.

Mat	Pro	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Enc	N170	L	1.85	1.22	2.47
			R	1.38	0.68	2.08
		VPP	L	1.15	0.70	1.59
			R	0.73	0.34	1.11
	Rtv	N170	L	2.46	1.68	3.25
			R	2.60	1.75	3.44
		VPP	L	1.66	1.06	2.26
			R	1.45	1.01	1.90

Non	Enc	N170	L	2.58	1.94	3.23
			R	3.73	3.02	4.44
		VPP	L	1.87	1.40	2.33
			R	1.61	1.22	2.00
	Rtv	N170	L	3.14	2.50	3.77
			R	3.71	3.02	4.40
		VPP	L	1.77	1.29	2.25
			R	2.45	2.06	2.84

4b.

ANOVA Factor	$F(1,21)$	p	η_p^2
Mat	44.24	<.001	.68
Pro	12.03	.002	.36
Reg	132.18	<.001	.86
Hem	0.70	.412	.03
Mat * Pro	3.80	.065	.15
Mat * Reg	23.88	<.001	.53
Mat * Hem	38.42	<.001	.65
Pro * Hem	5.89	.024	.22
Reg * Hem	0.73	.404	.03
Pro * Reg	1.03	.323	.05
Mat * Pro * Hem	1.82	.192	.08
Mat * Reg * Hem	1.41	.249	.06
Mat * Pro * Reg	4.04	.057	.16
Pro * Reg * Hem	2.79	.110	.12
Mat * Pro * Reg * Hem	7.25	.014	.26

4c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mat * Pro	Enc	Mat	2.74	-5.63	<.001	.47	-1.20
	Rtv	Mat	2.74	-4.72	<.001	.79	-1.03
	Ver	Pro	2.74	-3.68	.007	.59	-0.80
	Non	Pro	2.74	-1.79	.287	.63	-0.38
		Mat * Pro	2.74	-1.94	.227	.22	-0.42
Mat * Reg	N170	Mat	2.42	-7.22	<.001	.74	-1.54
	VPP	Mat	2.42	-5.03	<.001	.66	-1.08
		Mat * Reg	2.42	-4.87	<.001	.76	-1.08
Mat * Hem	L	Mat	2.71	-4.09	.002	.81	-0.89
	R	Mat	2.71	-7.78	<.001	.68	-1.68
	Ver	Hem	2.71	1.08	.657	.54	0.23
	Non	Hem	2.71	-3.55	.009	.72	-0.76
		Mat * Hem	2.71	6.22	<.001	.70	1.37
Pro * Hem	L	Pro	2.78	-2.57	.073	.80	-0.60
	R	Pro	2.78	-3.81	.005	.64	-0.82
	Enc	Hem	2.78	-0.01	.999	.56	0.00
	Rtv	Hem	2.78	-1.53	.419	.68	-0.33
		Pro * Hem	2.78	2.44	.095	.75	0.53
Reg * Hem	N170	Hem	2.38	-0.92	.616	.15	-0.20
	VPP	Hem	2.38	0.28	.958	.50	0.06
		Reg * Hem	2.38	-0.85	.664	-.34	-0.19
Pro * Reg	N170	Pro	2.42	-3.04	.013	.70	-0.68

	VPP	Pro	2.42	-3.93	.002	.71	-0.86
		Pro * Reg	2.42	-1.03	.500	.91	-0.31
Mat * Pro * Hem	Enc / L	Mat	3.18	-3.53	.025	.54	-0.75
	Enc / R	Mat	3.18	-6.84	<.001	.49	-1.46
	Rtv / L	Mat	3.18	-2.60	.166	.86	-0.60
	Rtv / R	Mat	3.18	-5.63	<.001	.72	-1.23
	Ver / L	Pro	3.18	-2.49	.208	.65	-0.55
	Ver / R	Pro	3.18	-4.51	.002	.63	-0.97
	Non / L	Pro	3.18	-1.48	.761	.76	-0.32
	Non / R	Pro	3.18	-1.81	.556	.50	-0.39
	Ver / Enc	Hem	3.18	2.05	.405	.56	0.44
	Ver / Rec	Hem	3.18	0.13	.999	.61	0.03
	Non / Enc	Hem	3.18	-2.49	.207	.68	-0.53
	Non / Rec	Hem	3.18	-3.96	.009	.76	-0.85
	Enc	Mat * Hem	3.18	5.79	<.001	.77	1.26
	Rtv	Mat * Hem	3.18	4.48	.002	.64	0.98
	Ver	Pro * Hem	3.18	2.86	.104	.79	0.61
	Non	Pro * Hem	3.18	1.19	.901	.74	0.28
Mat * Reg * Hem	N170 / L	Mat	3.03	-3.65	.011	.80	-0.78
	N170 / R	Mat	3.03	-7.09	<.001	.70	-1.54
	VPP / L	Mat	3.03	-2.34	.197	.64	-0.50
	VPP / R	Mat	3.03	-6.01	<.001	.59	-1.29
	Ver / N170	Hem	3.03	0.37	.999	.07	0.08
	Non / N170	Hem	3.03	-2.44	.166	.26	-0.52
	Ver / VPP	Hem	3.03	1.46	.674	.45	0.31
	Non / VPP	Hem	3.03	-1.14	.849	.48	-0.25
	N170	Mat * Hem	3.03	3.62	.013	.18	0.78
	VPP	Mat * Hem	3.03	2.63	.113	.30	0.56
Mat * Pro * Reg	Enc / N170	Mat	2.98	-6.17	<.001	.46	-1.32
	Rtv / N170	Mat	2.98	-4.68	<.001	.78	-1.01
	Enc / VPP	Mat	2.98	-4.05	.006	.38	-0.86
	Rtv / VPP	Mat	2.98	-4.14	.005	.75	-0.91
	N170 / N170	Pro	2.98	-3.53	.017	.56	-0.77
	VPP / N170	Pro	2.98	-1.19	.757	.62	-0.25
	N170 / VPP	Pro	2.98	-3.64	.013	.62	-0.79
	VPP / VPP	Pro	2.98	-2.41	.147	.61	-0.52
	N170	Mat * Pro	2.98	-2.24	.196	.16	-0.48
	VPP	Mat * Pro	2.98	-1.19	.758	.30	-0.26
Pro * Reg * Hem	N170 / L	Pro	2.98	-3.34	.024	.85	-0.74
	N170 / R	Pro	2.98	-2.30	.213	.66	-0.50
	VPP / L	Pro	2.98	-1.19	.839	.69	-0.27
	VPP / R	Pro	2.98	-5.34	<.001	.64	-1.15
	Enc / N170	Hem	2.98	-0.87	.951	.05	-0.19
	Rtv / N170	Hem	2.98	-0.90	.943	.30	-0.19
	Enc / VPP	Hem	2.98	2.19	.258	.57	0.47
	Rtv / VPP	Hem	2.98	-1.01	.913	.38	-0.22
	N170	Pro * Hem	2.98	0.07	.999	.57	0.02
	VPP	Pro * Hem	2.98	2.91	.057	.23	0.62
Mat * Pro * Reg * Hem	Enc / L / N170	Mat	3.47	-2.97	.141	.67	-0.63

Enc / R / N170	Mat	3.47	-6.58	<.001	.44	-1.40
Enc / L / VPP	Mat	3.47	-2.66	.262	.24	-0.57
Enc / R / VPP	Mat	3.47	-4.57	.003	.46	-0.97
Rtv / L / N170	Mat	3.47	-3.26	.077	.84	-0.73
Rtv / R / N170	Mat	3.47	-3.61	.036	.67	-0.79
Rtv / L / VPP	Mat	3.47	-0.58	.999	.70	-0.13
Rtv / R / VPP	Mat	3.47	-5.97	<.001	.65	-1.28
Ver / L / N170	Pro	3.47	-2.61	.285	.78	-0.58
Non / L / N170	Pro	3.47	-2.96	.144	.82	-0.63
Ver / L / VPP	Pro	3.47	-2.01	.650	.53	-0.44
Non / L / VPP	Pro	3.47	0.43	.999	.53	0.09
Ver / R / N170	Pro	3.47	-3.63	.034	.61	-0.79
Non / R / N170	Pro	3.47	0.05	.999	.44	0.01
Ver / R / VPP	Pro	3.47	-4.28	.007	.64	-0.92
Non / R / VPP	Pro	3.47	-4.78	.002	.57	-1.02
Ver / Enc / N170	Hem	3.47	1.08	.993	.10	0.23
Non / Enc / N170	Hem	3.47	-2.67	.257	.13	-0.57
Ver / Enc / VPP	Hem	3.47	2.11	.579	.52	0.45
Non / Enc / VPP	Hem	3.47	1.26	.980	.54	0.27
Ver / Rtv / N170	Hem	3.47	-0.27	.999	.20	-0.06
Non / Rtv / N170	Hem	3.47	-1.62	.881	.39	-0.35
Ver / Rtv / VPP	Hem	3.47	0.68	.999	.34	0.15
Non / Rtv / VPP	Hem	3.47	-2.73	.230	.30	-0.59
Enc / N170	Mat * Hem	3.47	4.50	.004	.35	0.99
Rtv / N170	Mat * Hem	3.47	0.66	.999	.44	0.14
Enc / VPP	Mat * Hem	3.47	1.22	.983	.06	0.27
Rtv / VPP	Mat * Hem	3.47	3.35	.065	.03	0.72
N170 / L	Pro * Hem	3.47	-0.27	.999	.36	-0.06
N170 / R	Pro * Hem	3.47	-1.85	.759	.06	-0.40
VPP / L	Pro * Hem	3.47	-2.72	.232	.14	-0.58
VPP / R	Pro * Hem	3.47	0.63	.999	.44	0.13

Mat = Material (Verbal - Nonverbal); Pro = Process (Encoding - Retrieval); Reg = Region (Parietal - Frontal); Hem = Hemisphere (Left - Right); Ver = Verbal; Non = Nonverbal; Enc = Encoding; Rtv = Retrieval; L = Left; R = Right.

Supplementary Table 5.

Descriptive and test statistics for N270/P300 mean amplitude

Mat	Pro	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Enc	P300	L	1.93	1.41	2.45
			R	3.70	2.93	4.47
		N270	L	2.06	1.74	2.37
			R	1.19	0.68	1.70
	Rtv	P300	L	1.98	1.41	2.55
			R	2.95	2.08	3.81
		N270	L	1.79	1.24	2.33
			R	1.38	0.92	1.84
Non	Enc	P300	L	1.47	1.02	1.92
			R	2.45	1.84	3.06
		N270	L	1.71	1.22	2.19
			R	0.66	0.29	1.02

	Rtv	P300	L	1.66	1.14	2.19
			R	2.13	1.39	2.86
		N270	L	1.15	0.57	1.72
			R	1.05	0.57	1.53

5b.

ANOVA Factor	$F(1,21)$	p	η_p^2
Mat	12.71	.002	.38
Pro	1.15	.296	.05
Reg	59.61	<.001	.74
Hem	3.76	.066	.15
Mat * Pro	0.27	.611	.01
Mat * Reg	4.56	.045	.18
Mat * Hem	6.03	.023	.22
Pro * Hem	0.05	.826	.00
Reg * Hem	32.73	<.001	.61
Pro * Reg	3.17	.089	.13
Mat * Pro * Hem	4.11	.056	.16
Mat * Reg * Hem	2.56	.125	.11
Mat * Pro * Reg	5.43	.030	.21
Pro * Reg * Hem	26.17	<.001	.56
Mat * Pro * Reg * Hem	0.15	.703	.01

5c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mat * Pro	Enc	Mat	2.82	-3.29	.020	.54	-0.71
	Rtv	Mat	2.82	-2.43	.103	.66	-0.52
	Ver	Pro	2.82	0.40	.975	.78	0.09
	Non	Pro	2.82	1.04	.724	.69	0.23
		Mat * Pro	2.82	-0.55	.941	.31	-0.12
Mat * Reg	P300	Mat	2.37	-3.36	.005	.69	-0.73
	N270	Mat	2.37	-3.50	.004	.74	-0.76
		Mat * Reg	2.37	-2.25	.066	.88	-0.67
Mat * Hem	L	Mat	2.76	-2.69	.057	.63	-0.58
	R	Mat	2.76	-3.83	.004	.73	-0.83
	Ver	Hem	2.76	-0.69	.891	.87	-0.16
	Non	Hem	2.76	-2.64	.064	.87	-0.69
		Mat * Hem	2.76	2.33	.115	.77	0.51
Pro * Hem	L	Pro	2.73	1.23	.622	.83	0.30
	R	Pro	2.73	0.72	.890	.81	0.16
	Enc	Hem	2.73	-1.45	.482	.79	-0.36
	Rtv	Hem	2.73	-2.15	.170	.92	-0.53
		Pro * Hem	2.73	0.28	.993	.68	0.06

Reg * Hem	P300	Hem	2.41	-5.23	<.001	.74	-1.20
	N270	Hem	2.41	3.58	.003	.60	0.77
		Reg * Hem	2.41	-5.66	<.001	-.25	-1.21
Pro * Reg	P300	Pro	2.46	1.62	.276	.88	0.37
	N270	Pro	2.46	0.38	.931	.74	0.09
		Pro * Reg	2.46	1.91	.167	.81	0.41
Mat * Pro * Hem	Enc / L	Mat	3.22	-2.05	.438	.39	-0.44
	Enc / R	Mat	3.22	-3.92	.009	.62	-0.87
	Rtv / L	Mat	3.22	-2.16	.376	.57	-0.46
	Rtv / R	Mat	3.22	-2.41	.249	.69	-0.51
	Ver / L	Pro	3.22	0.99	.966	.65	0.22
	Ver / R	Pro	3.22	-0.30	.999	.79	-0.07
	Non / L	Pro	3.22	0.66	.997	.69	0.15
	Non / R	Pro	3.22	1.24	.904	.69	0.26
	Ver / Enc	Hem	3.22	0.24	.999	.71	0.05
	Ver / Rec	Hem	3.22	-1.49	.787	.89	-0.34
	Non / Enc	Hem	3.22	-2.64	.167	.85	-0.77
	Non / Rec	Hem	3.22	-2.08	.420	.89	-0.49
	Enc	Mat * Hem	3.22	3.02	.078	.72	0.65
	Rtv	Mat * Hem	3.22	0.52	.999	.78	0.11
	Ver	Pro * Hem	3.22	1.39	.836	.56	0.30
	Non	Pro * Hem	3.22	-1.29	.884	.82	-0.30
Mat * Reg * Hem	P300 / L	Mat	3.05	-2.05	.312	.69	-0.44
	P300 / R	Mat	3.05	-3.34	.026	.58	-0.72
	N270 / L	Mat	3.05	-2.49	.146	.53	-0.54
	N270 / R	Mat	3.05	-3.39	.024	.83	-0.73
	Ver / P300	Hem	3.05	-2.98	.056	.61	-0.67
	Non / P300	Hem	3.05	-5.42	<.001	.72	-1.27
	Ver / N270	Hem	3.05	3.12	.042	.65	0.67
	Non / N270	Hem	3.05	3.02	.052	.42	0.65
	P300	Mat * Hem	3.05	2.23	.231	.41	0.51
	N270	Mat * Hem	3.05	-0.40	.999	.26	-0.09
Mat * Pro * Reg	Enc / P300	Mat	2.94	-3.43	.018	.54	-0.76
	Rtv / P300	Mat	2.94	-2.20	.206	.64	-0.47
	Enc / N270	Mat	2.94	-2.71	.080	.53	-0.58
	Rtv / N270	Mat	2.94	-2.62	.095	.70	-0.57
	P300 / P300	Pro	2.94	0.38	.997	.79	0.09
	N270 / P300	Pro	2.94	1.72	.433	.78	0.37
	P300 / N270	Pro	2.94	0.42	.996	.77	0.10
	N270 / N270	Pro	2.94	0.20	.999	.47	0.04
	P300	Mat * Pro	2.94	-1.05	.832	.40	-0.22
	N270	Mat * Pro	2.94	0.11	.999	.15	0.02
Pro * Reg * Hem	P300 / L	Pro	3.04	-0.99	.909	.87	-0.22
	P300 / R	Pro	3.04	2.81	.078	.82	0.62
	N270 / L	Pro	3.04	2.39	.178	.66	0.56
	N270 / R	Pro	3.04	-2.08	.304	.75	-0.45
	Enc / P300	Hem	3.04	-6.06	<.001	.62	-1.36
	Rtv / P300	Hem	3.04	-3.35	.027	.77	-0.78

	Enc / N270	Hem	3.04	5.05	.001	.42	1.10
	Rtv / N270	Hem	3.04	1.29	.771	.68	0.28
	P300	Pro * Hem	3.04	-3.53	.017	.36	-0.79
	N270	Pro * Hem	3.04	4.39	.003	.48	0.94
Mat * Pro * Reg * Hem	Enc / L / P300	Mat	3.50	-2.03	.637	.54	-0.44
	Enc / R / P300	Mat	3.50	-3.59	.043	.47	-0.78
	Enc / L / N270	Mat	3.50	-1.36	.961	.18	-0.30
	Enc / R / N270	Mat	3.50	-2.97	.152	.69	-0.68
	Rtv / L / P300	Mat	3.50	-1.50	.918	.69	-0.32
	Rtv / R / P300	Mat	3.50	-2.14	.567	.52	-0.46
	Rtv / L / N270	Mat	3.50	-2.33	.450	.48	-0.50
	Rtv / R / N270	Mat	3.50	-2.24	.503	.85	-0.48
	Ver / L / P300	Pro	3.50	-1.15	.990	.76	-0.25
	Non / L / P300	Pro	3.50	-0.29	.999	.83	-0.06
	Ver / L / N270	Pro	3.50	2.29	.472	.55	0.49
	Non / L / N270	Pro	3.50	1.08	.994	.37	0.25
	Ver / R / P300	Pro	3.50	1.32	.968	.73	0.29
	Non / R / P300	Pro	3.50	2.52	.341	.72	0.54
	Ver / R / N270	Pro	3.50	-2.70	.249	.75	-0.62
	Non / R / N270	Pro	3.50	-0.97	.998	.65	-0.21
	Ver / Enc / P300	Hem	3.50	-3.46	.056	.42	-0.76
	Non / Enc / P300	Hem	3.50	-6.58	<.001	.69	-1.54
	Ver / Enc / N270	Hem	3.50	4.13	.013	.26	0.90
	Non / Enc / N270	Hem	3.50	3.79	.028	.42	0.86
	Ver / Rtv / P300	Hem	3.50	-1.82	.766	.70	-0.42
	Non / Rtv / P300	Hem	3.50	-3.33	.075	.72	-0.80
	Ver / Rtv / N270	Hem	3.50	0.33	.999	.74	0.07
	Non / Rtv / N270	Hem	3.50	1.66	.846	.49	0.36
	Enc / P300	Mat * Hem	3.50	2.53	.334	.48	0.57
	Rtv / P300	Mat * Hem	3.50	0.61	.999	.09	0.13
	Enc / N270	Mat * Hem	3.50	1.49	.925	.47	0.35
	Rtv / N270	Mat * Hem	3.50	-1.44	.940	.48	-0.36
	P300 / L	Pro * Hem	3.50	-0.67	.999	.09	-0.14
	P300 / R	Pro * Hem	3.50	0.82	.999	-.02	0.17
	N270 / L	Pro * Hem	3.50	-1.12	.992	-.02	-0.24
	N270 / R	Pro * Hem	3.50	-1.22	.982	.40	-0.26

Mat = Material (Verbal - Nonverbal); Pro = Process (Encoding - Retrieval); Reg = Region (Parietal - Frontal); Hem = Hemisphere (Left - Right); Ver = Verbal; Non = Nonverbal; Enc = Encoding; Rtv = Retrieval; L = Left; R = Right.

Supplementary Table 6a.

Descriptive and test statistics for VPP/N170 mean amplitude - Repetition effect

Mat	Pro	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Old	N170	L	2.92	2.14	3.71
			R	3.85	2.97	4.72
		VPP	L	1.42	0.76	2.08
			R	1.72	0.90	2.53
	New	N170	L	3.04	2.45	3.64

			R	4.00	3.16	4.84
		VPP	L	1.99	1.38	2.60
			R	2.45	1.95	2.94
Non	Old	N170	L	2.49	1.67	3.31
			R	2.40	1.47	3.32
		VPP	L	1.54	0.96	2.12
			R	1.39	0.92	1.86
	New	N170	L	2.32	1.53	3.10
			R	2.77	1.95	3.59
		VPP	L	1.83	1.10	2.56
			R	1.53	0.99	2.07

6b.

ANOVA Factor	$F(1,21)$	p	η_p^2
Mat	16.39	.001	.44
Rep	3.15	.090	.13
Reg	102.13	<.001	.83
Hem	2.35	.140	.10
Mat * Rep	0.75	.396	.04
Mat * Reg	10.71	.004	.34
Mat * Hem	17.41	<.001	.45
Rep * Hem	0.89	.356	.04
Reg * Hem	0.68	.418	.03
Rep * Reg	4.22	.053	.17
Mat * Rep * Hem	0.14	.711	.01
Mat * Reg * Hem	0.09	.766	.00
Mat * Rep * Reg	1.29	.270	.06
Rep * Reg * Hem	0.60	.446	.03
Mat * Rep * Reg * Hem	1.82	.192	.08

6c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mat * Rep	Old	Mat	2.72	-2.62	.062	.70	-0.56
	New	Mat	2.72	-3.48	.009	.65	-0.75
	Ver	Rep	2.72	-1.25	.608	.89	-0.27
	Non	Rep	2.72	-1.49	.460	.45	-0.32
		Mat * Rep	2.72	0.87	.824	.15	0.19
Mat * Reg	N170	Mat	2.48	-4.88	<.001	.77	-1.06
	VPP	Mat	2.48	-1.84	.184	.64	-0.40
		Mat * Reg	2.48	-3.27	.009	.45	-0.70
Mat * Hem	L	Mat	2.73	-1.90	.247	.86	-0.47
	R	Mat	2.73	-5.01	<.001	.73	-1.07
	Ver	Hem	2.73	0.09	.999	.62	0.02

	Non	Hem	2.73	-3.40	.010	.67	-0.73
		Mat * Hem	2.73	4.17	.002	.59	0.91
Rep * Hem	L	Rep	2.72	-1.22	.639	.80	-0.26
	R	Rep	2.72	-1.94	.249	.77	-0.42
	Old	Hem	2.72	-1.01	.762	.59	-0.22
	New	Hem	2.72	-2.00	.226	.71	-0.43
		Rep * Hem	2.72	0.94	.793	.61	0.20
Reg * Hem	N170	Hem	2.37	-1.28	.407	.21	-0.27
	VPP	Hem	2.37	-0.30	.956	.35	-0.06
		Reg * Hem	2.37	-0.83	.689	-.37	-0.18
Rep * Reg	N170	Rep	2.36	-1.04	.535	.92	-0.23
	VPP	Rep	2.36	-1.99	.120	.49	-0.43
		Rep * Reg	2.36	2.05	.106	.74	0.57
Mat * Rep * Hem	Old / L	Mat	3.25	-0.77	.994	.74	-0.17
	Old / R	Mat	3.25	-3.70	.016	.69	-0.80
	New / L	Mat	3.25	-2.13	.418	.76	-0.49
	New / R	Mat	3.25	-3.91	.010	.51	-0.83
	Ver / L	Rep	3.25	-0.36	.999	.86	-0.08
	Ver / R	Rep	3.25	-1.76	.661	.87	-0.37
	Non / L	Rep	3.25	-1.38	.866	.50	-0.30
	Non / R	Rep	3.25	-1.40	.858	.44	-0.30
	Ver / Old	Hem	3.25	0.45	.999	.59	0.10
	Ver / Rec	Hem	3.25	-0.28	.999	.61	-0.06
	Non / Old	Hem	3.25	-2.31	.314	.60	-0.50
	Non / Rec	Hem	3.25	-4.24	.005	.79	-0.92
	Old	Mat * Hem	3.25	3.66	.018	.61	0.79
	New	Mat * Hem	3.25	2.92	.104	.63	0.65
	Ver	Rep * Hem	3.25	1.03	.969	.28	0.22
	Non	Rep * Hem	3.25	0.45	.999	.74	0.10
Mat * Reg * Hem	N170 / L	Mat	2.97	-2.76	.080	.83	-0.61
	N170 / R	Mat	2.97	-4.08	.004	.67	-0.87
	VPP / L	Mat	2.97	-0.09	.999	.63	-0.02
	VPP / R	Mat	2.97	-3.74	.009	.72	-0.80
	Ver / N170	Hem	2.97	-0.37	.999	.22	-0.08
	Non / N170	Hem	2.97	-2.03	.346	.15	-0.44
	Ver / VPP	Hem	2.97	0.77	.982	.40	0.17
	Non / VPP	Hem	2.97	-1.41	.735	.34	-0.30
	N170	Mat * Hem	2.97	1.97	.377	.02	0.43
	VPP	Mat * Hem	2.97	2.86	.064	.50	0.64
Mat * Rep * Reg	Old / N170	Mat	2.99	-4.43	.001	.77	-0.96
	New / N170	Mat	2.99	-4.01	.004	.65	-0.86
	Old / VPP	Mat	2.99	-0.33	.999	.35	-0.07
	New / VPP	Mat	2.99	-2.61	.108	.62	-0.56
	N170 / N170	Rep	2.99	-0.65	.978	.89	-0.14
	VPP / N170	Rep	2.99	-0.80	.953	.81	-0.17
	N170 / VPP	Rep	2.99	-1.59	.575	.83	-0.35
	VPP / VPP	Rep	2.99	-1.66	.533	-.03	-0.36
	N170	Mat * Rep	2.99	0.17	.999	.49	0.04
	VPP	Mat * Rep	2.99	1.10	.852	-.13	0.24
Rep * Reg * Hem	N170 / L	Rep	2.89	0.15	.999	.87	0.03

	N170 / R	Rep	2.89	-1.91	.425	.94	-0.43
	VPP / L	Rep	2.89	-1.85	.464	.64	-0.40
	VPP / R	Rep	2.89	-1.62	.620	.41	-0.35
	Old / N170	Hem	2.89	-0.86	.974	.18	-0.18
	New / N170	Hem	2.89	-1.71	.559	.24	-0.37
	Old / VPP	Hem	2.89	-0.28	.999	.43	-0.06
	New / VPP	Hem	2.89	-0.26	.999	.34	-0.06
	N170	Rep * Hem	2.89	1.28	.826	.01	0.28
	VPP	Rep * Hem	2.89	0.00	.999	.49	0.00
Mat * Rep * Reg * Hem	Old / L / N170	Mat	3.43	-1.67	.881	.77	-0.36
	Old / R / N170	Mat	3.43	-4.05	.010	.66	-0.87
	Old / L / VPP	Mat	3.43	0.34	.999	.32	0.07
	Old / R / VPP	Mat	3.43	-0.93	.999	.46	-0.22
	New / L / N170	Mat	3.43	-3.13	.104	.79	-0.72
	New / R / N170	Mat	3.43	-3.30	.069	.56	-0.70
	New / L / VPP	Mat	3.43	-0.62	.999	.70	-0.14
	New / R / VPP	Mat	3.43	-3.67	.027	.50	-0.78
	Ver / L / N170	Rep	3.43	0.97	.999	.89	0.21
	Non / L / N170	Rep	3.43	-0.48	.999	.74	-0.11
	Ver / L / VPP	Rep	3.43	-1.20	.988	.72	-0.27
	Non / L / VPP	Rep	3.43	-1.61	.902	.33	-0.34
	Ver / R / N170	Rep	3.43	-2.14	.597	.92	-0.48
	Non / R / N170	Rep	3.43	-0.63	.999	.82	-0.13
	Ver / R / VPP	Rep	3.43	-0.69	.999	.69	-0.15
	Non / R / VPP	Rep	3.43	-1.51	.937	-.13	-0.33
	Ver / Old / N170	Hem	3.43	0.18	.999	.23	0.04
	Non / Old / N170	Hem	3.43	-1.67	.879	.05	-0.36
	Ver / Old / VPP	Hem	3.43	0.50	.999	.35	0.11
	Non / Old / VPP	Hem	3.43	-0.88	.999	.56	-0.19
	Ver / New / N170	Hem	3.43	-0.95	.999	.24	-0.20
	Non / New / N170	Hem	3.43	-2.20	.554	.24	-0.48
	Ver / New / VPP	Hem	3.43	0.79	.999	.26	0.17
	Non / New / VPP	Hem	3.43	-1.60	.908	.44	-0.35
	Old / N170	Mat * Hem	3.43	2.21	.543	-.08	0.48
	New / N170	Mat * Hem	3.43	1.39	.962	.59	0.30
	Old / VPP	Mat * Hem	3.43	1.31	.978	.26	0.29
	New / VPP	Mat * Hem	3.43	2.58	.307	.32	0.55
	N170 / L	Rep * Hem	3.43	1.15	.992	.34	0.25
	N170 / R	Rep * Hem	3.43	0.71	.999	.20	0.16
	VPP / L	Rep * Hem	3.43	-0.67	.999	-.17	-0.14
	VPP / R	Rep * Hem	3.43	1.16	.991	.07	0.27

Mat = Material (Verbal - Nonverbal); Pro = Process (Encoding - Retrieval); Reg = Region (Parietal - Frontal); Hem = Hemisphere (Left - Right); Ver = Verbal; Non = Nonverbal; Enc = Encoding; Rtv = Retrieval; L = Left; R = Right.

Supplementary Table 7a.

Descriptive and test statistics for N270/P300 mean amplitude - Repetition effect

Mat	Pro	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Old	P300	L	2.02	1.50	2.54
			R	3.15	2.26	4.04
		N270	L	1.31	0.72	1.91
			R	0.99	0.35	1.63
	New	P300	L	1.97	1.30	2.64
			R	3.06	2.22	3.89
		N270	L	1.86	1.27	2.44
			R	1.33	0.89	1.77
Non	Old	P300	L	1.53	0.98	2.09
			R	1.84	0.89	2.79
		N270	L	0.87	0.25	1.48
			R	0.99	0.54	1.43
	New	P300	L	1.54	1.03	2.06
			R	2.09	1.39	2.79
		N270	L	1.23	0.66	1.80
			R	0.98	0.47	1.48

7b.

ANOVA Factor	$F(1,21)$	*p*	η_p^2
Mat	7.14	.014	.25
Rep	0.74	.398	.03
Reg	45.15	<.001	.68
Hem	5.57	.028	.21
Mat * Rep	0.03	.874	.00
Mat * Reg	5.04	.036	.19
Mat * Hem	0.84	.370	.04
Rep * Hem	0.62	.440	.03
Reg * Hem	9.33	.006	.31
Rep * Reg	2.86	.106	.12
Mat * Rep * Hem	0.08	.780	.00
Mat * Reg * Hem	3.41	.079	.14
Mat * Rep * Reg	2.20	.153	.10
Rep * Reg * Hem	2.13	.159	.09
Mat * Rep * Reg * Hem	1.12	.302	.05

7c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mat * Rep	Old	Mat	2.57	-2.11	.145	.48	-0.46
	New	Mat	2.57	-2.90	.022	.68	-0.62
	Ver	Rep	2.57	-0.78	.899	.74	-0.17
	Non	Rep	2.57	-0.77	.903	.53	-0.17
		Mat * Rep	2.57	0.16	.999	.68	0.04

Mat * Reg	P300	Mat	2.45	-2.89	.019	.56	-0.62
	N270	Mat	2.45	-1.87	.159	.51	-0.42
		Mat * Reg	2.45	-2.25	.078	.70	-0.52
Mat * Hem	L	Mat	2.73	-2.36	.105	.48	-0.51
	R	Mat	2.73	-2.60	.066	.57	-0.56
	Ver	Hem	2.73	-1.34	.536	.88	-0.32
	Non	Hem	2.73	-2.33	.110	.84	-0.58
		Mat * Hem	2.73	0.92	.788	.73	0.20
Rep * Hem	L	Rep	2.60	-0.96	.789	.43	-0.21
	R	Rep	2.60	-0.67	.917	.75	-0.14
	Old	Hem	2.60	-2.27	.108	.88	-0.61
	New	Hem	2.60	-1.88	.238	.89	-0.41
		Rep * Hem	2.60	-0.79	.871	.85	-0.18
Reg * Hem	P300	Hem	2.41	-3.47	.004	.73	-0.81
	N270	Hem	2.41	1.40	.305	.55	0.30
		Reg * Hem	2.41	-3.05	.012	-.39	-0.65
Rep * Reg	P300	Rep	2.19	-0.18	.990	.82	-0.04
	N270	Rep	2.19	-1.22	.466	.24	-0.26
		Rep * Reg	2.19	1.69	.257	.77	0.42
Mat * Rep * Hem	Old / L	Mat	3.19	-1.72	.650	.31	-0.38
	Old / R	Mat	3.19	-2.18	.357	.52	-0.47
	New / L	Mat	3.19	-2.53	.197	.66	-0.55
	New / R	Mat	3.19	-2.72	.131	.62	-0.58
	Ver / L	Rep	3.19	-0.89	.988	.65	-0.19
	Ver / R	Rep	3.19	-0.59	.999	.78	-0.13
	Non / L	Rep	3.19	-0.84	.991	.23	-0.18
	Non / R	Rep	3.19	-0.57	.999	.71	-0.12
	Ver / Old	Hem	3.19	-1.39	.847	.88	-0.32
	Ver / Rec	Hem	3.19	-1.04	.968	.86	-0.23
	Non / Old	Hem	3.19	-2.13	.384	.76	-0.52
	Non / Rec	Hem	3.19	-1.82	.579	.84	-0.39
	Old	Mat * Hem	3.19	0.89	.988	.73	0.19
	New	Mat * Hem	3.19	0.69	.997	.65	0.15
	Ver	Rep * Hem	3.19	-0.53	.999	.82	-0.11
	Non	Rep * Hem	3.19	-0.67	.998	.78	-0.15
Mat * Reg * Hem	P300 / L	Mat	3.03	-2.07	.314	.63	-0.45
	P300 / R	Mat	3.03	-2.62	.115	.39	-0.56
	N270 / L	Mat	3.03	-2.02	.336	.29	-0.45
	N270 / R	Mat	3.03	-1.06	.882	.68	-0.23
	Ver / P300	Hem	3.03	-1.59	.585	.70	-0.39
	Non / P300	Hem	3.03	-3.33	.027	.58	-0.76
	Ver / N270	Hem	3.03	0.35	.999	.70	0.08
	Non / N270	Hem	3.03	1.86	.418	.28	0.40
	P300	Mat * Hem	3.03	1.66	.543	.35	0.39
	N270	Mat * Hem	3.03	-1.59	.584	.53	-0.37
Mat * Rep * Reg	Old / P300	Mat	2.84	-2.63	.078	.44	-0.56
	New / P300	Mat	2.84	-2.78	.058	.66	-0.61
	Old / N270	Mat	2.84	-0.80	.961	.34	-0.17
	New / N270	Mat	2.84	-2.83	.051	.70	-0.61
	P300 / P300	Rep	2.84	-0.57	.990	.74	-0.13

	N270 / P300	Rep	2.84	0.44	.997	.86	0.10
	P300 / N270	Rep	2.84	-1.01	.902	.73	-0.22
	N270 / N270	Rep	2.84	-1.21	.807	-.19	-0.26
	P300	Mat * Rep	2.84	-0.87	.945	.73	-0.20
	N270	Mat * Rep	2.84	0.99	.911	.37	0.22
Rep * Reg * Hem	P300 / L	Rep	2.87	0.12	.999	.76	0.03
	P300 / R	Rep	2.87	-0.47	.998	.88	-0.10
	N270 / L	Rep	2.87	-1.43	.722	.10	-0.31
	N270 / R	Rep	2.87	-0.72	.984	.48	-0.15
	Old / P300	Hem	2.87	-3.04	.034	.76	-0.77
	New / P300	Hem	2.87	-3.66	.008	.72	-0.80
	Old / N270	Hem	2.87	0.47	.998	.55	0.10
	New / N270	Hem	2.87	1.97	.366	.64	0.42
	P300	Rep * Hem	2.87	0.84	.965	.76	0.18
	N270	Rep * Hem	2.87	-1.30	.797	.71	-0.30
Mat * Rep * Reg * Hem	Old / L / P300	Mat	3.36	-1.77	.796	.44	-0.38
	Old / R / P300	Mat	3.36	-2.48	.337	.29	-0.53
	Old / L / N270	Mat	3.36	-1.23	.981	.22	-0.26
	Old / R / N270	Mat	3.36	-0.01	.999	.53	0.00
	New / L / P300	Mat	3.36	-2.01	.636	.76	-0.46
	New / R / P300	Mat	3.36	-2.49	.326	.46	-0.54
	New / L / N270	Mat	3.36	-2.39	.388	.55	-0.51
	New / R / N270	Mat	3.36	-2.46	.347	.81	-0.54
	Ver / L / P300	Rep	3.36	-0.04	.999	.66	-0.01
	Non / L / P300	Rep	3.36	0.27	.999	.79	0.06
	Ver / L / N270	Rep	3.36	-1.53	.911	.66	-0.33
	Non / L / N270	Rep	3.36	-1.21	.983	-.27	-0.26
	Ver / R / P300	Rep	3.36	-0.91	.999	.79	-0.21
	Non / R / P300	Rep	3.36	0.51	.999	.91	0.11
	Ver / R / N270	Rep	3.36	0.07	.999	.73	0.02
	Non / R / N270	Rep	3.36	-1.02	.996	.23	-0.22
	Ver / Old / P300	Hem	3.36	-0.97	.998	.73	-0.25
	Non / Old / P300	Hem	3.36	-3.10	.095	.53	-0.73
	Ver / Old / N270	Hem	3.36	-0.57	.999	.70	-0.13
	Non / Old / N270	Hem	3.36	1.06	.994	.48	0.23
	Ver / New / P300	Hem	3.36	-2.21	.504	.68	-0.50
	Non / New / P300	Hem	3.36	-3.33	.054	.61	-0.73
	Ver / New / N270	Hem	3.36	1.12	.991	.63	0.24
	Non / New / N270	Hem	3.36	2.20	.511	.55	0.48
	Old / P300	Mat * Hem	3.36	1.67	.852	.38	0.39
	New / P300	Mat * Hem	3.36	-1.50	.921	.59	-0.33
	Old / N270	Mat * Hem	3.36	1.46	.937	.35	0.34
	New / N270	Mat * Hem	3.36	-1.13	.990	.40	-0.27
	P300 / L	Rep * Hem	3.36	-0.29	.999	.45	-0.06
	P300 / R	Rep * Hem	3.36	0.53	.999	.66	0.14
	N270 / L	Rep * Hem	3.36	-1.06	.994	.06	-0.23
	N270 / R	Rep * Hem	3.36	1.31	.970	.60	0.33

Mat = Material (Verbal - Nonverbal); Pro = Process (Encoding - Retrieval);
Reg = Region (Parietal - Frontal); Hem = Hemisphere (Left - Right); Ver =

Verbal; Non = Nonverbal; Enc = Encoding; Rtv = Retrieval; L = Left; R = Right.

Segue to Chapter 4

In Chapter 3 the effects of material and processing type on lateralisation were compared using event-related potential measures from healthy participants. In Chapter 4, the same effects were explored using measures of electroencephalographic (EEG) power in the theta and alpha frequency bands. Accordingly, some sections of Chapter 4 are identical to those in Chapter 3, including Sections 2.1 to 2.4 and 2.6.3 of the Materials and Methods, and parts of Section 3.1 of the Results which pertain to behavioural measures of participant accuracy and response time.

EEG is an overlooked method through which to potentially investigate the relative effects of material and processing on hemispheric lateralisation. While ERPs predominantly measure neural activity evoked by sensory stimulation and are modulated by different attentional and cognitive demands, EEG oscillations index aspects of neural activity that ERPs filter out, including recurrent and reciprocal changes between cortical regions. Event-related EEG is also particularly well-suited to measure longer-lasting cognitive processes (up to many seconds after the stimulus), whilst ERPs predominantly index activity within 0 to 500 ms. For short periods after a stimulus (e.g., 0 to 500 ms), event-related EEG is partially correlated with and partially independent of ERP measures. In sum, EEG is a temporally and qualitatively different measure of neural activity than ERPs that usefully complements ERP measures.

Importantly, memory performance has been associated with patterns of oscillatory synchronisation in specific frequency bands: changes in the theta band (4 to 7 Hz) have been related to working memory and encoding processes, while changes in the alpha band (8 to 13 Hz) have been related memory retrieval and may also show material specific lateralisation (see Chapter 3 for more details). It is therefore possible that the use of frequency measures of neural activity may lead to new insights about the nature of lateralisation effects as mediated by the type of material and the type of processing, and their interaction.

Chapter 4: The effects of material type and memory processing type on lateralisation of event-related theta and alpha power

Adam Bentvelzen[1,2], Nicholas A. Badcock[1,3], Genevieve McArthur[1,3], & Greg Savage[1,2]

[1] ARC Centre of Excellence in Cognition and its Disorders;

[2] Department of Psychology, Macquarie University, NSW, 2109, Australia;

[3] Department of Cognitive Science, Macquarie University, NSW, 2109, Australia;

Key words: nonverbal memory, lateralisation, frequency, temporal lobe epilepsy, HERA.

Running title: Type of material and processing affect EEG lateralisation

Corresponding author: Adam Bentvelzen, ARC Centre of Excellence in Cognition and its Disorders, Department of Cognitive Science, Macquarie University, NSW, 2109, Australia.

Email: adam.bentvelzen@students.mq.edu.au

Acknowledgements

This work was funded by an Australian Postgraduate Award (APA) to Adam Bentvelzen and a Macquarie University Research Development Grant to Greg Savage, and supported by the Australian Research Council Centre of Excellence for Cognition and its Disorders (CE110001021) http://www.ccd.edu.au

Abstract

There is an urgent need for reliable neuropsychological tools to assess right hemisphere pathology in clinical settings. Recent neuroimaging evidence suggests that lateralisation due to material (verbal, nonverbal) and memory process (encoding, retrieval) may interact across different brain regions. Little is known about the electroencephalography (EEG) time-frequency dimensions of such findings, however, despite the demonstrated role of theta (4-7 Hz) and alpha (8-13 Hz) oscillations in memory, which have included material specific lateralisation. Moreover, previous findings have suggested a possible frequency-by-process dissociation with greater involvement of theta frequency during encoding and greater involvement of alpha during retrieval. In order to examine the interaction of material (verbal, nonverbal) and processing (encoding, retrieval) in the time-frequency domain, we measured event-related theta and alpha power in 22 healthy adults during encoding and retrieval of verbal (printed pseudoword) and nonverbal (dot pattern) materials. Memory (old/new) for nonverbal material was right-lateralised in late (500 to 1500 ms) theta power, while memory for verbal material was not left-lateralised. During encoding there was right-lateralised theta power (0 to 500 ms) than during retrieval, opposing the predictions of the hemispheric encoding retrieval model (HERA) for the effect of processing type. Early alpha power also showed an old/new memory effect but material and process did not affect lateralisation. Our data support the idea that the lateralising influences of material and process type both affect theta power from 500 to 1500 ms, and support previous findings of an association between spatial-navigational memory and right-lateralised theta power in the medial temporal region. These findings suggest that considering both material specific and processing specific lateralisation effects improve the clinical assessment of right hemispheric pathology.

1. Introduction

Material specificity is the most influential model of the hemispheric division of memory function. Classical and contemporary findings have shown that memory for verbal material (e.g., lists of words) is specifically impaired after left temporal lobe damage (Alpherts et al., 2006; Glosser, Deutsch, Cole, Corwin, & Saykin, 1998; Ojemann & Dodrill, 1985; Pillon et al., 1999). Conversely, early findings connected right temporal damage and impaired memory for nonverbal material (e.g., spatial locations, Smith & Milner, 1981), however, this association is inconsistently replicated (Barr, 1997; Bell & Davies, 1998; Smith, Malec, & Ivnik, 1992; Vaz, 2004).

In attempts to resolve this issue, neuroimaging findings have converged to support both the verbal and nonverbal accounts of material specific lateralisation, with the caveat that right hemispheric memory function may be confounded by the relative verbalisability of the nonverbal material (e.g., Golby et al., 2001; Kelley et al., 1998). That is, memory for difficult-to-verbalise stimuli such as abstract spatial patterns or unfamiliar faces appears to invoke right-lateralisation compared with non-lateralised findings for easily nameable pictures (Bellgowan, Buffalo, Bodurka, & Martin, 2009; Igloi, Doeller, Berthoz, Rondi-Reig, & Burgess, 2010; Kelley et al., 1998; Kohler, Danckert, Gati, & Menon, 2005; Martin, Wiggs, & Weisberg, 1997). In addition, neuroimaging studies have shown that tasks placing strong demands on purely positional aspects of spatial memory are more closely associated with right medial temporal lobe (MTL) function than tasks requiring memory for non-spatial information including object identity which involves greater left MTL activity (e.g., see the meta-analysis by Kuhn & Gallinat, 2014), with a similar pattern reported in studies of right temporal lobe epilepsy patients (Kessels, de Haan, Kappelle, & Postma, 2001; Spiers et al., 2001). Therefore, the use of nonverbal memory tests that are difficult to verbalise and focused on spatial memory may improve the neuropsychological diagnosis of right MTL pathology.

Neuroimaging studies have also cast light on the lateralising effect of task-related factors. Among these, perhaps the most important have provided evidence in support of the

hemispheric encoding retrieval asymmetry model (HERA; see Nyberg, Cabeza, & Tulving, 1996 for a review), which predicts that the left prefrontal cortex is more involved with the initial learning of stimuli (encoding) than with the later remembering of previously learned stimuli (retrieval), while the right prefrontal cortex shows a greater involvement in retrieval than in encoding (Habib, Nyberg, & Tulving, 2003). Importantly, HERA predicts that the encoding/retrieval effect occurs independently of the material type, and across a variety of conditions of encoding (e.g., incidental or intentional) and retrieval (e.g., recall and recognition; Nyberg, Cabeza, & Tulving, 1996).

While there is evidence that patterns of lateralisation in the prefrontal cortices of healthy participants support the predictions of HERA (e.g., Babiloni et al., 2006; Cabeza & Nyberg, 2000; Desgranges, Baron, & Eustache, 1998), there is also evidence suggesting that prefrontal lateralisation relates to material type rather than the type of processing (e.g., Lee, Robbins, Pickard, & Owen, 2000; Opitz, Mecklinger, & Friederici, 2000). However, the proponents of HERA have argued rather than one or the other model necessarily having to predominate, material type and process may have simultaneous and independent effects on hemispheric lateralisation (Habib et al., 2003). Supporting this idea, one study using whole-brain PET found that lateralisation patterns consistent with HERA could operate within material specific networks across multiple brain regions (Nyberg et al., 2000). Similarly, an fMRI study showed that lateralisation related to both material and processing could occur within the MTL (Kennepohl, Sziklas, Garver, Wagner, & Jones-Gotman, 2007). In sum, consideration of the lateralising effects of both material type and processing type may help guide clinical assessment of the right MTL.

Measures of task-related changes in electroencephalographic (EEG) power in the theta (4 to 7 Hz) and alpha (8 to 13 Hz) EEG rhythms have been linked to memory processing. Changes in theta power appear to reflect working memory processes (Klimesch, Freunberger, & Sauseng, 2010; Klimesch, Freunberger, Sauseng, & Gruber, 2008; Klimesch, Schack, & Sauseng, 2005), positively correlating with working memory load (Fingelkurts, Fingelkurts,

Krause, & Sams, 2002; Gevins, Smith, McEvoy, & Yu, 1997; Jensen & Tesche, 2002; Mecklinger, Kramer, & Strayer, 1992; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010), episodic over semantic components of encoding (Klimesch, Schimke, & Schwaiger, 1994), and superior memory performance (Klimesch, 1999; Klimesch, Doppelmayr, Schimke, & Ripper, 1997), including performance on the Rey Auditory Verbal Learning Test (RAVLT) in patients with unilateral temporal lobe epilepsy (Babiloni et al., 2009). The association between theta and memory is most commonly observed within the medial temporal region, particularly the hippocampus, and the prefrontal cortex, as well as between and within different structures in each region (Anderson et al., 2010; Babiloni et al., 2009; Nyhus & Curran, 2010; Rutishauser, Ross, Mamelak, & Schuman, 2010). In sum, there is abundant evidence for a link between changes in theta power and memory phenomena in regions known to be involved in memory.

Episodic encoding success is also associated with increased theta activity during the specific time period of the N170 event-related potential (ERP) peak (i.e., approximately 120 to 200 ms; Klimesch, Doppelmayr, Pachinger, & Russegger, 1997; Klimesch, Doppelmayr, Schwaiger, Winkler, & Gruber, 2000; Klimesch, Freunberger, Sauseng, & Gruber, 2008; Klimesch et al., 2001, 2004). This finding is particularly intriguing since it contrasts with previous findings that lateralisation of the N170 relates to higher-order perceptual processing rather than memory-related processing (e.g., Maillard et al., 2011), and suggests that early theta power could also show material specific lateralisation mediated by memory demands.

Alpha power change may play a particularly important role during memory retrieval and has been proposed to relate preferentially to the reactivation of semantic and perceptual aspects of stored memory traces (Klimesch, 1999; Klimesch, Doppelmayr, Pachinger, et al., 1997; Klimesch et al., 2005; Klimesch et al., 2008; Klimesch et al., 2010). Furthermore, there is evidence that alpha power suppression from 750 to 1250 ms post-stimulus is lateralised to the left for word memory and to the right for face memory (Burgess & Gruzelier, 2000). However, few studies have used EEG power to systematically investigate hemispheric

lateralisation. One study testing memory for scenes found some support for HERA but only in the posterior parietal cortex and only for power in the gamma band, but different materials were not compared (Babilioni et al., 2006).

In summary, changes in EEG rhythms have been associated with memory tasks and may show functional dissociation by frequency, with theta power associated with encoding processes and alpha power related to retrieval processes (Dujardin, Bourriez, & Guieu, 1994; Fell et al., 2011; Guderian & Duzel, 2005; Klimesch, 1999; Klimesch et al., 2005). To our knowledge, no study has explicitly tested the material specificity and HERA models of hemispheric lateralisation using EEG frequency bands in the same participants. This question will be explored here using EEG to examine the relative time-frequency profile of these lateralising influences and whether they interact.

The current study asked healthy adults to encode and retrieve two types of visual stimuli: printed pseudowords (verbal) and spatial dot patterns (nonverbal). The effects of stimulus familiarity were minimised as neither material type contained semantic information, and the memory task, which involved an encoding phase followed by yes/no recognition judgments, was matched. The recognition format is more appropriate than recall for comparing verbal and nonverbal tasks as it avoids confounding the modality of the response (spoken for verbal recall and drawn for nonverbal recall) with the learned material type. The HERA model has been supported across a variety of different types of retrieval conditions, including recall, in which retrieving the memory involves a deliberate search of memory, and recognition, in which memory retrieval does not require an explicit search since the original stimulus is re-presented (see review by Nyberg, Cabeza, & Tulving, 1996). Therefore, we used a recognition task and considered this an appropriate format to test the predictions of HERA.

We measured hemispheric lateralisation of these materials during both encoding and retrieval processes using event-related power change in the theta and alpha frequency bands. The frequency ranges chosen for the theta (4 to 7 Hz) and alpha bands (8 to 13 Hz) closely

reflect the "classical" ranges most commonly used (Rosanova et al., 2009). These measures were recorded from frontal and parietal regions as these areas are commonly associated with memory effects using EEG (e.g., see Friedman & Johnson, 2000, for a review of ERP studies involving encoding and retrieval). Based on previous research, we focused on two time windows of theoretical interest: 0 to 500 ms (early) and 500 to 1500 ms (late) following stimulus onset. These two time windows were selected based on the differential temporal response of theta and alpha: theta power shows a very rapid increase peaking at about 250 ms following stimulus onset before declining rapidly to approach baseline level by 500 ms, while alpha power decreases more slowly until reaching a minimum approximately 600 ms following stimulus onset and then maintaining this level for several hundred milliseconds (Klimesch, 1999). Power change was measured in both frequency bands in both time ranges as memory-related effects have been reported for all four of these frequency-by-time combinations (Klimesch, Sauseng, & Hanslmayr, 2007; Mitchell, McNaughton, Flanagan, & Kirk, 2008).

It was predicted that material would have an effect on hemispheric lateralisation, with left-lateralisation of theta and alpha for verbal materials and right-lateralisation of theta and alpha for nonverbal materials. It was also predicted that the type of memory processing would affect lateralisation with greater involvement of the left hemisphere during encoding than during retrieval, and greater involvement of the right hemisphere during retrieval than during encoding. As a secondary aim, we explored whether changes in different frequency bands were related to the type of memory processing, specifically whether the theta band was more involved in encoding than retrieval, and whether the alpha band was conversely more involved in retrieval than encoding.

2. Materials and Methods

2.1 Participants

Twenty-two adults (mean age = 22.23 years, *SD* = 5.00, range 18 to 37; 17 females) were paid $30 to participate in the experiment. Data from two additional participants were

excluded due to significant EEG artefacts (i.e., more than 30% of epochs rejected). All participants reported normal or corrected-to-normal vision and that they were right-handed for writing. The experimental methods were approved by the Macquarie University Human Research Ethics Committee (Ref# 5201100342) in accordance with the Declaration of Helsinki. Informed consent was obtained from all participants.

2.2 Apparatus

Testing occurred in a dimly lit room, with participants sitting 60 cm away from an 18" Sony Trinitron CRT monitor (resolution 1024 x 768 pixels, 32 bit, 96 dpi, 100 Hz refresh rate) showing a light grey background colour. Task instructions for both conditions were displayed onscreen. Stimuli were controlled using Presentation (Neurobehavioral Systems Inc, Version 10.3) and EEG data were recorded with NeuroScan Synamps2 software. Participants responded with a Cedrus® RB830 button box, pressing one of two buttons that were positioned to the immediate left and right of the box's midline.

2.3 Stimuli

2.3.1 Verbal (printed pseudowords)

Target stimuli for the verbal condition were six, disyllabic, eight-letter pseudowords (*boltrens*, *morphalt*, *prealent*, *breatish*, *calthern*, *slempern*). Foils always differed from the target stimuli by one letter, which could be any of the eight letters regardless of position in the word or whether a consonant or vowel (e.g. *boltrons, morthalt, crealent,* etc.) as long as the syllabic structure of the word was not altered. The resulting target-foil visual similarity was designed to require careful analysis of the entire pseudoword. These pseudowords were presented on the computer screen in Courier New font, subtending a maximum of 6.5 x 1.1^0 visual angle. There were 48 foils, 96 in total, and eight different foils per target stimulus.

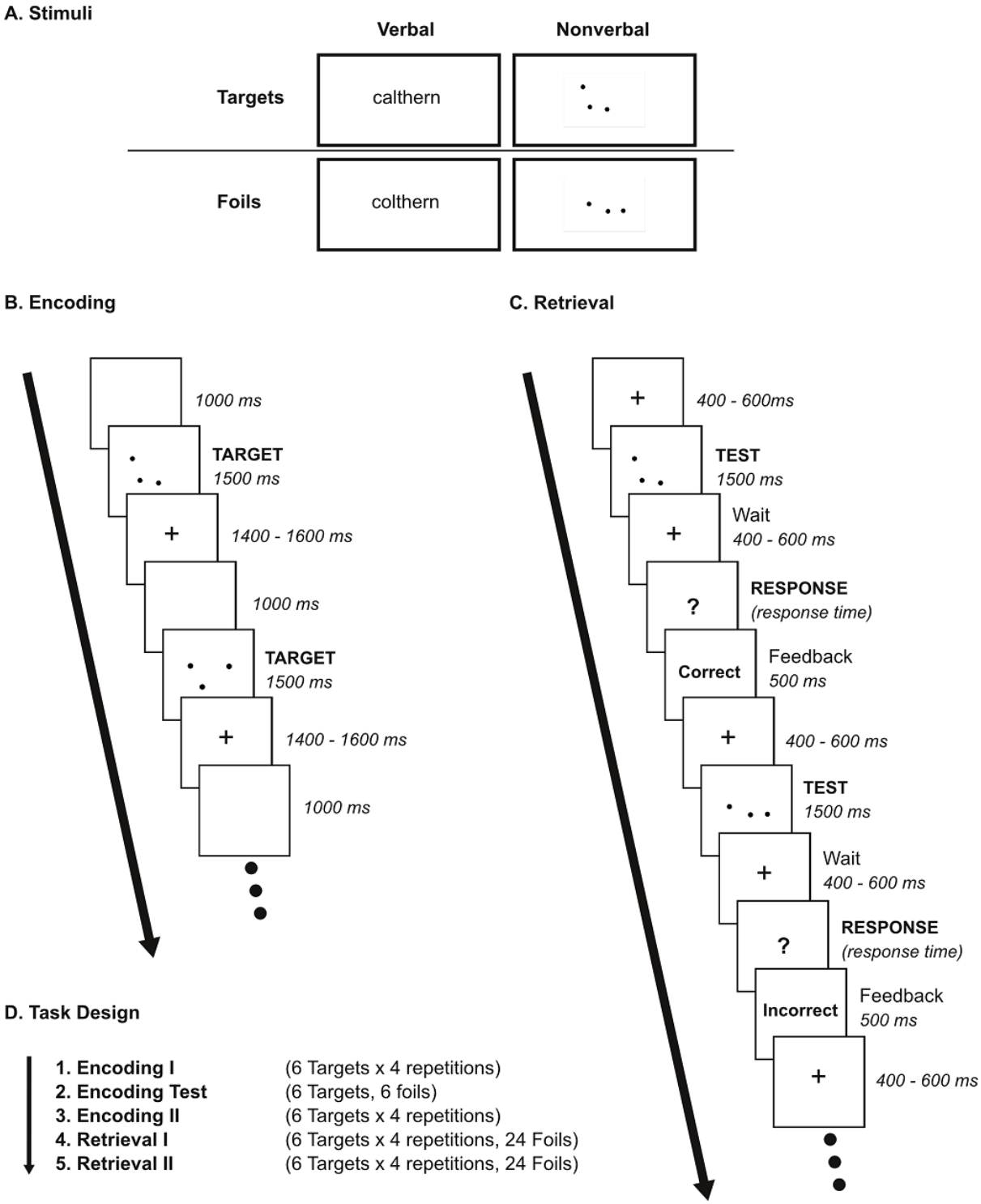

Fig 1. Experimental design. (a) Experimental stimuli - examples of targets and related foils for both material types. (b) Encoding phase - target presentation followed by interval of randomised duration; (c) Retrieval phase - test stimulus presentation (intermixed sequence of targets and foils) followed by interval of randomised duration, response screen and feedback. (d) Task Design – list of task phases including number of targets and foils per phase.

2.3.2 *Nonverbal (dot patterns)*

Target stimuli for the nonverbal condition were six spatial arrays of three dark grey dots each with a diameter subtending a 0.63^0 visual angle, as shown in Figure 1(a). Pilot experiments indicated that these three-dot arrays were both difficult to verbalise in healthy participants and difficult to remember for people with right temporal lobe damage, suggesting their potential value in activating the right hemisphere (Lee, Gonzalez, & Savage, 2007). Each three-dot array was freely positioned, without a grid or outer boundary, within a maximum two-dimensional range of 9.12^0 by 6.30^0 visual angle centred on the screen.

Arrays could take any combination of positions within the specified range with five restrictions: 1) no pair of dots was completely aligned along the horizontal or vertical axis; 2) dots could not be aligned to form a straight line along any angle or point directly towards a corner of the screen as these may be verbalised (e.g., as “line”, “top left corner”); 3) no array configuration (i.e., the specific combination of angles between dots) could be repeated, transposed or rotated; 4) there was a minimum of a 0.81^0 visual angle between the nearest outer edges of adjacent dots; and 5) dots were separated from each other by at least this minimum distance. These restrictions encouraged encoding of exact dot locations and also their spatial inter-relation. The foils corresponding with each target stimulus were produced by rearrangement of target dot positions such that there was one to three with a changed position, and the average positional change in any direction was 1.11^0 visual angle per dot (SD = 0.13, maximum 5.37). Otherwise, foil arrays had the same restrictions as target stimuli.

2.4 *Procedure*

2.4.1 *Task design*

The format of the memory task, depicted in Figure 1(b,c), was equivalent for both material types, and involved five phases: Encoding I; Encoding Test; Encoding II; Retrieval I; Retrieval II. In Encoding I, participants were instructed to remember the target stimuli, with no instructions to categorise or label the stimuli. The six stimuli were presented sequentially

in pseudorandom order, then repeated four times with the restriction that immediate repetitions were avoided. This was followed by an Encoding Test (six target items and six foils with no repetitions, intermixed in pseudorandom order) in order to ensure that participants were learning and understood the task. Encoding I was then repeated with a re-randomised stimulus order (Encoding II). Note that memory performance and ERP data were analysed from Encoding I and II phases but not the Encoding Test.

The Encoding phases were followed by two consecutive Retrieval phases in which the six target items were repeated four times (48 total target trials), intermixed with 24 different foils, shown once each (with 24 foil trials over 2 phases, eight unique foils per target stimulus, and no foil repeated). Each target was repeated 8 times and foils were refreshed with each repetition to ensure that memory for multiple aspects of the target stimuli were being tested. For example, for different pseudoword foils, different letters within the words were changed in order to ensure that memory for the target word as a whole was tested rather than only the initial letter cluster, thereby requiring encoding, and subsequent recognition, of all associated word features.

Across all phases the stimuli were presented for 1500 ms, and, to enhance sustained attention to the task, the duration of pre- and post-stimulus intervals, during which participants were instructed to fixate a cross, was jittered randomly (Encoding: between 1400 and 1600 ms; Retrieval: 400 to 600 ms) as shown in Figure 1(b,c). During the Encoding Test and Retrieval I and II phases, participants fixated the cross before either a target or foil stimulus was presented and pressed one button to indicate a match to a target stimulus ("yes—seen before") or a second button to indicate a new item ("no—unseen"). On-screen feedback was provided in both the Encoding Test and Retrieval I and II phases ("correct" or "incorrect"). Participants were encouraged to respond quickly and accurately. To account for potential response-hand-related hemispheric lateralisation in ERP peaks, response-hand was counterbalanced between participants: half used the right button for "yes" and the left for "no" for both types of task, with the assignment reversed for the other half.

2.5 EEG recording and offline analysis

EEG was recorded during all five phases using sintered Ag-AgCl electrodes mounted in an Easy-Cap according to the 10-20 system (FP1, FP2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz, and O2). The ground electrode was positioned between FPz and Fz. Activity from both mastoids was recorded and the left mastoid served as the online reference. Vertical eye movements (VEOG; vertical electrooculogram) were measured with electrodes placed above and below the left eye. Horizontal eye movements (HEOG; horizontal electrooculogram) were measured with electrodes on the outer canthi of each eye. Electrode impedance was kept below 5 kΩ. The signal was amplified 20,000 times (SynAmps2 amplifier, Compumedics Limited), sampled at 500 Hz, low-pass filtered at 100 Hz online and saved to a hard disk.

Offline analysis was conducted using BESA Research software (version 6.0, BESA GMbH, Grafelfing, Germany). First, portions of EEG containing large movement-related artefacts were manually rejected. EEG was then set to reference-free and filtered (highpass 0.53Hz, forward, 6 db/octave; lowpass 8Hz, zero phase, 24 db/octave roll-off), for artefact correction which was carried out using the adaptive method of the automatic artefact correction tool in BESA. This method applied a predefined source model to the data, combining three topographies accounting for EOG activities (HEOG, VEOG, blink) with a set of 12 regional sources modelling the different scalp regions. If the EOG signals exceeded set thresholds (HEOG amplitude 150μV, VEOG/Blink threshold 250μV), then the current EEG topography was accumulated and averaged over the whole EEG. The first principle component of this averaged EOG signal served as the artefact topography that was used for artefact correction, which was performed using an adaptive method (see Ille, Berg, & Scherg, 2002 for further details).

The EEG data were then divided into 2500 ms epochs with a 1000 ms pre-stimulus interval and 1500 ms post-stimulus interval. These epochs were then re-referenced to the average of the left and right mastoids, band pass filtered (highpass 0.53 Hz, forward phase, 6

dB/octave roll-off; lowpass 200 Hz, zero phase, 24 dB/octave roll-off) and baseline corrected the using mean pre-stimulus amplitude for the epoch. EEG artefacts, including blinks and eye-movements, were rejected using the BESA artefact scan tool, which rejects trials based on abnormally high amplitudes (120 μV), abrupt gradients in amplitude exceeding 75 μV, or unusually low signal (below 0.01 μV). The mean number of epochs rejected was low (verbal 5.96%, nonverbal 5.38%, encoding 7.29%, retrieval 4.86 %). Epochs associated with incorrect responses were also excluded from further analysis, resulting in the average percentage of trials accepted: verbal 90.25%, nonverbal 84.31%, encoding 92.71%, retrieval 84.56%.

2.5.1 Event-related power change

EEG amplitudes for each accepted epoch and channel were squared in order to obtain simple power estimates and averaged separately for each experimental condition and participant. BESA was then used to conduct time-frequency analysis (frequency range 2 to 20 Hz, frequency/time sampling of 1 Hz/50 ms) resulting in 969 time-frequency measures (19 frequency samples x 51 time samples) per electrode. Based on these data, event-related power change (power) values were calculated as the percentage decrease or increase in band power during the test interval (stimulus onset to 1500 ms post-stimulus) compared with the reference interval (1000 ms pre-stimulus to stimulus onset; Pfurtscheller & da Silva, 1999). Positive power values indicated a mean power increase relative to baseline while negative values indicated a mean power decrease. These power measures were then averaged to create 128 frequency- and time-specific power measures per participant: eight hemispherically lateralised sites in frontal and parietal regions (F7, F3, F4, F8, P7, P4, P3, P8) by two materials (verbal, nonverbal) by two processes (encoding, retrieval) by two frequency bands (theta: 4 to 7 Hz; alpha: 8 to 13 Hz) by two time windows (early: 0 to 500 ms; late: 500 to 1500 ms). Region-wide measures were then obtained by averaging the mean power of F3 and F7 (left frontal), F4 and F8 (right frontal), P3 and P7 (left parietal), P4 and P8 (right parietal), resulting in 64 total measures used for analysis: Material (2) x Process (2) x Region (2) x

Frequency (2) x Time (2) x Hemisphere (2).

2.6 Statistical analyses

2.6.1 Memory performance

Mean percentage correct responses to targets and foils were calculated during the Retrieval Phase, from which mean percentage correct and sensitivity (*d'*) values for target/foil discrimination were calculated to ensure the different kinds of stimuli in each condition were adequately learned. *d'* is based on z-score transformations and takes into account both hits and false alarms, controlling for response biases (McNicol, 1972). Response times (RTs) were calculated by subtracting the time of response from the onset time of the response screen (see Figure 1), and median RTs were calculated for each participant. Response times were inverse-transformed (i.e, 1/RT) to reduce the impact of outliers in the analysis.

In order to determine whether task performance had a significant impact on EEG measures, correlations were calculated between: 1) the difference in retrieval accuracy (*d'*) between the materials (i.e. $d'_{\text{verbal}} - d'_{\text{nonverbal}}$), and 2) the difference in power measures between the materials (i.e. $power_{\text{verbal}} - power_{\text{nonverbal}}$), for the 32 relevant power measures (all combinations of Frequency [theta, alpha] x Process [encoding, retrieval] x Time [early, late] x Region [frontal, parietal] x Hemisphere [left, right] combinations). Equivalent correlations were calculated between (inverse-transformed) RTs and EEG measures. To calculate 95% confidence intervals for each correlation, a bootstrap method was conducted with 1000 samples (IBM SPSS Statistics version 22).

2.6.2 EEG hemispheric lateralisation and memory (old/new) effects

Using SPSS, the key predictions of material and process effects on hemispheric differences were tested by comparing mean amplitudes using four-way repeated measures ANOVA with factors material (verbal, nonverbal), process (encoding, retrieval), region (frontal, parietal), and hemisphere (left, right). Separate ANOVAs were run for each of the four combinations of frequency band (theta, alpha) and time window (early, late). We

analysed main effects and interactions between these factors as well as planned simple effects to compare material and process effects. As we used an experimental procedure with multiple repeated items and trials in order to maximise the proportion of correct responses, we did not compare differential power change between correct and incorrect stimuli due to the likely low proportion, and hence poor reliability, of incorrect trials. Instead, to assess correlates of memory for the Retrieval Phase we also compared correct responses to repeated (old) and foil (new) trials using separate Material x Repetition (repeated, non-repeated) x Region x Hemisphere ANOVAs and contrast tests for each time window. In-text reporting of contrasts is restricted to comparisons of direct theoretical relevance; for brevity, using p_p values only. Complete inferential statistics for theta are reported in Supplementary Tables 4 to 7 (see Appendix).

2.6.3 Data treatment, effect size and accounting for multiple comparisons

To ensure that analyses were robust to the effect of outliers, extreme values were subjected to a Winsorisation procedure where values greater than the 95th or less than the 5th percentiles were adjusted to these respective cut-off values. Extreme values accounted for less than 5% of the data across variables. Effect size for all ANOVAs was reported as partial eta-squared (η_p^2), the proportion of variance explained controlling for other effects (interpreted as small: .01 to .09; medium: .09 to .25; or large: > 0.25; Kenny, 1987). For interaction contrast tests the effect size (*d*) was reported, adjusted for repeated measures using Morris and DeShon's (2002) method and appraised according to the review of Lipsey and Wilson (2001), i.e., small: < 0.3; medium: 0.3 to 0.7; large: > 0.7). For contrasts analyses, *p* values were adjusted for multiple comparisons (reported as p_p) using a permutation testing procedure designed for repeated measures (10000 permutations, MATLAB function "mult_comp_perm_t1" by Groppe, Urbach, & Kutas, 2011). Like Bonferroni correction, this method adjusts *p* values in a way that controls the family-wise error rate. However, for EEG data the permutation method is more powerful than Bonferroni correction due to high within-subject correlations between sites and conditions (Blair & Karniski, 1993; Burgess &

Gruzelier, 2000; Good, 1994; Manly, 1997).

3. Results

3.1 Behavioural results and correlation with EEG measures

Retrieval accuracy (*d'*) was significantly higher for verbal stimuli, $M = 3.53$ [CI_{95}: 3.14 3.93] (94.31% correct), than nonverbal stimuli, $M = 2.22$ [1.90 2.54] (84.54%), $t(21) = 5.49$, $p < .001$. RTs did not significantly differ between verbal stimuli, $M = 324$ ms [291 365], and nonverbal stimuli, $M = 326$ ms [294 366], $F(1,21) = 0.01$, $p = .91$. Differences in *d*' between the materials (i.e., verbal – nonverbal) and equivalent differences in EEG measures were not significantly correlated with the exception of alpha measures during encoding in the left hemisphere, $r(18) = .41$ [$CI_{95(bootstrap)}$: .04 .75] and the right hemisphere, $r(18) = .39$ [$CI_{95(bootstrap)}$: .01 .75] during encoding. Equivalent comparisons for response time differences did not show any significant correlations.

To confirm whether *d'* had an independent effect on lateralisation it was entered as a predictor along with variables material, process, and subject (i.e., differences between participants) into a repeated-measures regression (sequential entry via "Enter" method) onto all lateralised EEG (left – right) measures. It was found that *d'* did not independently predict lateralisation for any of these measures, *p*s > .14, indicating the impact of retrieval accuracy and speed on lateralisation of EEG measures was negligible. See Supplementary Tables 1, 2 and 3, respectively, in the Appendix for complete inferential statistics for *d'*, RT and regression analyses.

3.2 EEG hemispheric lateralisation – material, process, and memory (old/new) effects

3.2.1 Early theta power (0 to 500 ms)

Figure 2 shows the left and right hemisphere mean event-related theta power change across all combinations of material, process, and scalp region. As expected, for encoding the theta response showed a rapid increase and subsequent decrease within approximately 500 ms post-stimulus. For retrieval, the overall pattern was similar though there was a pre-stimulus

power decrease, the early theta increase was smaller, and after 500 ms theta power was maintained below (rather than at) the pre-stimulus baseline.

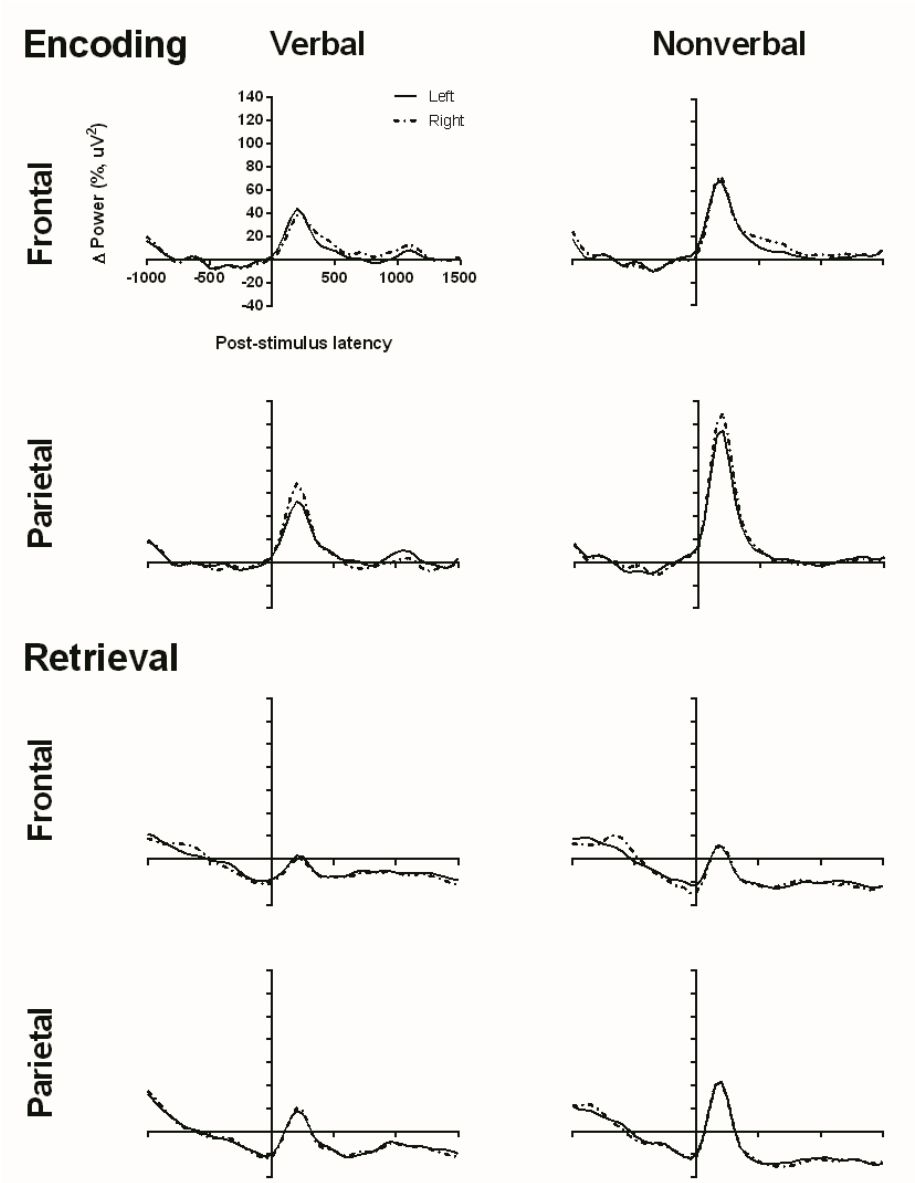

Fig. 2. Mean percentage theta power change from 0 to 1500 ms post-stimulus for verbal and nonverbal materials during encoding and retrieval at frontal and parietal sites in both hemispheres.

Stimuli induced an early theta power increase and revealed a significant main effect of material (nonverbal > verbal), $p = .02$, process (encoding > retrieval), $p < .001$, region (parietal > frontal), $p < .001$, and hemisphere (right > left), $p = .04$. The following interactions were significant: Material x Region, $p < .001$; Process x Hemisphere, $p = .02$; Process x Region, $p = .04$; Material x Process x Region, $p < .001$. Interaction contrasts showed that the main effect of material (nonverbal > verbal) did not differ between the hemispheres, $p_p = .50$, failing to support the material hypothesis. Early theta was significantly right-lateralised during

encoding, p_p = .006, but not during retrieval, p_p = .94 (difference, p_p = .048), opposing the process hypothesis (see Figure 3). Early theta did not show a significant main effect of repetition, p = .86, or interactions, ps > .17. Overall, the early theta response did not show any material-specific pattern, and opposed our predictions for processing, with encoding shown to be more right-lateralised than retrieval.

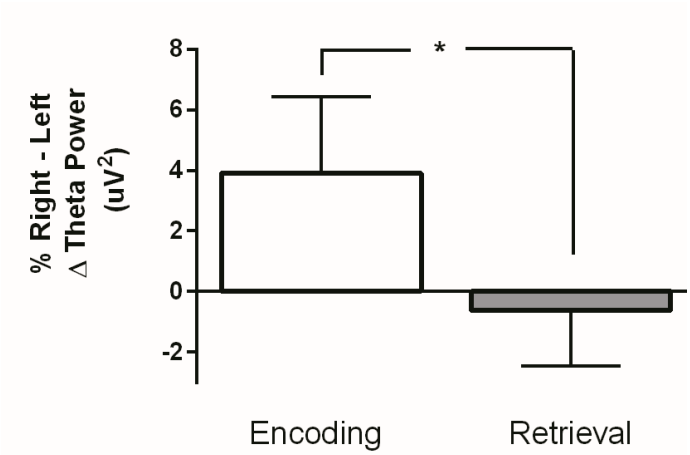

Fig. 3. Mean percentage theta power change (right – left hemisphere, with standard error of difference) from 0 to 500 ms during encoding and retrieval. Asterisks located above bars refers to significant main effect of process (encoding > retrieval). * p < .05.

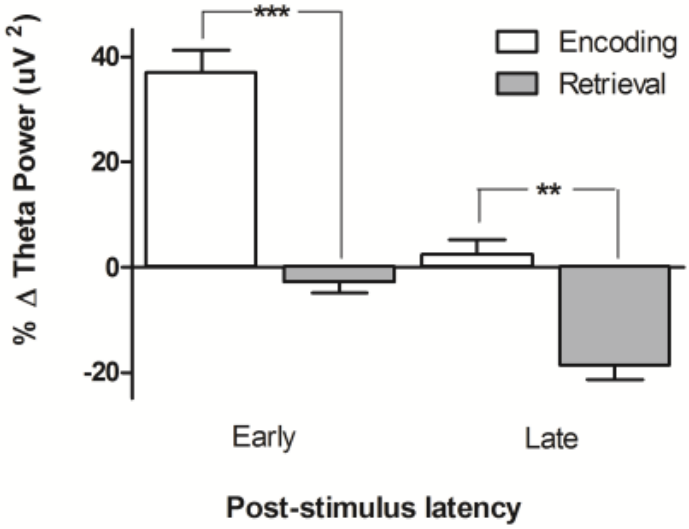

Fig. 4. Mean percentage theta power change (with standard errors) for early and late post-stimulus latencies during encoding and retrieval in both hemispheres. Early: 0 to 500 ms. Late: 500 to 1500 ms. Asterisks above the bars refer to significant main effect of process within each time window (early: encoding increase > retrieval increase; late: retrieval decrease > encoding decrease). ** p < .01, *** p < .001.

3.2.2 Late theta power (500 to 1500 ms)

Late theta power revealed a significant main effect of material (nonverbal > verbal decrease), $p = .049$, process (retrieval > encoding decrease; see Figure 4), $p < .001$, and region (parietal > frontal), $p = .001$. All interaction contrasts testing associations between material, process, and lateralisation were not significant.

The main effect of Repetition was not significant, $p = .16$; however, the following interactions were significant: Repetition x Hemisphere, $p < .001$; Material x Repetition x Hemisphere, $p < .001$; Repetition x Region x Hemisphere, $p < .001$; Material x Repetition x Region x Hemisphere, $p < .001$. There was a right-lateralised old/new effect (old > new) overall, $p_p < .001$ (see Figure 5, upper panel), with right-lateralisation for nonverbal materials in isolation, $p_p < .001$, but no lateralisation for verbal materials, $p_p = .99$ ($p_p < .001$ for material difference; see Figure 5, lower panel), supporting the material hypothesis.

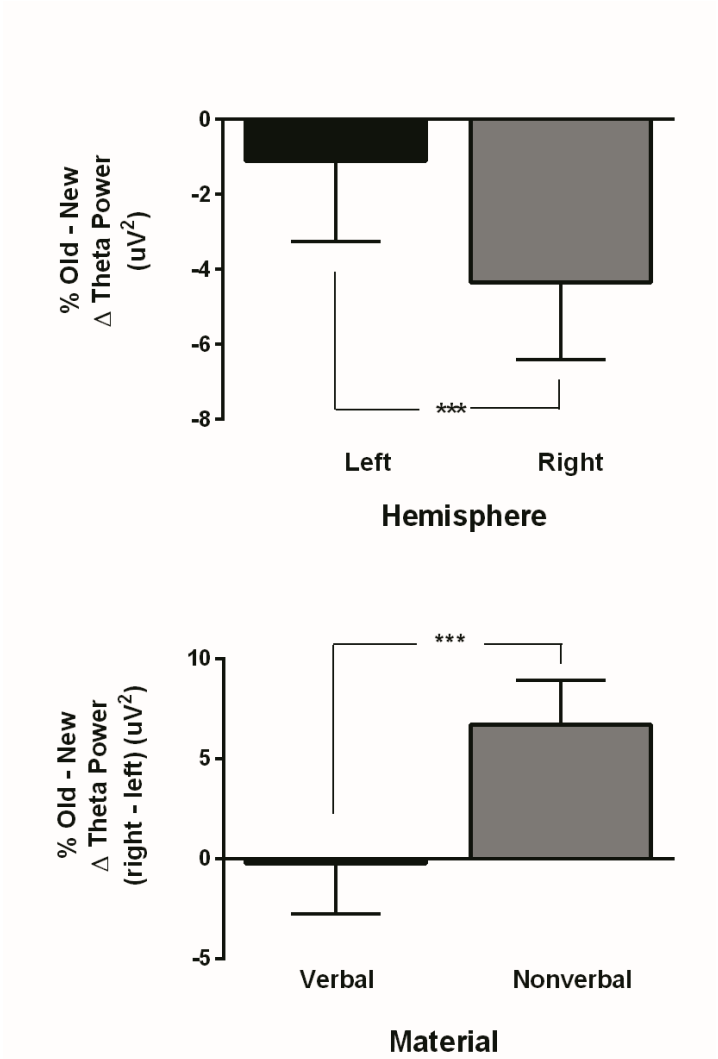

Fig. 5. Mean percentage theta power change (with standard errors) from 500 to 1500 ms during retrieval-stage memory effects. Upper panel: repetition effect (old decrease > new decrease) in left and right hemisphere; asterisks below bars refers to significant lateralisation (right decrease > left decrease). Lower panel: hemispheric difference (right decrease > left decrease) in repetition effect (old – new) for verbal and nonverbal materials; asterisks above bars refers to significant main effect of material (nonverbal > verbal). *** $p < .001$.

3.2.3 Early alpha power, 0 to 500 ms

Figure 6 shows alpha power increased very rapidly within the first 300 ms post-stimullus, followed by a rapid and large decrease below baseline levels that was greatest at approximately 500 ms and was maintained for several hundred millseconds. The pattern and magnitude of power change were similar for encoding and retrieval with the exception of a pre-stimulus power increase for retrieval. Complete inferential statistics for alpha are reported

in the Appendix (Supplementary Tables 8 to 11).

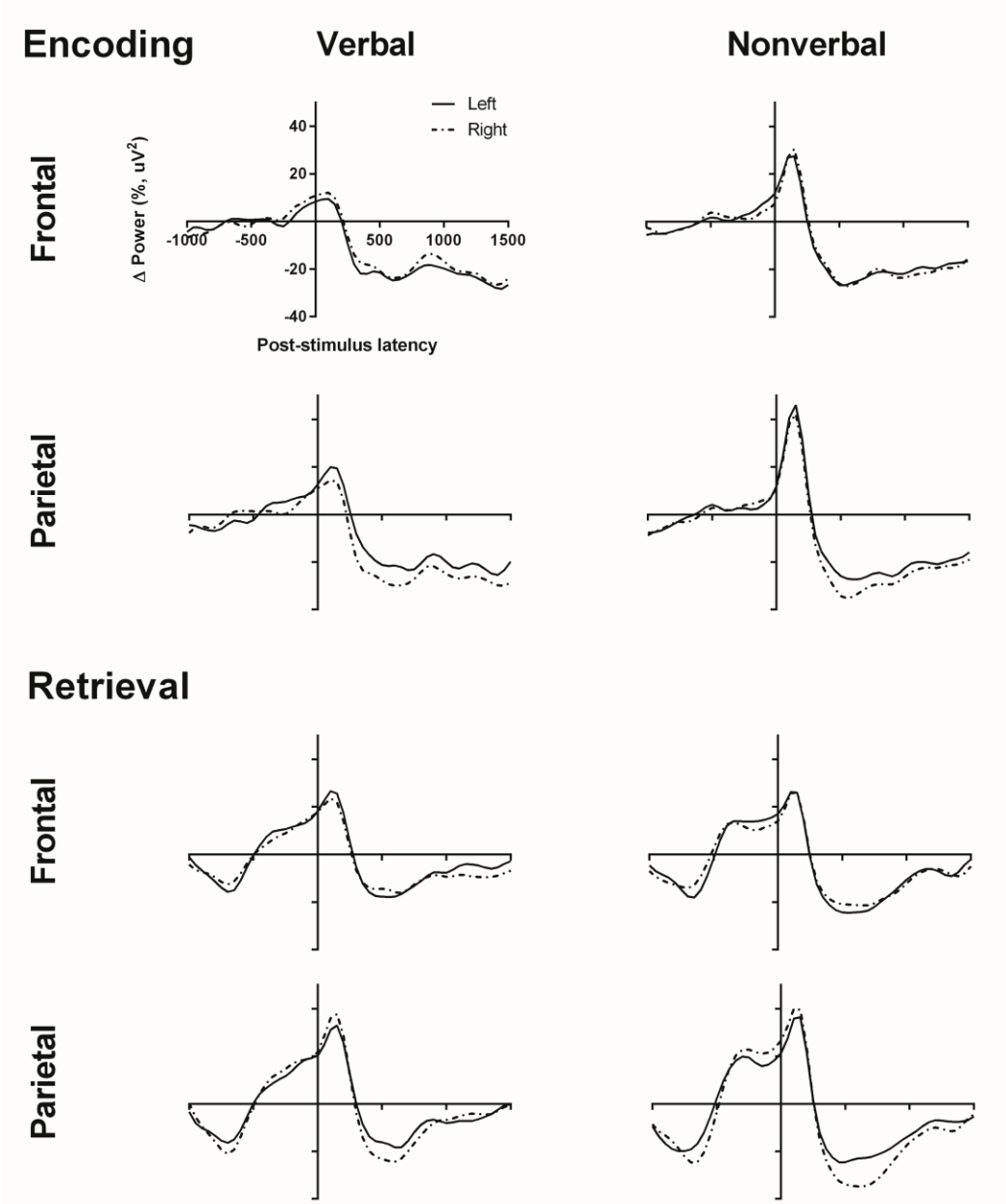

Fig. 6. Mean percent alpha power change from 0 to 1500 ms post-stimulus for verbal and nonverbal materials during encoding and retrieval at frontal and parietal sites in both hemispheres.

ANOVA main effects were all non-significant, *p*s > .08. The Region x Hemisphere, p = .01, and the Material x Process x Region, p = .02, interactions were significant. The Region x Hemisphere interaction was explained by opposing, non-significant patterns of lateralisation between the parietal (left > right, p_p = .06) and frontal regions (right > left, p_p = .14). The main effect of repetition was significant (old > new), p = .03 (see Figure 7, left), but there were no significant interactions, *p*s > .29. Contrasts showed the repetition effect was significant in the right hemisphere, p_p = .04, but not in the left, p_p = .32 (lateralisation, p_p

= .70). In summary, lateralisation of early alpha power was not affected by the type of material or process, and there was a right-lateralised old/new memory effect.

3.2.4 Late alpha power, 500 to 1500 ms

For late alpha power, there was a significant main effect of Process (encoding > retrieval decrease), $p = .004$, Region (parietal > frontal), $p < .03$, and Hemisphere (right > left), $p = .02$. The Process x Region, $p = .03$, and Material x Process x Region x Hemisphere, $p = .02$, interactions were significant. The main effect of Process (encoding > retrieval) was highly specific to verbal material, showing significant differences for all combinations of region and hemisphere, p_ps < .03, except for in the right frontal region, $p_p = .19$ (nonverbal, p_ps > .12). However, the Process effect was not lateralised, $p_p = .94$. All old/new main effects, interactions, and contrasts were not significant, p_ps > .07. In summary, late alpha showed right-lateralisation (see Figure 7, right), but this was not affected by the type of material, process, or memory demands.

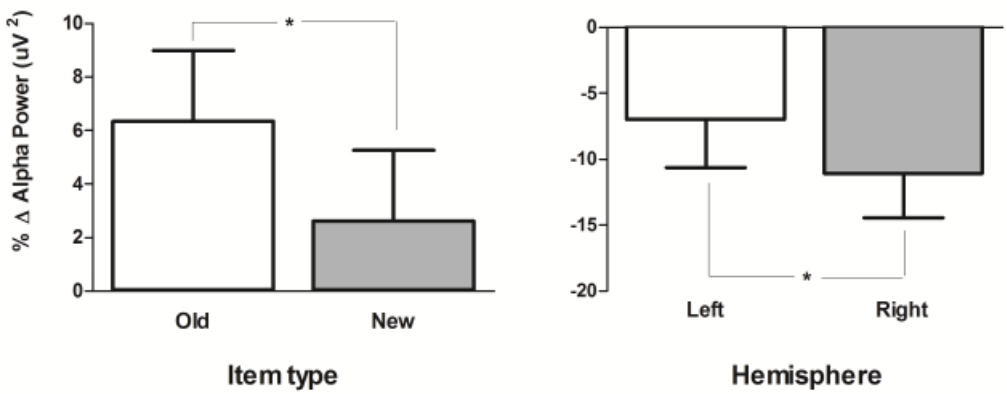

Fig. 7. Mean percentage alpha power change (with standard errors), collapsed across type of material and processing. Left: early alpha, repeated (old) and non-repeated (new) stimuli. Right: late alpha, left and right hemisphere. * $p < .05$.

4. Discussion

The aim of this study was to investigate the separate and interacting effects of material (verbal, nonverbal) and processing (encoding, retrieval) on hemispheric lateralisation in the theta and alpha frequency bands during a memory task. The first prediction was that changes

in EEG power would show relative left-lateralisation for verbal materials and relative right-lateralisation for nonverbal materials, consistent with the material specificity model. The second prediction was that changes in EEG power would show relative left-lateralisation for encoding and relative right-lateralisation for retrieval, consistent with the HERA model. Overall, our prediction for material was partially supported, with nonverbal material showing a right-lateralised old/new memory effect in theta power, however verbal materials did not show relative left-lateralisation. For the second prediction, the results were in the opposite direction, with theta power showing right-lateralisation during encoding relative to retrieval, regardless of material. Alpha power did not show any hemispheric differences related to material or processing type, in contrast to theta power.

A right-lateralised theta response while retrieving spatially arranged dot patterns material is consistent with previous MEG findings for the retrieval of scenes (Osipova et al., 2006) and an association between right parahippocampal theta in memory for navigated routes (Baker & Holroyd, 2013). More broadly, the data are consistent with fMRI studies showing selective right hippocampal activity during spatial and navigational memory tasks (Bellgowan et al., 2009; Kuhn & Gallinat, 2014; Maguire et al., 1998; Maguire, Frith, & Cipolotti, 2001; Suthana, Ekstrom, Moshirvaziri, Knowlton, & Bookheimer, 2009; White, Congedo, Ciorciari, & Silberstein, 2012). The findings also correspond with lesion studies showing right-lateralised involvement when encoding abstract spatial information (Bohbot et al., 1998; Kessels, Postma, de Haan, & Kappelle, 2002; Spiers et al., 2001), and single-cell recording evidence for “grid cells” and “place cells” in the human right hippocampal and parahippocampal regions (Burgess, 2002; Ekstrom et al., 2003; Suthana et al., 2009).

In contrast to the results for the nonverbal memory task, the absence of left hemispheric lateralisation for verbal material is inconsistent with previous electrophysiological and neuropsychological studies showing left hemisphere dominance for pseudoword processing (e.g., Bentin et al., 1999; Falk, Cole, & Glosser, 2002), but is consistent with other findings showing less left hemisphere involvement (Doyle, Rugg &

Wells, 1996; Evans & Federmeier, 2007; Sekiguchi, Koyama, & Kakigi, 2001; Swick & Knight, 1997). Meaningful words were not used in this study in order to more precisely match the novel, non-semantic nature of the spatial nonverbal stimuli. The right-lateralisation found for nonverbal stimuli can therefore be directly attributable to their greater reliance on spatial processing and less to their relative novelty or a lack of semantic processing per se.

Our results using EEG frequency offer little support for HERA, in contrast to much existing literature (e.g., PET: Lee et al., 2000; Nyberg et al., 1996; review of PET and fMRI studies: Cabeza & Nyberg, 2000). It is possible that frequency-specific measures of EEG power are less sensitive to the process-related lateralisation effects that have been found using blood flow measures. However, as there were effects in the opposite direction to those predicted, this suggests that the theta frequency may be sensitive to other aspects of process type than those found in neuroimaging studies. One possible explanation is that early theta is sensitive to the relative novelty of the stimulus within the experimental context, since the relative novelty is greater during encoding than retrieval. This type of novelty has been linked to right-lateralisation regardless of material type (e.g., Martin, 1999).

Another possible source of the discrepancy may be the considerably shorter timescale of the effect in theta power from 0 to 500 ms after stimulus onset, compared to a resolution of at least 5 seconds for neuroimaging measures such as fMRI. Therefore, lateralisation of the very rapid theta effect could be cancelled out across a 5 second span by other, later changes in brain activity that are lateralised in the opposite pattern. More speculatively, a negative correlation may exist between EEG frequency measures and blood flow measures (fMRI). While some studies using simultaneous EEG-fMRI recordings have shown positive correlations between theta power change and BOLD response using tasks involving memory formation (Hanslmayr et al., 2011) and the encoding phase of a working memory task (Ozelo et al., 2014), others using working memory tasks have found negative correlations between theta power and the BOLD response (e.g. Michels et al., 2010; Scheeringa et al., 2009). Therefore, it is possible that the observed right-lateralisation of theta power during encoding

rather than retrieval (opposing HERA) could actually be associated with greater left-lateralisation of BOLD response for encoding rather than for retrieval (consistent with HERA). In contrast to theta, decreases in alpha as observed in this study are more reliably associated with increases in BOLD response in the neocortex (Goldman et al., 2002; Laufs et al., 2003; Moosmann et al., 2003; Scheeringa et al., 2009), causing no potential conflict in interpreting the direction of lateralisation effects. Taken together, our findings regarding the HERA model must be interpreted with caution as aspects of our methodology differ from those of previous investigations, including the use of multiple repetitions of stimuli across encoding trials (versus a simple study-test design) and the use of ERPs (versus PET or fMRI). Future studies with simultaneous scalp EEG-fMRI may cast light on this matter.

As a secondary aim of this study we explored whether changes in different frequency bands were related to the type of memory processing, specifically whether the theta band was more involved during encoding than retrieval, and whether the alpha band showed the opposite pattern. There was some support for this when the time window was considered, as the increase in early theta power was more associated with encoding than retrieval, while the decrease in late theta power was more strongly associated with retrieval than encoding (see Figures 2 and 4 showing this distinction). This supports previous findings showing that theta power is critical to both memory formation and retrieval (e.g., Klimesch et al., 2001; Nyhus & Curran, 2010). In contrast, for alpha the effects were mixed, with early alpha showing an old/new effect indicating some sensitivity to retrieval-related processing consistent with previous studies (e.g., Burgess & Gruzelier, 2000), but late alpha showed larger power change to encoding than retrieval, hence opposing the prediction. In sum, the results of this study suggest that both theta and alpha band were involved in performing the memory tasks, with the direction of theta power more affected by the particular kind of memory-related processing involved.

Another important issue relating to interpretation of the material effects is the potential role of low-level stimulus characteristics, since the dot arrays were larger in size and lower in

spatial frequency than the pseudowords. ERPs are sensitive to differences in both size and spatial frequency, with stimuli that are larger in size and lower in spatial frequency associated with right-lateralisation of ERPs, and particularly the N170 (Luck, 2005; Martinez, di Russo, Anllo-Vento, & Hillyard, 2001; Sergent, 1982; van der Ham, Postma, & Laeng, 2014). Therefore, it is possible that size and/or spatial frequency may confound interpretation of the material effects as related to the memory task. While this is possible, it seems unlikely since the material-related lateralisation old/new effects in theta occurred in the time window from 500 to 1500 ms after stimulus onset, well after the period (within first 200 ms) typically associated with these stimulus sizes and spatial frequency effects (e.g., Martinez et al., 2001). However, to rule out these factors this study could be replicated with spatial frequency and size controlled between the verbal and nonverbal stimuli.

The memory-related (old/new) effects we found in late theta and early alpha are consistent with previous findings, with some minor divergence in the timing of the effects (cf. early theta and late alpha; Burgess & Gruzelier, 1997, 2000). These studies also showed material specific lateralisation of the old/new effect (i.e., left for real words and right for faces), whereas we found a right-lateralised old/new effect for dot patterns but no left-lateralised effect for pseudowords. These differences may be associated with the different stimuli and therefore processing demands in this study relative to these previous studies. In addition, these previous findings used narrower frequency bands and were also measured relative to individualised peak alpha frequency (approximately, theta: 4 to 6 Hz; lower alpha: 7 to 10 Hz; upper alpha: 11 to 13 Hz; see Klimesch, 1999, for details), while we used the broader, more commonly used “traditional” frequency band ranges (theta: 4 to 7 Hz; alpha 8 to 13 Hz). While the authors of these studies have argued that their method is required to distinguish functionally different memory-related effects in the theta band from those in the alpha band, there are many studies that have found effects relating to memory using the traditional bands (e.g., Babiloni et al., 2009; Baker & Holroyd, 2013; Ekstrom et al., 2005; Osipova et al., 2006). In addition, as the traditional frequency ranges are the most commonly

used, they more readily permit comparison of our data with a wide range of studies with differing methodologies (e.g., intracranial EEG, fMRI, animal studies). This is particularly important as there remain very few investigations into memory-related lateralisation employing frequency measures, fewer that have compared verbal with nonverbal material, and none to our knowledge that have directly compared material specific lateralisation effects to those relating to processing.

As scalp-measured EEG frequency measures have poor spatial resolution the precise localisation of the observed effects is unknown. However, given the wealth of evidence for a direct connection between spatial memory and theta band changes in the right medial temporal lobe (e.g., Baker & Holroyd, 2013), this region is most likely involved. Replication of our findings using fMRI of the medial temporal and prefrontal lobes would clarify the localisation of EEG lateralisation effects due to material and processing. Nevertheless, our findings suggest that EEG frequency measures usefully complement neuroimaging techniques with high spatial resolution in testing the validity of the HERA model versus the material specificity model.

4.1 Conclusion

The results of this study indicate that lateralisation of theta power is dependent on both the type of material and the type of memory processing. Specifically, theta power shows right-lateralisation of the old/new memory effect for nonverbal material compared with verbal material, supporting the material specificity model, and during memory retrieval compared with encoding, contradicting the HERA model. Alpha power, by contrast, was not sensitive to material or process but early alpha power (0 to 500 ms) correlated with memory performance. Previous findings of a correlation between spatial memory and theta power were confirmed. The finding that opposed HERA may have been due to methodological differences between this and previous studies. This study indicates that considering both material specific and processing specific lateralisation effects may have relevance in the clinical assessment of right hemispheric pathology.

References

Alpherts, W. C. J., Vermeulen, J., van Rijen, P. C., da Silva, F. H. L., van Veelen, C. W. M., & Dutch Collaborative Epilepsy, S. (2006). Verbal memory decline after temporal epilepsy surgery? A 6-year multiple assessments follow-up study. *Neurology, 67*(4), 626-631. doi: 10.1212/01.wnl.0000230139.45304.eb

Anderson, K. L., Rajagovindan, R., Ghacibeh, G. A., Meador, K. J., & Ding, M. Z. (2010). Theta Oscillations Mediate Interaction between Prefrontal Cortex and Medial Temporal Lobe in Human Memory. *Cerebral Cortex, 20*(7), 1604-1612. doi:10.1093/cercor/bhp223

Babiloni, C., Vecchio, F., Cappa, S., Pasqualetti, P., Rossi, S., Miniussi, C., & Rossini, P. M. (2006). Functional frontoparietal connectivity during encoding and retrieval processes follows HERA model - A high-resolution study. *Brain Research Bulletin, 68*(4), 203-212. doi: 10.1016/j.brainresbull.2005.04.019

Babiloni, C., Vecchio, F., Mirabella, G., Buttiglione, M., Sebastiano, F., Picardi, A., . . . Eusebi, F. (2009). Hippocampal, Amygdala, and Neocortical Synchronization of Theta Rhythms is Related to an Immediate Recall During Rey Auditory Verbal Learning Test. *Human Brain Mapping, 30*(7), 2077-2089. doi:10.1002/hbm.20648

Baker, T. E., & Holroyd, C. B. (2013). The topographical N170: Electrophysiological evidence of a neural mechanism for human spatial navigation. *Biological Psychology, 94*(1), 90-105.

Barr, W. B. (1997). Examining the right temporal lobe's role in nonverbal memory. *Brain and Cognition, 35*(1), 26-41.

Bell, B. D., & Davies, K. G. (1998). Anterior temporal lobectomy, hippocampal sclerosis, and memory: Recent neuropsychological findings. *Neuropsychology Review, 8*(1), 25-41. doi: 10.1023/a:1025679122911

Bellgowan, P. S. F., Buffalo, E. A., Bodurka, J., & Martin, A. (2009). Lateralized spatial and object memory encoding in entorhinal and perirhinal cortices. *Learning & Memory, 16*(7), 433-438. doi: 10.1101/lm.1357309

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience, 11*(3), 235-260.

Blair, R. C., & Karniski, W. (1993). An alternative method for significance testing of waveform difference potentials. *Psychophysiology, 30*(5), 518-524.

Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia, 36*(11), 1217-1238. doi: 10.1016/s0028-3932(97)00161-9

Burgess, N. (2002). The hippocampus, space, and viewpoints in episodic memory. *The Quarterly Journal of Experimental Psychology: Section A, 55*(4), 1057-1080.

Burgess, A. P., & Gruzelier, J. H. (1997). Short duration synchronization of human theta rhythm during recognition memory. *Neuroreport, 8*(4), 1039-1042.

Burgess, A. P., & Gruzelier, J. H. (2000). Short duration power changes in the EEG during recognition memory for words and faces. *Psychophysiology, 37*(5), 596-606.

Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience, 12*(1), 1-47.

Cohen, J. (1977). *Statistical power for behavioural sciences (revised edition)*. New York: Academic Press.

Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. In S. E. Hyman, T. M. Jessell, C. J. Shatz, C. F. Stevens, & H. Y. Zoghbi (Eds.), *Annual Review of Neuroscience, Vol 34* (Vol. 34, pp. 569-599).

Desgranges, B., Baron, J. C., & Eustache, F. (1998). The functional neuroanatomy of episodic memory: The role of the frontal lobes, the hippocampal formation, and other areas. *Neuroimage, 8*(2), 198-213. doi: 10.1006/nimg.1998.0359

Doyle, M. C., Rugg, M. D., & Wells, T. (1996). A comparison of the electrophysiological effects of formal and repetition priming. *Psychophysiology, 33*(2), 132-147. doi: 10.1111/j.1469-8986.1996.tb02117.x

Dujardin, K., Bourriez, J. L., & Guieu, J. D. (1994). Event-related desynchronization (ERD) patterns during verbal memory tasks: effect of age. *International Journal of Psychophysiology*, *16*(1), 17-27. doi: 10.1016/0167-8760(94)90038-8

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., & et al. (2003). Cellular networks underlying human spatial navigation. *Nature, 425*(6954), 184-188.

Evans, K. M., & Federmeier, K. D. (2007). The memory that's right and the memory that's left: Event-related potentials reveal hemispheric asymmetries in the encoding and retention of verbal information. *Neuropsychologia, 45*(8), 1777-1790. doi: 10.1016/j.neuropsychologia.2006.12.014

Falk, M. C., Cole, L. C., & Glosser, G. (2002). Pseudoword and real word memory in unilateral temporal lobe epilepsy. *Journal of Clinical and Experimental Neuropsychology, 24*(3), 327-334. doi: 10.1076/jcen.24.3.327.979

Fell, J., Ludowig, E., Staresina, B. P., Wagner, T., Kranz, T., Elger, C. E., & Axmacher, N. (2011). Medial Temporal Theta/Alpha Power Enhancement Precedes Successful Memory Encoding: Evidence Based on Intracranial EEG. *Journal of Neuroscience, 31*(14), 5392-5397. doi: 10.1523/jneurosci.3668-10.2011

Fernandez, G., & Tendolkar, I. (2001). Integrated brain activity in medial temporal and prefrontal areas predicts subsequent memory performance: Human declarative memory formation at the system level. *Brain Research Bulletin, 55*(1), 1-9. doi: 10.1016/s0361-9230(01)00494-4

Fingelkurts, A. A., Fingelkurts, A. A., Krause, C. M., & Sams, M. (2002). Probability interrelations between pre-/post-stimulus intervals and ERD/ERS during a memory task. *Clinical Neurophysiology, 113*(6), 826-843. doi: 10.1016/s1388-2457(02)00058-5

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing, and practice. *Cerebral Cortex, 7*(4), 374-385. doi: 10.1093/cercor/7.4.374

Glosser, G., Deutsch, G. K., Cole, L. C., Corwin, J., & Saykin, A. J. (1998). Differential lateralization of memory discrimination and response bias in temporal lobe epilepsy patients. *Journal of the International Neuropsychological Society, 4*(5), 502-511.

Golby, A. J., Poldrack, R. A., Brewer, J. B., Spencer, D., Desmond, J. E., Aron, A. P., & Gabrieli, J. D. E. (2001). Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. *Brain, 124*, 1841-1854. doi: 10.1093/brain/124.9.1841

Goldman, R. I., Stern, J. M., Engel Jr, J., & Cohen, M. S. (2002). Simultaneous EEG and fMRI of the alpha rhythm. *Neuroreport, 13*(18), 2487.

Good, P. (1994). *Permutation Tests: A Practical Guide to Resampling Methods for Testing Hypotheses.* New York: Springer-Verlag.

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

Guderian, S., & Duzel, E. (2005). Induced theta oscillations mediate large-scale synchrony with mediotemporal areas during recollection in humans. *Hippocampus, 15*(7), 901-912. doi: 10.1002/hipo.20125

Habib, R., Nyberg, L., & Tulving, E. (2003). Hemispheric asymmetries of memory: the HERA model revisited. *Trends in Cognitive Sciences, 7*(6), 241-245. doi: 10.1016/s1364-6613(03)00110-4

Hanslmayr, S., Volberg, G., Wimber, M., Raabe, M., Greenlee, M. W., & Bäuml, K.-H. T. (2011). The relationship between brain oscillations and BOLD signal during memory formation: a combined EEG–fMRI study. *The Journal of Neuroscience, 31*(44), 15674-15680.

Ille, N., Berg, P., & Scherg, M. (2002). Artefact Correction of the Ongoing EEG Using Spatial Filters Based on Artefact and Brain Signal Topographies. *Journal of Clinical Neurophysiology, 19*(2), 113-124.

Igloi, K., Doeller, C. F., Berthoz, A., Rondi-Reig, L., & Burgess, N. (2010). Lateralized human hippocampal activity predicts navigation based on sequence or place memory. *Proceedings of the National Academy of Sciences of the United States of America, 107*(32), 14466-14471. doi: 10.1073/pnas.1004243107

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience, 15*(8), 1395-1399. doi: 10.1046/j.1460-9568.2002.01975.x

Johnson, M. K., Raye, C. L., Mitchell, K. J., Greene, E. J., & Anderson, A. W. (2003). fMRI evidence for an organization of prefrontal cortex by both type of process and type of information. *Cerebral Cortex, 13*(3), 265-273. doi: 10.1093/cercor/13.3.265

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., . . . Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron, 20*(5), 927-936. doi: 10.1016/s0896-6273(00)80474-2

Kennepohl, S., Sziklas, V., Garver, K. E., Wagner, D. D., & Jones-Gotman, M. (2007). Memory and the medial temporal lobe: Hemispheric specialization reconsidered. *Neuroimage, 36*(3), 969-978. doi: 10.1016/j.neuroimage.2007.03.049

Kenny, D. A. (1987). *Statistics for the social and behavioral sciences.* Boston: Little, Brown.

Kessels, R. P. C., de Haan, E. H. F., Kappelle, L. J., & Postma, A. (2001). Varieties of human spatial memory: a meta-analysis on the effects of hippocampal lesions. *Brain Research Reviews, 35*(3), 295-303.

Kessels, R. P. C., Kappelle, L. J., de Haan, E. H. F., & Postma, A. (2002). Lateralization of spatial-memory processes: evidence on spatial span, maze learning, and memory for object locations. *Neuropsychologia, 40*(8), 1465-1473.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews, 29*(2-3), 169-195. doi: 10.1016/s0165-0173(98)00056-3

Klimesch, W., Doppelmayr, M., Pachinger, T., & Russegger, H. (1997a). Event-related desynchronization in the alpha band and the processing of semantic information. *Cognitive Brain Research, 6*(2), 83-94. doi: 10.1016/s0926-6410(97)00018-9

Klimesch, W., Doppelmayr, M., Schimke, H., & Ripper, B. (1997b). Theta synchronization and alpha desynchronization in a memory task. *Psychophysiology, 34*(2), 169-176. doi: 10.1111/j.1469-8986.1997.tb02128.x

Klimesch, W., Doppelmayr, M., Schwaiger, J., Winkler, T., & Gruber, W. (2000). Theta oscillations and the ERP old/new effect: independent phenomena? *Clinical Neurophysiology, 111*(5), 781-793. doi: 10.1016/s1388-2457(00)00254-6

Klimesch, W., Doppelmayr, M., Yonelinas, A., Kroll, N. E., Lazzara, M., Roehm, D., & Gruber, W. (2001). Theta synchronization during episodic retrieval: neural correlates of conscious awareness. *Cognitive Brain Research, 12*(1), 33-38.

Klimesch, W., Freunberger, R., & Sauseng, P. (2010). Oscillatory mechanisms of process binding in memory. *Neuroscience and Biobehavioral Reviews*, *34*(7), 1002-1014. doi: 10.1016/j.neubiorev.2009.10.004

Klimesch, W., Freunberger, R., Sauseng, P., & Gruber, W. (2008). A short review of slow phase synchronization and memory: Evidence for control processes in different memory systems? *Brain Research*, *1235,* 31-44. doi: 10.1016/j.brainres.2008.06.049

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, 53(1), 63-88. doi: 10.1016/j.brainresrev.2006.06.003

Klimesch, W., Schack, B., & Sauseng, P. (2005). The functional significance of theta and upper alpha oscillations. *Experimental Psychology, 52*(2), 99-108. doi: 10.1027/1618-3169.52.2.99

Klimesch, W., Schack, B., Schabus, M., Doppelmayr, M., Gruber, W., & Sauseng, P. (2004). Phase-locked alpha and theta oscillations generate the P1-N1 complex and are related to memory performance. *Brain research. Cognitive brain research, 19*(3), 302-316.

Klimesch, W., Schimke, H., & Schwaiger, J. (1994). Episodic and semantic memory: an analysis in the EEG theta and alpha band. *Electroencephalography and Clinical Neurophysiology, 91*(6), 428-441. doi: 10.1016/0013-4694(94)90164-3

Kohler, S., Danckert, S., Gati, J. S., & Menon, R. S. (2005). Novelty responses to relational and non-relational information in the hippocampus and the parahippocampal region: A comparison based on event-related fMRI. *Hippocampus, 15*(6), 763-774. doi: 10.1002/hipo.20098

Kuhn, S., & Gallinat, J. (2014). Segregating Cognitive Functions Within Hippocampal Formation: A Quantitative Meta-analysis on Spatial Navigation and Episodic Memory. *Human Brain Mapping, 35*(4), 1129-1142. doi: 10.1002/hbm.22239

Laufs, H., Kleinschmidt, A., Beyerle, A., Eger, E., Salek-Haddadi, A., Preibisch, C., & Krakow, K. (2003). EEG-correlated fMRI of human alpha activity. *Neuroimage, 19*(4), 1463-1476.

Lee, S., Gonzalez, L., & Savage, G. (2007). Eye-tunes: Memory for spatial and melodic form. *Australian Journal of Psychology, 59*(S1), 222.

Lee, A. C. H., Robbins, T. W., Pickard, J. D., & Owen, A. M. (2000). Asymmetric frontal activation during episodic memory: the effects of stimulus type on encoding and retrieval. *Neuropsychologia, 38*(5), 677-692. doi: 10.1016/s0028-3932(99)00094-9

Lipsey, M.W. and Wilson, D.B. (2001) *Practical Meta-analysis*. Thousand Oaks, CA: Sage

Luck, S. (2005). *An Introduction To The Event-Related Potential Technique*. Cambridge, Massachusetts: The MIT Press.

Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. J., Frith, C. D., & O'Keefe, J. (1998). Knowing where and getting there: A human navigation network. *Science, 280*(5365), 921-924. doi: 10.1126/science.280.5365.921

Maguire, E. A., Frith, C. D., & Cipolotti, L. (2001). Distinct neural systems for the encoding and recognition of topography and faces. *Neuroimage, 13*(4), 743-750. doi: 10.1006/nimg.2000.0712

Maillard, L., Barbeau, E. J., Baumann, C., Koessler, L., Benar, C., Chauvel, P., & Liegeois-Chauvel, C. (2011). From Perception to Recognition Memory: Time Course and Lateralization of Neural Substrates of Word and Abstract Picture Processing. *Journal of Cognitive Neuroscience, 23*(4), 782-800. doi:10.1162/jocn.2010.21434

Manly, B. F. J. (1997). *Randomization, Bootstrap, and Monte Carlo Methods in Biology* (2nd ed.). London: Chapman and Hall.

Martin, A. (1999). Automatic activation of the medial temporal lobe during encoding: Lateralized influences of meaning and novelty. *Hippocampus, 9*(1), 62-70. doi: 10.1002/(sici)1098-1063(1999)9:1<62::aid-hipo7>3.0.co;2-k

Martin, A., Wiggs, C. L., & Weisberg, J. (1997). Modulation of human medial temporal lobe activity by form, meaning, and experience. *Hippocampus, 7*(6), 587-593. doi: 10.1002/(sici)1098-1063(1997)7:6<587::aid-hipo1>3.0.co;2-c

Martinez, A., Di Russo, F., Anllo-Vento, L., & Hillyard, S. A. (2001). Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clinical Neurophysiology, 112*(11), 1980-1998.

McNicol, D. (1972). *A primer of signal detection theory*. Sydney: Australasian Publishing Company.

Mecklinger, A., Kramer, A. F., & Strayer, D. L. (1992). Event related potentials and EEG components in a semantic memory-search task. *Psychophysiology, 29*(1), 104-119. doi: 10.1111/j.1469-8986.1992.tb02021.x

Michels, L., Bucher, K., Lüchinger, R., Klaver, P., Martin, E., Jeanmonod, D., & Brandeis, D. (2010). Simultaneous EEG-fMRI during a working memory task: modulations in low and high frequency bands. *Plos One, 5*(4), e10298.

Mitchell, D. J., McNaughton, N., Flanagan, D., & Kirk, I. J. (2008). Frontal-midline theta from the perspective of hippocampal "theta". *Progress in Neurobiology, 86*(3), 156-185. doi: 10.1016/j.pneurobio.2008.09.005

Morris, S. B., & DeShon, R. P. (2002). Combining effect size estimates in meta-analysis with repeated measures and independent-groups designs. *Psychological Methods, 7*, 105-125.

Moosmann, M., Ritter, P., Krastel, I., Brink, A., Thees, S., Blankenburg, F., . . . Villringer, A. (2003). Correlates of alpha rhythm in functional magnetic resonance imaging and near infrared spectroscopy. *Neuroimage, 20*(1), 145-158.

Nyberg, L., Cabeza, R., & Tulving, E. (1996). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin & Review, 3*(2), 135-148. doi: 10.3758/bf03212412

Nyberg, L., Persson, J., Habib, R., Tulving, E., McIntosh, A. R., Cabeza, R., & Houle, S. (2000). Large scale neurocognitive networks underlying episodic memory. *Journal of Cognitive Neuroscience, 12*(1), 163-173.

Nyhus, E., & Curran, T. (2010). Functional role of gamma and theta oscillations in episodic memory. *Neuroscience and Biobehavioral Reviews, 34*(7), 1023-1035. doi: 10.1016/j.neubiorev.2009.12.014

Ojemann, G. A., & Dodrill, C. B. (1985). Verbal memory deficits after left temporal lobectomy for epilepsy. Mechanism and intraoperative prediction. *Journal of Neurosurgery, 62*(1), 101-107.

Opitz, B., Mecklinger, A., & Friederici, A. D. (2000). Functional asymmetry of human prefrontal cortex: Encoding and retrieval of verbally and nonverbally coded information. *Learning & Memory, 7*(2), 85-96. doi: 10.1101/lm.7.2.85

Osipova, D., Takashima, A., Oostenveld, R., Fernandez, G., Maris, E., & Jensen, O. (2006). Theta and gamma oscillations predict encoding and retrieval of declarative memory. *Journal of Neuroscience, 26*(28), 7523-7531. doi: 10.1523/jneurosci.1948-06.2006

Ozelo, H. F., Alessio, A., Sercheli, M. S., Bilevicius, E., Pedro, T., Pereira, F. R., . . . Covolan, R. J. (2014). Pattern changes of EEG oscillations and BOLD signals associated with temporal lobe epilepsy as revealed by a working memory task. *BMC neuroscience, 15*(1), 1.

Papanicolaou, A. C., Simos, P. G., Castillo, E. M., Breier, J. I., Katz, J. S., & Wright, A. A. (2002). The hippocampus and memory of verbal and pictorial material. *Learning & Memory, 9*(3), 99-104. doi: 10.1101/lm.44302

Pfurtscheller, G., & da Silva, F. H. L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical Neurophysiology*, *110*(11), 1842-1857. doi: 10.1016/s1388-2457(99)00141-8

Pillon, B., Bazin, B., Deweer, B., Ehrle, N., Baulac, M., & Dubois, B. (1999). Specificity of memory deficits after right or left temporal lobectomy. *Cortex, 35*(4), 561-571. doi: 10.1016/s0010-9452(08)70819-0

Rosanova, M., Casali, A., Bellina, V., Resta, F., Mariotti, M., & Massimini, M. (2009). Natural Frequencies of Human Corticothalamic Circuits. *The Journal of Neuroscience*, *29*(24), 7679-7685. doi: 10.1523/jneurosci.0445-09.2009

Rutishauser, U., Ross, I. B., Mamelak, A. N., & Schuman, E. M. (2010). Human memory strength is predicted by theta-frequency phase-locking of single neurons. *Nature*, *464*(7290), 903-U116. doi: 10.1038/nature08860

Sauseng, P., Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: A possible function of EEG theta oscillations. *Neuroscience and Biobehavioral Reviews*, *34*(7), 1015-1022. doi: 10.1016/j.neubiorev.2009.12.006

Scheeringa, R., Fries, P., Petersson, K.-M., Oostenveld, R., Grothe, I., Norris, D. G., . . . Bastiaansen, M. C. (2011). Neuronal dynamics underlying high-and low-frequency EEG oscillations contribute independently to the human BOLD signal. *Neuron, 69*(3), 572-583.

Sekiguchi, T., Koyama, S., & Kakigi, R. (2001). The Effect of Stimulus Repetition on Cortical Magnetic Responses Evoked by Words and Nonwords. *Neuroimage, 14*(1), 118-128. doi: http://dx.doi.org/10.1006/nimg.2001.0774

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation. *Journal of Experimental Psychology-Human Perception and Performance, 8*(2), 253-272. doi:10.1037/0096-1523.8.2.253

Smith, G. E., Malec, J. F., & Ivnik, R. J. (1992). Validity of the construct of nonverbal memory: A factor-analytic study in a normal elderly sample. *Journal of Clinical and Experimental Neuropsychology, 14*(2), 211-221. doi: 10.1080/01688639208402824

Smith, M. L., & Milner, B. (1981). The role of the right hippocampus in the recall of spatial location. *Neuropsychologia, 19*(6), 781-793.

Spiers, H. J., Burgess, N., Maguire, E. A., Baxendale, S. A., Hartley, T., Thompson, P. J., & O'Keefe, J. (2001). Unilateral temporal lobectomy patients show lateralized topographical and episodic memory deficits in a virtual town. *Brain*, *124*, 2476-2489. doi: 10.1093/brain/124.12.2476

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.

Suthana, N. A., Ekstrom, A. D., Moshirvaziri, S., Knowlton, B., & Bookheimer, S. Y. (2009). Human Hippocampal CA1 Involvement during Allocentric Encoding of Spatial

Information. *Journal of Neuroscience*, *29*(34), 10512-10519. doi: 10.1523/jneurosci.0621-09.2009

van der Ham, I. J. M., Postma, A., & Laeng, B. (2014). Lateralized perception: The role of attention in spatial relation processing. *Neuroscience and Biobehavioral Reviews, 45*, 142-148. doi:10.1016/j.neubiorev.2014.05.006

Vaz, S. A. M. (2004). Nonverbal memory functioning following right anterior temporal lobectomy: a meta-analytic review. *Seizure-European Journal of Epilepsy, 13*(7), 446-452. doi: 10.1016/j.seizure.2003.12.004

White, D. J., Congedo, M., Ciorciari, J., & Silberstein, R. B. (2012). Brain Oscillatory Activity during Spatial Navigation: Theta and Gamma Activity Link Medial Temporal and Parietal Regions. *Journal of Cognitive Neuroscience, 24*(3), 686-697.

Supplementary Table 1

Correlations between $d'_{verbal} - d'_{nonverbal}$ and $Power_{verbal} - Power_{nonverbal}$ (averages)

EEG measure	*r*	*[CI95]*	*p*
θ - L - Enc	-.28	[-.56 .08]	.21
θ - R - Enc	-.31	[-.61 .10]	.16
α - L - Enc	.41	[.04 .75]*	.06
α - R - Enc	.39	[.01 .75]*	.07
θ - L - Rtv	-.16	[-.50 .20]	.48
θ - R - Rtv	-.25	[-.54 .04]	.26
α - L - Rtv	.18	[-.33 .60]	.26
α - R - Rtv	.15	[-.36 .56]	.51

d' = d-prime (recognition accuracy); Power = event-related power change; θ = Theta; α = Alpha; Enc = Encoding; Rtv = Retrieval; L = Left; R = Right; t1 = 0-500ms; t2 = 500-1500ms; *r* = correlation coefficient; [CI_{95}] = lower and upper bounds of 95% confidence interval (1000x bootstrapped); *p* = significance test (not corrected for multiple comparisons)

* = bootstrapped CI is different from zero or *p* value significant (as appr opriate).

Supplementary Table 2

Correlations between average *RT* differences and *Power* differences

EEG measure	*r*	*[CI95]*	*p*
A. Material (Verbal - Nonverbal)			
θ - L - Enc	-.18	[-.61 .40]	.42
θ - R - Enc	-.21	[-.64 .40]	.35
α - L - Enc	-.23	[-.64 .35]	.30
α - R - Enc	-.37	[-.74 .24]	.09
θ - L - Rtv	-.19	[-.54 .20]	.40
θ - R - Rtv	-.16	[-.54 .24]	.47
α - L - Rtv	.30	[-.11 .64]	.18
α - R - Rtv	.22	[-.21 .59]	.32
B. Processing (Encoding - Retrieval)			
θ - L - Ver	.13	[-.26 .42]	.58
θ - R - Ver	.15	[-.30 .47]	.50
α - L - Ver	.06	[-.41 .53]	.78
α - R - Ver	.09	[-.35 .50]	.70
θ - L - Non	.28	[-.24 .57]	.21
θ - R - Non	.36	[-.03 .62]	.10
α - L - Non	.40	[-.24 .75]	.06
α - R - Non	.45	[-.19 .78]	.04*

RT = response time; Power = event-related power change; θ = Theta; α = Alpha; Enc = Encoding; Rtv = Retrieval; t1 = 0-500ms; t2 = 500-1500ms; Fro = Frontal; Par = Parietal; L = Left; R = Right. Ver = Verbal; Non = Nonverbal; *r* = correlation coefficient; [CI_{95}] = lower and upper bounds of 95% confidence interval (1000x bootstrapped); *p* = significance test (not corrected for multiple comparisons).

* = bootstrapped CI is different from zero and/or p < 05 (as appropriate).

Supplementary Table 3

Regression analysis of Subject, Material, Process, and *d'* on EEG lateralisation

EEG measure	Predictor	R^2	ΔR^2	*p*
Lat_Fro_Th_t1	1. Subj	.32	.32	.11
	2. Mat	.32	.00	.58
	3. Pro	.33	.01	.40
	4. Mat x Pro	.33	.00	.94
	5. Acc	.34	.01	.45
Lat_Fro_Th_t2	1. Subj	.40	.40	.01*
	2. Mat	.41	.01	.24
	3. Pro	.45	.04	.03*
	4. Mat x Pro	.46	.00	.63
	5. Acc	.46	.01	.44
Lat_Fro_Al_t1	1. Subj	.24	.24	.46
	2. Mat	.24	.00	.96
	3. Pro	.26	.02	.20
	4. Mat x Pro	.27	.00	.65
	5. Acc	.27	.00	.53
Lat_Fro_Al_t2	1. Subj	.37	.37	.04*
	2. Mat	.37	.00	.99
	3. Pro	.39	.03	.11
	4. Mat x Pro	.45	.06	.01*
	5. Acc	.45	.00	.82
Lat_Par_Th_t1	1. Subj	.25	.25	.44
	2. Mat	.26	.01	.41
	3. Pro	.33	.07	.01*
	4. Mat x Pro	.33	.00	.79
	5. Acc	.35	.02	.22
Lat_Par_Th_t2	1. Subj	.34	.34	.08
	2. Mat	.34	.01	.38
	3. Pro	.35	.00	.65
	4. Mat x Pro	.37	.02	.17
	5. Acc	.39	.02	.14
Lat_Par_Al_t1	1. Subj	.37	.37	.03*
	2. Mat	.38	.01	.42
	3. Pro	.39	.01	.24
	4. Mat x Pro	.39	.00	.65
	5. Acc	.40	.01	.31
Lat_Par_Al_t2	1. Subj	.47	.47	<.001*
	2. Mat	.48	.00	.51
	3. Pro	.48	.00	.51
	4. Mat x Pro	.49	.01	.18
	5. Acc	.49	.00	.75

d' = d-prime (recognition accuracy); Power = event-related power change; Lat: Laterality Index (left - right hemisphere); Th = Theta; Al = Alpha; Fro = Frontal; Par = Parietal; t1 = 0-500ms; t2 = 500-1500ms; R^2 = correlation coefficient; [CI_{95}] = lower and upper bounds of 95% confidence interval (1000x bootstrapped); *p* = significance test (not corrected for multiple comparisons)
* $p < .05$.

Supplementary Table 4a.
Descriptive and test statistics for mean theta power change (0 to 500 ms)

Mat	Pro	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Enc	Par	L	30.52	20.86	40.18
			R	34.95	23.19	46.72
		Fro	L	23.99	12.93	35.05
			R	25.32	17.23	33.41
	Rtv	Par	L	0.14	-7.06	7.34
			R	-1.90	-10.68	6.89
		Fro	L	-8.39	-15.23	-1.55
			R	-9.11	-16.95	-1.26
Non	Enc	Par	L	52.35	38.71	66.00
			R	59.84	45.68	74.00
		Fro	L	33.51	23.21	43.81
			R	35.93	24.42	47.44
	Rtv	Par	L	5.08	-1.75	11.91
			R	4.66	-2.49	11.81
		Fro	L	-7.05	-10.83	-3.26
			R	-6.35	-12.77	0.07

4b.

ANOVA Factor	$F(1,21)$	*p*	η_p^2
Mat	7.01	.015	.25
Pro	94.00	<.001	.82
Reg	56.80	<.001	.73
Hem	4.71	.042	.18
Mat * Pro	3.52	.075	.14
Mat * Reg	25.46	<.001	.55
Mat * Hem	1.82	.192	.08
Pro * Hem	7.09	.015	.25
Reg * Hem	0.37	.551	.02
Pro * Reg	4.68	.042	.18
Mat * Pro * Hem	0.05	.821	.00
Mat * Reg * Hem	0.10	.757	.06
Mat * Pro * Reg	18.90	<.001	.47
Pro * Reg * Hem	1.20	.285	.05
Mat * Pro * Reg * Hem	0.05	.827	.00

4c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mat * Pro	Enc	Mat	2.73	-2.81	.043	.34	-0.61
	Rtv	Mat	2.73	-0.91	.779	.02	-0.20
	Ver	Pro	2.73	6.85	<.001	.25	1.48
	Non	Pro	2.73	8.03	<.001	.21	1.88
		Mat * Pro	2.73	-1.88	.242	.14	-0.41
Mat * Reg	Par	Mat	2.44	-3.29	.008	.32	-0.71

	Fro	Mat	2.44	-1.73	.182	.30	-0.37
		Mat * Reg	2.44	-5.05	<.001	.94	-1.28
Mat * Hem	L	Mat	2.64	-2.65	.049	.36	-0.57
	R	Mat	2.64	-2.60	.056	.22	-0.56
	Ver	Hem	2.64	-0.80	.821	.96	-0.17
	Non	Hem	2.64	-2.38	.093	.96	-0.57
		Mat * Hem	2.64	1.35	.504	.96	0.35
Pro * Hem	L	Pro	2.65	9.37	<.001	.31	2.19
	R	Pro	2.65	9.63	<.001	.24	2.18
	Enc	Hem	2.65	-3.57	.006	.97	-0.77
	Rtv	Hem	2.65	0.52	.940	.87	0.12
		Pro * Hem	2.65	-2.66	.048	.92	-0.58
Reg * Hem	Par	Hem	2.47	-1.64	.225	.90	-0.35
	Fro	Hem	2.47	-0.68	.754	.85	-0.15
		Reg * Hem	2.47	-0.61	.799	-.42	-0.13
Pro * Reg	Par	Pro	2.47	9.53	<.001	.39	2.28
	Fro	Pro	2.47	9.14	<.001	.17	2.04
		Pro * Reg	2.47	2.16	.086	.86	0.47
Mat * Pro * Hem	Enc / L	Mat	3.13	-2.77	.113	.37	-0.60
	Enc / R	Mat	3.13	-2.80	.107	.30	-0.61
	Rtv / L	Mat	3.13	-0.84	.979	.12	-0.18
	Rtv / R	Mat	3.13	-0.94	.963	-.02	-0.20
	Ver / L	Pro	3.13	6.54	<.001	.27	1.43
	Ver / R	Pro	3.13	6.91	<.001	.22	1.48
	Non / L	Pro	3.13	8.00	<.001	.20	1.89
	Non / R	Pro	3.13	7.79	<.001	.20	1.78
	Ver / Enc	Hem	3.13	-2.25	.289	.96	-0.48
	Ver / Rec	Hem	3.13	1.01	.947	.94	0.24
	Non / Enc	Hem	3.13	-3.17	.045	.97	-0.74
	Non / Rec	Hem	3.13	-0.09	.999	.87	-0.02
	Enc	Mat * Hem	3.13	1.13	.913	.96	0.26
	Rtv	Mat * Hem	3.13	0.86	.976	.95	0.25
	Ver	Pro * Hem	3.13	-2.31	.261	.93	-0.50
	Non	Pro * Hem	3.13	-2.09	.372	.93	-0.47
Mat * Reg * Hem	Par / L	Mat	2.96	-3.19	.028	.37	-0.69
	Par / R	Mat	2.96	-3.21	.026	.27	-0.69
	Fro / L	Mat	2.96	-1.66	.520	.42	-0.36
	Fro / R	Mat	2.96	-1.67	.511	.19	-0.36
	Ver / Par	Hem	2.96	-0.57	.993	.84	-0.12
	Non / Par	Hem	2.96	-2.39	.166	.94	-0.51
	Ver / Fro	Hem	2.96	-0.16	.999	.83	-0.03
	Non / Fro	Hem	2.96	-1.00	.894	.88	-0.23
	Par	Mat * Hem	2.96	1.05	.875	.89	0.24
	Fro	Mat * Hem	2.96	0.59	.990	.85	0.13
Mat * Pro * Reg	Enc / Par	Mat	2.89	-3.62	.012	.40	-0.79
	Rtv / Par	Mat	2.89	-1.19	.682	-.01	-0.25
	Enc / Fro	Mat	2.89	-1.79	.346	.30	-0.38
	Rtv / Fro	Mat	2.89	-0.53	.973	.17	-0.12
	Par / Par	Pro	2.89	6.56	<.001	.31	1.43
	Fro / Par	Pro	2.89	8.18	<.001	.33	1.94
	Par / Fro	Pro	2.89	6.75	.000	.21	1.45
	Fro / Fro	Pro	2.89	7.43	<.001	.03	1.69

	Par	Mat * Pro	2.89	-2.45	.119	.21	-0.53
	Fro	Mat * Pro	2.89	-1.21	.673	.05	-0.26
Pro * Reg * Hem	Par / L	Pro	2.94	9.12	<.001	.41	2.11
	Par / R	Pro	2.94	8.72	<.001	.25	2.04
	Fro / L	Pro	2.94	8.06	<.001	.14	1.87
	Fro / R	Pro	2.94	9.76	<.001	.21	2.11
	Enc / Par	Hem	2.94	-2.41	.148	.88	-0.53
	Rtv / Par	Hem	2.94	0.59	.989	.68	0.13
	Enc / Fro	Hem	2.94	-0.91	.927	.88	-0.21
	Rtv / Fro	Hem	2.94	0.01	.999	.87	0.00
	Par	Pro * Hem	2.94	-2.03	.294	.74	-0.45
	Fro	Pro * Hem	2.94	-0.85	.944	.87	-0.19
Mat * Pro * Reg * Hem	Enc / L / Par	Mat	3.44	-3.28	.069	.33	-0.72
	Enc / R / Par	Mat	3.44	-3.73	.027	.44	-0.80
	Enc / L / Fro	Mat	3.44	-1.75	.795	.44	-0.37
	Enc / R / Fro	Mat	3.44	-1.63	.859	.08	-0.35
	Rtv / L / Par	Mat	3.44	-1.17	.986	.22	-0.25
	Rtv / R / Par	Mat	3.44	-1.14	.988	-.11	-0.24
	Rtv / L / Fro	Mat	3.44	-0.38	.999	.14	-0.09
	Rtv / R / Fro	Mat	3.44	-0.63	.999	.20	-0.14
	Ver / L / Par	Pro	3.44	6.66	<.001	.40	1.45
	Non / L / Par	Pro	3.44	7.26	<.001	.27	1.69
	Ver / L / Fro	Pro	3.44	5.51	.001	.13	1.22
	Non / L / Fro	Pro	3.44	7.78	<.001	.04	1.84
	Ver / R / Par	Pro	3.44	5.75	.001	.18	1.24
	Non / R / Par	Pro	3.44	8.30	<.001	.30	1.94
	Ver / R / Fro	Pro	3.44	7.47	<.001	.28	1.59
	Non / R / Fro	Pro	3.44	6.77	<.001	.03	1.50
	Ver / Enc / Par	Hem	3.44	-1.36	.954	.82	-0.30
	Non / Enc / Par	Hem	3.44	-2.79	.190	.92	-0.60
	Ver / Enc / Fro	Hem	3.44	-0.40	.999	.77	-0.09
	Non / Enc / Fro	Hem	3.44	-1.01	.996	.90	-0.22
	Ver / Rtv / Par	Hem	3.44	0.74	.999	.76	0.16
	Non / Rtv / Par	Hem	3.44	0.18	.999	.76	0.04
	Ver / Rtv / Fro	Hem	3.44	0.45	.999	.91	0.10
	Non / Rtv / Fro	Hem	3.44	-0.40	.999	.87	-0.12
	Enc / Par	Mat * Hem	3.44	0.91	.998	.87	0.19
	Rtv / Par	Mat * Hem	3.44	0.26	.999	.78	0.06
	Enc / Fro	Mat * Hem	3.44	0.56	.999	.87	0.14
	Rtv / Fro	Mat * Hem	3.44	0.74	.999	.90	0.17
	Par / L	Pro * Hem	3.44	-2.30	.435	.16	-0.50
	Par / R	Pro * Hem	3.44	-1.27	.973	.33	-0.27
	Fro / L	Pro * Hem	3.44	-2.38	.385	.31	-0.51
	Fro / R	Pro * Hem	3.44	-1.03	.996	.03	-0.22

Mat = Material (Verbal - Nonverbal); Repetition (Old - New); Reg = Region (Parietal - Frontal); Hem = Hemisphere (Left - Right); Ver = Verbal; Non = Nonverbal; Par = Parietal; Fro = Frontal; L = Left; R = Right.

Supplementary Table 5a.

Descriptive and test statistics for mean theta power change (500 to 1500 ms)

Mat	Pro	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Enc	Par	L	4.70	-1.79	11.19

			R	0.67	-7.56	8.89
		Fro	L	3.78	-2.81	10.36
			R	3.24	-4.10	10.59
	Rtv	Par	L	-15.42	-22.29	-8.54
			R	-16.48	-23.81	-9.14
		Fro	L	-13.68	-20.43	-6.94
			R	-11.97	-17.59	-6.35
Non	Enc	Par	L	1.30	-4.19	6.80
			R	0.92	-7.21	9.05
		Fro	L	2.18	-6.35	10.71
			R	2.59	-5.56	10.74
	Rtv	Par	L	-25.17	-31.72	-18.63
			R	-27.04	-33.88	-20.20
		Fro	L	-21.80	-28.37	-15.24
			R	-17.90	-23.94	-11.86

5b.

ANOVA Factor	$F(1,21)$	p	η_p^2
Mat	4.36	.049	.17
Pro	35.51	<.001	.63
Reg	16.31	.001	.44
Hem	0.13	.721	.01
Mat * Pro	2.39	.137	.10
Mat * Reg	3.08	.094	.13
Mat * Hem	3.67	.069	.15
Pro * Hem	1.96	.176	.09
Reg * Hem	4.05	.057	.16
Pro * Reg	4.25	.052	.17
Mat * Pro * Hem	2.68	.117	.11
Mat * Reg * Hem	0.01	.939	.00
Mat * Pro * Reg	1.62	.218	.07
Pro * Reg * Hem	0.68	.420	.03
Mat * Pro * Reg * Hem	2.15	.157	.09

5c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mat * Pro	Enc	Mat	2.76	0.36	.980	.37	0.08
	Rtv	Mat	2.76	3.05	.029	.57	0.65
	Ver	Pro	2.76	3.97	.004	.04	0.85
	Non	Pro	2.76	6.06	<.001	.21	1.30
		Mat * Pro	2.76	-1.54	.409	.02	-0.33
Mat * Reg	Par	Mat	2.47	2.29	.073	.47	0.49
	Fro	Mat	2.47	1.77	.191	.55	0.38
		Mat * Reg	2.47	1.76	.196	.92	0.39
Mat * Hem	L	Mat	2.75	2.50	.081	.51	0.54
	R	Mat	2.75	1.67	.353	.52	0.36
	Ver	Hem	2.75	1.15	.653	.94	0.27
	Non	Hem	2.75	-0.82	.834	.97	-0.18
		Mat * Hem	2.75	1.92	.236	.95	0.43
Pro * Hem	L	Pro	2.68	6.28	<.001	.13	1.34
	R	Pro	2.68	5.47	<.001	.19	1.17
	Enc	Hem	2.68	0.94	.762	.93	0.22
	Rtv	Hem	2.68	-1.51	.411	.99	-0.32
		Pro * Hem	2.68	1.40	.478	.94	0.30

Reg * Hem	Par	Hem	2.46	1.74	.197	.90	0.41
	Fro	Hem	2.46	-1.40	.336	.90	-0.30
		Reg * Hem	2.46	2.01	.122	-.22	0.43
Pro * Reg	Par	Pro	2.49	6.44	<.001	.18	1.37
	Fro	Pro	2.49	5.16	<.001	.12	1.10
		Pro * Reg	2.49	2.06	.115	.88	0.44
Mat * Pro * Hem	Enc / L	Mat	3.15	0.70	.993	.35	0.15
	Enc / R	Mat	3.15	0.05	.999	.40	0.01
	Rtv / L	Mat	3.15	3.08	.058	.56	0.66
	Rtv / R	Mat	3.15	2.94	.076	.57	0.63
	Ver / L	Pro	3.15	4.26	.004	-.03	0.91
	Ver / R	Pro	3.15	3.60	.018	.11	0.77
	Non / L	Pro	3.15	6.35	<.001	.21	1.36
	Non / R	Pro	3.15	5.60	<.001	.20	1.21
	Ver / Enc	Hem	3.15	1.74	.585	.94	0.42
	Ver / Rec	Hem	3.15	-0.49	.999	.98	-0.11
	Non / Enc	Hem	3.15	-0.01	.999	.94	0.00
	Non / Rec	Hem	3.15	-1.86	.505	.98	-0.40
	Enc	Mat * Hem	3.15	2.30	.264	.97	0.56
	Rtv	Mat * Hem	3.15	0.82	.985	.96	0.18
	Ver	Pro * Hem	3.15	2.15	.336	.96	0.46
	Non	Pro * Hem	3.15	0.65	.996	.94	0.14
Mat * Reg * Hem	Par / L	Mat	2.97	2.69	.091	.45	0.57
	Par / R	Mat	2.97	1.81	.451	.49	0.39
	Fro / L	Mat	2.97	2.03	.328	.54	0.45
	Fro / R	Mat	2.97	1.41	.703	.56	0.30
	Ver / Par	Hem	2.97	1.86	.420	.86	0.41
	Non / Par	Hem	2.97	0.99	.919	.93	0.26
	Ver / Fro	Hem	2.97	-0.48	.998	.86	-0.11
	Non / Fro	Hem	2.97	-2.12	.281	.93	-0.46
	Par	Mat * Hem	2.97	1.04	.900	.88	0.23
	Fro	Mat * Hem	2.97	1.46	.670	.90	0.31
Mat * Pro * Reg	Enc / Par	Mat	2.96	0.41	.993	.34	0.09
	Rtv / Par	Mat	2.96	3.35	.022	.56	0.72
	Enc / Fro	Mat	2.96	0.28	.999	.40	0.06
	Rtv / Fro	Mat	2.96	2.59	.100	.57	0.55
	Par / Par	Pro	2.96	4.03	.005	.06	0.86
	Fro / Par	Pro	2.96	7.15	<.001	.28	1.52
	Par / Fro	Pro	2.96	3.78	.009	.01	0.81
	Fro / Fro	Pro	2.96	4.76	.001	.11	1.03
	Par	Mat * Pro	2.96	-1.87	.317	.11	-0.40
	Fro	Mat * Pro	2.96	-1.18	.710	-.09	-0.25
Pro * Reg * Hem	Par / L	Pro	2.99	6.88	<.001	.15	1.48
	Par / R	Pro	2.99	5.63	<.001	.19	1.20
	Fro / L	Pro	2.99	5.17	.001	.07	1.10
	Fro / R	Pro	2.99	4.94	.001	.19	1.06
	Enc / Par	Hem	2.99	1.36	.688	.88	0.35
	Rtv / Par	Hem	2.99	1.10	.839	.90	0.24
	Enc / Fro	Hem	2.99	0.05	.999	.90	0.01
	Rtv / Fro	Hem	2.99	-2.52	.124	.92	-0.57
	Par	Pro * Hem	2.99	0.36	.999	.85	0.08
	Fro	Pro * Hem	2.99	1.87	.375	.92	0.41

Mat * Pro * Reg * Hem	Enc / L / Par	Mat	3.44	1.00	.994	.32	0.22
	Enc / R / Par	Mat	3.44	-0.06	.999	.36	-0.01
	Enc / L / Fro	Mat	3.44	0.39	.999	.37	0.08
	Enc / R / Fro	Mat	3.44	0.16	.999	.43	0.03
	Rtv / L / Par	Mat	3.44	3.15	.091	.54	0.67
	Rtv / R / Par	Mat	3.44	3.40	.055	.59	0.73
	Rtv / L / Fro	Mat	3.44	2.77	.198	.58	0.59
	Rtv / R / Fro	Mat	3.44	2.27	.441	.57	0.48
	Ver / L / Par	Pro	3.44	4.66	.004	.10	0.99
	Non / L / Par	Pro	3.44	7.23	<.001	.21	1.55
	Ver / L / Fro	Pro	3.44	3.61	.035	-.14	0.77
	Non / L / Fro	Pro	3.44	4.98	.001	.14	1.07
	Ver / R / Par	Pro	3.44	3.31	.068	.05	0.71
	Non / R / Par	Pro	3.44	6.52	<.001	.30	1.40
	Ver / R / Fro	Pro	3.44	3.79	.024	.19	0.82
	Non / R / Fro	Pro	3.44	4.37	.006	.08	0.94
	Ver / Enc / Par	Hem	3.44	1.95	.643	.86	0.45
	Non / Enc / Par	Hem	3.44	0.21	.999	.92	0.06
	Ver / Enc / Fro	Hem	3.44	0.31	.999	.87	0.07
	Non / Enc / Fro	Hem	3.44	-0.27	.999	.93	-0.06
	Ver / Rtv / Par	Hem	3.44	0.72	.999	.91	0.16
	Non / Rtv / Par	Hem	3.44	1.25	.967	.89	0.27
	Ver / Rtv / Fro	Hem	3.44	-1.19	.978	.90	-0.27
	Non / Rtv / Fro	Hem	3.44	-3.69	.030	.94	-0.81
	Enc / Par	Mat * Hem	3.44	1.75	.778	.89	0.43
	Rtv / Par	Mat * Hem	3.44	0.53	.999	.90	0.11
	Enc / Fro	Mat * Hem	3.44	-0.62	.999	.91	-0.13
	Rtv / Fro	Mat * Hem	3.44	1.84	.717	.91	0.41
	Par / L	Pro * Hem	3.44	-1.49	.903	.44	-0.32
	Par / R	Pro * Hem	3.44	-1.21	.973	.38	-0.26
	Fro / L	Pro * Hem	3.44	-2.11	.542	.43	-0.46
	Fro / R	Pro * Hem	3.44	-1.08	.990	.38	-0.23

Mat = Material (Verbal - Nonverbal); Repetition (Old - New); Reg = Region (Parietal - Frontal); Hem = Hemi sphere (Left - Right); Ver = Verbal; Non = Nonverbal; Par = Parietal; Fro = Frontal; L = Left; R = Right.

Supplementary Table 6a.

Descriptive and test statistics for mean theta power change - Repetition effect (0 to 500 ms)

Mat	Rep	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Old	Par	L	1.16	-5.41	7.72
			R	-2.68	-11.05	5.69
		Fro	L	-9.49	-16.33	-2.65
			R	-7.97	-16.76	0.83
	New	Par	L	-1.12	-10.18	7.94
			R	-2.66	-12.03	6.72
		Fro	L	-7.99	-15.86	-0.13
			R	-9.78	-17.75	-1.81
Non	Old	Par	L	5.37	-2.79	13.52
			R	4.87	-3.29	13.03
		Fro	L	-7.82	-13.28	-2.36
			R	-7.59	-14.51	-0.67

	New	Par	L	6.15	-1.08	13.38
			R	5.01	-3.57	13.58
		Fro	L	-6.06	-10.55	-1.57
			R	-4.89	-12.25	2.47

6b.

ANOVA Factor	$F(1,21)$	p	η_p^2
Mat	1.16	.294	.05
Rep	0.03	.858	.00
Reg	38.51	<.001	.65
Hem	0.39	.541	.02
Mat * Rep	0.20	.660	.01
Mat * Reg	6.07	.023	.22
Mat * Hem	0.62	.438	.03
Rep * Hem	0.02	.884	.00
Reg * Hem	0.69	.416	.03
Rep * Reg	1.36	.256	.06
Mat * Rep * Hem	0.10	.758	.01
Mat * Reg * Hem	0.09	.770	.00
Mat * Rep * Reg	0.08	.782	.00
Rep * Reg * Hem	1.31	.265	.06
Mat * Rep * Reg * Hem	2.01	.171	.09

6c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mat * Rep	Old	Mat	2.78	-0.72	.879	-.10	-0.15
	New	Mat	2.78	-1.19	.621	.12	-0.26
	Ver	Rep	2.78	0.22	.996	.67	0.05
	Non	Rep	2.78	-0.46	.967	.53	-0.10
		Mat * Rep	2.78	0.45	.969	.55	0.10
Mat * Reg	Par	Mat	2.46	-1.42	.314	.01	-0.30
	Fro	Mat	2.46	-0.60	.789	.20	-0.13
		Mat * Reg	2.46	-2.46	.050	.94	-0.63
Mat * Hem	L	Mat	2.70	-1.03	.700	.13	-0.22
	R	Mat	2.70	-1.09	.665	.03	-0.23
	Ver	Hem	2.70	1.02	.705	.93	0.23
	Non	Hem	2.70	0.04	.999	.88	0.01
		Mat * Hem	2.70	0.79	.834	.95	0.21
Rep * Hem	L	Rep	2.75	-0.24	.994	.68	-0.05
	R	Rep	2.75	-0.12	.999	.66	-0.03
	Old	Hem	2.75	0.49	.958	.86	0.11
	New	Hem	2.75	0.61	.930	.87	0.13
		Rep * Hem	2.75	-0.15	.999	.84	-0.03
Reg * Hem	Par	Hem	2.46	0.89	.676	.71	0.19
	Fro	Hem	2.46	-0.20	.981	.86	-0.05
		Reg * Hem	2.46	0.83	.710	-.04	0.18
Rep * Reg	Par	Rep	2.50	0.16	.983	.68	0.03
	Fro	Rep	2.50	-0.54	.852	.69	-0.11
		Rep * Reg	2.50	1.17	.492	.84	0.25
Mat * Rep * Hem	Old / L	Mat	3.24	-0.66	.997	-.10	-0.14
	Old / R	Mat	3.24	-0.75	.993	-.05	-0.16
	New / L	Mat	3.24	-1.13	.936	.22	-0.25
	New / R	Mat	3.24	-1.20	.913	.06	-0.26
	Ver / L	Rep	3.24	0.13	.999	.64	0.03

	Ver / R	Rep	3.24	0.29	.999	.69	0.06
	Non / L	Rep	3.24	-0.45	.999	.49	-0.10
	Non / R	Rep	3.24	-0.42	.999	.55	-0.09
	Ver / Old	Hem	3.24	0.75	.993	.93	0.19
	Ver / Rec	Hem	3.24	1.15	.929	.93	0.25
	Non / Old	Hem	3.24	0.08	.999	.88	0.02
	Non / Rec	Hem	3.24	-0.01	.999	.86	0.00
	Old	Mat * Hem	3.24	0.58	.999	.95	0.14
	New	Mat * Hem	3.24	0.75	.992	.92	0.19
	Ver	Rep * Hem	3.24	-0.45	.999	.93	-0.10
	Non	Rep * Hem	3.24	0.07	.999	.81	0.02
Mat * Reg * Hem	Par / L	Mat	3.03	-1.33	.746	.19	-0.28
	Par / R	Mat	3.03	-1.39	.715	-.06	-0.30
	Fro / L	Mat	3.03	-0.54	.995	.19	-0.12
	Fro / R	Mat	3.03	-0.62	.989	.22	-0.13
	Ver / Par	Hem	3.03	1.04	.892	.77	0.23
	Non / Par	Hem	3.03	0.36	.999	.78	0.08
	Ver / Fro	Hem	3.03	0.08	.999	.88	0.02
	Non / Fro	Hem	3.03	-0.43	.999	.88	-0.13
	Par	Mat * Hem	3.03	0.66	.987	.86	0.15
	Fro	Mat * Hem	3.03	0.43	.999	.89	0.10
Mat * Rep * Reg	Old / Par	Mat	2.96	-1.12	.787	-.11	-0.24
	New / Par	Mat	2.96	-1.40	.622	.07	-0.30
	Old / Fro	Mat	2.96	-0.22	.999	-.02	-0.05
	New / Fro	Mat	2.96	-0.86	.912	.26	-0.19
	Par / Par	Rep	2.96	0.37	.998	.69	0.08
	Fro / Par	Rep	2.96	-0.14	.999	.59	-0.03
	Par / Fro	Rep	2.96	0.05	.999	.64	0.01
	Fro / Fro	Rep	2.96	-0.77	.943	.46	-0.16
	Par	Mat * Rep	2.96	0.33	.999	.59	0.07
	Fro	Mat * Rep	2.96	0.52	.990	.45	0.11
Rep * Reg * Hem	Par / L	Rep	3.05	0.35	.999	.74	0.08
	Par / R	Rep	3.05	-0.03	.999	.65	-0.01
	Fro / L	Rep	3.05	-0.87	.962	.64	-0.19
	Fro / R	Rep	3.05	-0.20	.999	.69	-0.04
	Old / Par	Hem	3.05	0.92	.947	.60	0.20
	New / Par	Hem	3.05	0.74	.982	.82	0.16
	Old / Fro	Hem	3.05	-0.62	.994	.86	-0.15
	New / Fro	Hem	3.05	0.18	.999	.81	0.04
	Par	Rep * Hem	3.05	0.57	.996	.80	0.12
	Fro	Rep * Hem	3.05	-0.77	.978	.74	-0.17
Mat * Rep * Reg * Hem	Old / L / Par	Mat	3.49	-0.82	.999	-.05	-0.17
	Old / R / Par	Mat	3.49	-1.33	.961	-.02	-0.28
	Old / L / Fro	Mat	3.49	-0.38	.999	-.06	-0.08
	Old / R / Fro	Mat	3.49	-0.07	.999	.03	-0.02
	New / L / Par	Mat	3.49	-1.51	.912	.26	-0.33
	New / R / Par	Mat	3.49	-1.19	.984	-.11	-0.25
	New / L / Fro	Mat	3.49	-0.49	.999	.20	-0.11
	New / R / Fro	Mat	3.49	-1.15	.988	.33	-0.24
	Ver / L / Par	Rep	3.49	0.70	.999	.66	0.16
	Non / L / Par	Rep	3.49	-0.24	.999	.60	-0.05
	Ver / L / Fro	Rep	3.49	-0.47	.999	.61	-0.10

	Non / L / Fro	Rep	3.49	-0.59	.999	.23	-0.13
	Ver / R / Par	Rep	3.49	-0.01	.999	.73	0.00
	Non / R / Par	Rep	3.49	-0.04	.999	.54	-0.01
	Ver / R / Fro	Rep	3.49	0.55	.999	.67	0.12
	Non / R / Fro	Rep	3.49	-0.85	.999	.57	-0.18
	Ver / Old / Par	Hem	3.49	1.32	.964	.70	0.29
	Non / Old / Par	Hem	3.49	0.19	.999	.78	0.04
	Ver / Old / Fro	Hem	3.49	-0.75	.999	.88	-0.18
	Non / Old / Fro	Hem	3.49	-0.14	.999	.86	-0.03
	Ver / New / Par	Hem	3.49	0.60	.999	.83	0.13
	Non / New / Par	Hem	3.49	0.42	.999	.75	0.09
	Ver / New / Fro	Hem	3.49	0.95	.998	.88	0.20
	Non / New / Fro	Hem	3.49	-0.53	.999	.81	-0.14
	Old / Par	Mat * Hem	3.49	1.14	.989	.86	0.25
	New / Par	Mat * Hem	3.49	-0.53	.999	.89	-0.12
	Old / Fro	Mat * Hem	3.49	0.10	.999	.80	0.02
	New / Fro	Mat * Hem	3.49	1.38	.952	.87	0.30
	Par / L	Rep * Hem	3.49	0.61	.999	-.18	0.13
	Par / R	Rep * Hem	3.49	0.05	.999	-.25	0.01
	Fro / L	Rep * Hem	3.49	0.02	.999	-.11	0.00
	Fro / R	Rep * Hem	3.49	0.98	.997	-.02	0.21

Supplementary Table 7a.

Descriptive and test statistics for mean theta power change - Repetition effect (500 to 1500 ms)

Mat	Rep	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Old	Par	L	-16.42	-21.76	-11.07
			R	-18.18	-23.84	-12.52
		Fro	L	-15.54	-21.12	-9.96
			R	-13.35	-17.87	-8.83
	New	Par	L	-13.38	-23.21	-3.54
			R	-14.51	-24.14	-4.88
		Fro	L	-11.48	-20.07	-2.88
			R	-10.39	-17.78	-3.01
Non	Old	Par	L	-23.35	-31.27	-15.43
			R	-25.99	-33.67	-18.30
		Fro	L	-22.51	-29.21	-15.82
			R	-17.56	-24.62	-10.49
	New	Par	L	-27.28	-33.15	-21.40
			R	-14.33	-17.91	-10.75
		Fro	L	-21.26	-27.60	-14.91
			R	-18.45	-23.73	-13.18

7b.

ANOVA Factor	$F(1,21)$	p	η_p^2
Mat	7.15	.014	.25
Rep	2.16	.156	.09
Reg	12.83	.002	.38
Hem	22.70	<.001	.52
Mat * Rep	0.16	.691	.01
Mat * Reg	0.02	.883	.00
Mat * Hem	25.29	<.001	.55

Rep * Hem	22.84	<.001	.52
Reg * Hem	0.18	.673	.01
Rep * Reg	2.77	.111	.12
Mat * Rep * Hem	22.74	<.001	.52
Mat * Reg * Hem	5.32	.031	.20
Mat * Rep * Reg	3.13	.091	.13
Rep * Reg * Hem	34.07	<.001	.62
Mat * Rep * Reg * Hem	20.72	<.001	.50

7c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mat * Rep	Old	Mat	2.74	2.00	.202	.42	0.44
	New	Mat	2.74	2.50	.084	.65	0.62
	Ver	Rep	2.74	-1.21	.602	.75	-0.32
	Non	Rep	2.74	-0.92	.775	.77	-0.22
		Mat * Rep	2.74	-0.40	.974	.41	-0.09
Mat * Reg	Par	Mat	2.49	2.51	.048	.58	0.55
	Fro	Mat	2.49	2.77	.027	.58	0.59
		Mat * Reg	2.49	-0.15	.987	.94	-0.03
Mat * Hem	L	Mat	2.69	3.34	.012	.57	0.71
	R	Mat	2.69	1.90	.229	.57	0.41
	Ver	Hem	2.69	-0.14	.999	.98	-0.03
	Non	Hem	2.69	-7.02	<.001	.98	-1.63
		Mat * Hem	2.69	5.03	<.001	.95	1.10
Rep * Hem	L	Rep	2.74	-0.55	.944	.78	-0.13
	R	Rep	2.74	-2.51	.082	.79	-0.54
	Old	Hem	2.74	-1.27	.572	.98	-0.27
	New	Hem	2.74	-6.17	<.001	.99	-1.82
		Rep * Hem	2.74	4.78	.001	.95	1.13
Reg * Hem	Par	Hem	2.43	-1.48	.286	.90	-0.32
	Fro	Hem	2.43	-2.59	.036	.92	-0.57
		Reg * Hem	2.43	0.43	.889	-.66	0.09
Rep * Reg	Par	Rep	2.48	-1.71	.213	.74	-0.37
	Fro	Rep	2.48	-1.07	.527	.81	-0.24
		Rep * Reg	2.48	-1.66	.227	.87	-0.38
Mat * Rep * Hem	Old / L	Mat	3.22	2.08	.401	.38	0.46
	Old / R	Mat	3.22	1.85	.540	.44	0.41
	New / L	Mat	3.22	3.59	.024	.64	0.84
	New / R	Mat	3.22	1.26	.885	.65	0.33
	Ver / L	Rep	3.22	-1.18	.917	.74	-0.31
	Ver / R	Rep	3.22	-1.21	.905	.75	-0.31
	Non / L	Rep	3.22	0.57	.999	.74	0.13
	Non / R	Rep	3.22	-2.40	.241	.80	-0.65
	Ver / Old	Hem	3.22	-0.28	.999	.95	-0.06
	Ver / Rec	Hem	3.22	0.03	.999	.99	0.01
	Non / Old	Hem	3.22	-1.45	.788	.97	-0.31
	Non / Rec	Hem	3.22	-8.52	<.001	.97	-2.95
	Old	Mat * Hem	3.22	0.82	.989	.94	0.18
	New	Mat * Hem	3.22	6.97	<.001	.94	1.51
	Ver	Rep * Hem	3.22	-0.30	.999	.96	-0.07
	Non	Rep * Hem	3.22	5.83	<.001	.87	1.25
Mat * Reg * Hem	Par / L	Mat	2.97	3.58	.015	.59	0.77
	Par / R	Mat	2.97	1.30	.726	.56	0.29

	Fro / L	Mat	2.97	2.88	.061	.55	0.62
	Fro / R	Mat	2.97	2.52	.129	.61	0.54
	Ver / Par	Hem	2.97	0.97	.892	.91	0.21
	Non / Par	Hem	2.97	-3.67	.011	.89	-0.83
	Ver / Fro	Hem	2.97	-1.20	.786	.90	-0.27
	Non / Fro	Hem	2.97	-3.86	.006	.94	-0.83
	Par	Mat * Hem	2.97	4.55	.001	.88	0.97
	Fro	Mat * Hem	2.97	2.02	.303	.93	0.48
Mat * Rep * Reg	Old / Par	Mat	2.93	2.16	.206	.44	0.48
	New / Par	Mat	2.93	1.88	.327	.63	0.50
	Old / Fro	Mat	2.93	1.78	.380	.40	0.39
	New / Fro	Mat	2.93	3.11	.035	.65	0.70
	Par / Par	Rep	2.93	-1.03	.810	.73	-0.27
	Fro / Par	Rep	2.93	-1.43	.581	.68	-0.35
	Par / Fro	Rep	2.93	-1.34	.632	.73	-0.34
	Fro / Fro	Rep	2.93	-0.10	.999	.82	-0.02
	Par	Mat * Rep	2.93	0.12	.999	.28	0.03
	Fro	Mat * Rep	2.93	-1.12	.759	.52	-0.24
Rep * Reg * Hem	Par / L	Rep	3.07	0.18	.999	.71	0.04
	Par / R	Rep	3.07	-3.97	.006	.77	-0.85
	Fro / L	Rep	3.07	-1.37	.708	.81	-0.32
	Fro / R	Rep	3.07	-0.62	.987	.81	-0.14
	Old / Par	Hem	3.07	1.65	.535	.88	0.35
	New / Par	Hem	3.07	-4.19	.004	.91	-0.95
	Old / Fro	Hem	3.07	-3.37	.027	.90	-0.72
	New / Fro	Hem	3.07	-1.50	.632	.92	-0.34
	Par	Rep * Hem	3.07	7.30	<.001	.89	1.72
	Fro	Rep * Hem	3.07	-1.57	.586	.84	-0.35
Mat * Rep * Reg * Hem	Old / L / Par	Mat	3.45	1.91	.672	.41	0.43
	Old / R / Par	Mat	3.45	2.25	.454	.45	0.49
	Old / L / Fro	Mat	3.45	2.04	.590	.34	0.44
	Old / R / Fro	Mat	3.45	1.34	.948	.44	0.30
	New / L / Par	Mat	3.45	3.74	.026	.62	0.90
	New / R / Par	Mat	3.45	-0.05	.999	.62	-0.01
	New / L / Fro	Mat	3.45	3.06	.117	.64	0.69
	New / R / Fro	Mat	3.45	3.02	.126	.66	0.69
	Ver / L / Par	Rep	3.45	-0.85	.999	.66	-0.22
	Non / L / Par	Rep	3.45	1.33	.951	.64	0.30
	Ver / L / Fro	Rep	3.45	-1.39	.934	.71	-0.33
	Non / L / Fro	Rep	3.45	-0.63	.999	.80	-0.14
	Ver / R / Par	Rep	3.45	-1.20	.977	.77	-0.32
	Non / R / Par	Rep	3.45	-4.30	.008	.73	-1.25
	Ver / R / Fro	Rep	3.45	-1.15	.982	.70	-0.28
	Non / R / Fro	Rep	3.45	0.45	.999	.81	0.10
	Ver / Old / Par	Hem	3.45	1.06	.991	.80	0.23
	Non / Old / Par	Hem	3.45	1.64	.838	.91	0.35
	Ver / Old / Fro	Hem	3.45	-1.34	.950	.79	-0.30
	Non / Old / Fro	Hem	3.45	-4.48	.005	.95	-0.97
	Ver / New / Par	Hem	3.45	0.67	.999	.93	0.14
	Non / New / Par	Hem	3.45	-7.89	<.001	.85	-2.20
	Ver / New / Fro	Hem	3.45	-0.70	.999	.93	-0.16
	Non / New / Fro	Hem	3.45	-2.09	.561	.90	-0.48

Old / Par	Mat * Hem	3.45	-0.46	.999	.86	-0.10
New / Par	Mat * Hem	3.45	1.51	.893	.85	0.33
Old / Fro	Mat * Hem	3.45	7.88	<.001	.89	1.68
New / Fro	Mat * Hem	3.45	1.32	.954	.92	0.31
Par / L	Rep * Hem	3.45	-1.56	.874	.08	-0.33
Par / R	Rep * Hem	3.45	-0.89	.998	.21	-0.19
Fro / L	Rep * Hem	3.45	1.86	.708	-.11	0.40
Fro / R	Rep * Hem	3.45	-1.21	.975	.04	-0.26

Mat = Material (Verbal - Nonverbal); Repetition (Old - New); Reg = Region (Parietal - Frontal); Hem = Hemisphere (Left - Right); Ver = Verbal; Non = Nonverbal; Par = Parietal; Fro = Frontal; L = Left; R = Right.

Supplementary Table 8a.
Descriptive and test statistics for mean alpha power change (0 to 500 ms)

Mat	Pro	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Enc	Par	L	-1.71	-11.70	8.29
			R	-7.66	-18.23	2.92
		Fro	L	-6.76	-16.34	2.82
			R	-4.33	-12.93	4.26
	Rtv	Par	L	8.83	0.99	16.67
			R	6.25	0.25	12.25
		Fro	L	4.08	-0.91	9.08
			R	4.11	-2.13	10.36
Non	Enc	Par	L	4.38	-11.16	19.92
			R	1.05	-16.11	18.20
		Fro	L	-2.15	-15.16	10.85
			R	-0.29	-13.87	13.29
	Rtv	Par	L	3.98	-2.79	10.76
			R	2.11	-2.78	7.01
		Fro	L	1.94	-4.20	8.07
			R	2.67	-3.28	8.61

8b.

ANOVA Factor	$F(1,21)$	*p*	η_p^2
Mat	0.19	.668	.01
Pro	1.40	.251	.06
Reg	3.33	.082	.14
Hem	2.33	.142	.10
Mat * Pro	2.69	.116	.11
Mat * Reg	0.02	.900	.00
Mat * Hem	0.92	.348	.04
Pro * Hem	0.19	.668	.01
Reg * Hem	7.28	.013	.26
Pro * Reg	0.04	.838	.00
Mat * Pro * Hem	0.04	.853	.00
Mat * Reg * Hem	0.24	.629	.01
Mat * Pro * Reg	6.13	.022	.23
Pro * Reg * Hem	1.46	.241	.07

Mat * Pro * Reg * Hem		0.49	.491	.02			

8c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mat * Pro	Enc	Mat	2.72	-1.12	.661	.67	-0.27
	Rtv	Mat	2.72	1.17	.633	.52	0.25
	Ver	Pro	2.72	-2.27	.131	.18	-0.50
	Non	Pro	2.72	-0.27	.993	.14	-0.06
		Mat * Pro	2.72	-1.64	.365	.16	-0.37
Mat * Reg	Par	Mat	2.52	-0.43	.903	.62	-0.10
	Fro	Mat	2.52	-0.42	.906	.60	-0.09
		Mat * Reg	2.52	-0.13	.991	.90	-0.03
Mat * Hem	L	Mat	2.75	-0.29	.990	.60	-0.07
	R	Mat	2.75	-0.57	.939	.63	-0.13
	Ver	Hem	2.75	1.79	.297	.96	0.38
	Non	Hem	2.75	0.78	.858	.98	0.17
		Mat * Hem	2.75	0.96	.765	.96	0.20
Pro * Hem	L	Pro	2.68	-1.16	.633	.14	-0.27
	R	Pro	2.68	-1.20	.611	.18	-0.28
	Enc	Hem	2.68	1.33	.526	.99	0.30
	Rtv	Hem	2.68	1.43	.466	.97	0.31
		Pro * Hem	2.68	0.44	.969	.99	0.09
Reg * Hem	Par	Hem	2.45	2.37	.057	.91	0.51
	Fro	Hem	2.45	-1.91	.143	.98	-0.42
		Reg * Hem	2.45	2.70	.029	-.26	0.60
Pro * Reg	Par	Pro	2.46	-1.06	.496	.17	-0.25
	Fro	Pro	2.46	-1.31	.355	.16	-0.30
		Pro * Reg	2.46	0.21	.973	.98	0.05
Mat * Pro * Hem	Enc / L	Mat	3.18	-1.07	.948	.67	-0.25
	Enc / R	Mat	3.18	-1.16	.925	.66	-0.28
	Rtv / L	Mat	3.18	1.23	.901	.51	0.26
	Rtv / R	Mat	3.18	1.06	.950	.52	0.23
	Ver / L	Pro	3.18	-2.15	.361	.14	-0.47
	Ver / R	Pro	3.18	-2.35	.264	.23	-0.52
	Non / L	Pro	3.18	-0.27	.999	.17	-0.06
	Non / R	Pro	3.18	-0.27	.999	.12	-0.07
	Ver / Enc	Hem	3.18	1.53	.757	.97	0.33
	Ver / Rec	Hem	3.18	1.40	.824	.95	0.30
	Non / Enc	Hem	3.18	0.64	.998	.99	0.15
	Non / Rec	Hem	3.18	0.72	.996	.96	0.17
	Enc	Mat * Hem	3.18	0.76	.994	.97	0.17
	Rtv	Mat * Hem	3.18	0.64	.998	.92	0.14
	Ver	Pro * Hem	3.18	0.40	.999	.97	0.09
	Non	Pro * Hem	3.18	0.16	.999	.99	0.04
Mat * Reg * Hem	Par / L	Mat	3.03	-0.17	.999	.53	-0.04
	Par / R	Mat	3.03	-0.67	.981	.66	-0.15
	Fro / L	Mat	3.03	-0.40	.999	.61	-0.09
	Fro / R	Mat	3.03	-0.41	.999	.55	-0.09
	Ver / Par	Hem	3.03	2.29	.209	.84	0.49
	Non / Par	Hem	3.03	1.48	.645	.92	0.32
	Ver / Fro	Hem	3.03	-1.23	.796	.93	-0.26
	Non / Fro	Hem	3.03	-1.32	.745	.97	-0.29
	Par	Mat * Hem	3.03	0.76	.965	.82	0.16

	Fro	Mat * Hem	3.03	0.05	.999	.89	0.01
Mat * Pro * Reg	Enc / Par	Mat	2.94	-1.31	.651	.69	-0.32
	Rtv / Par	Mat	2.94	1.47	.549	.46	0.32
	Enc / Fro	Mat	2.94	-0.86	.888	.62	-0.20
	Rtv / Fro	Mat	2.94	0.71	.942	.57	0.15
	Par / Par	Pro	2.94	-2.42	.130	.24	-0.53
	Fro / Par	Pro	2.94	-0.04	.999	.13	-0.01
	Par / Fro	Pro	2.94	-2.04	.245	.15	-0.45
	Fro / Fro	Pro	2.94	-0.54	.979	.18	-0.13
	Par	Mat * Pro	2.94	-1.97	.274	.14	-0.44
	Fro	Mat * Pro	2.94	-1.18	.730	.19	-0.27
Pro * Reg * Hem	Par / L	Pro	2.96	-0.82	.932	.08	-0.19
	Par / R	Pro	2.96	-1.27	.714	.29	-0.32
	Fro / L	Pro	2.96	-1.53	.556	.24	-0.36
	Fro / R	Pro	2.96	-1.08	.824	.07	-0.24
	Enc / Par	Hem	2.96	2.49	.134	.95	0.55
	Rtv / Par	Hem	2.96	1.25	.731	.80	0.29
	Enc / Fro	Hem	2.96	-2.12	.247	.98	-0.45
	Rtv / Fro	Hem	2.96	-0.40	.998	.93	-0.09
	Par	Pro * Hem	2.96	1.08	.823	.93	0.23
	Fro	Pro * Hem	2.96	-1.21	.754	.96	-0.27
Mat * Pro * Reg * Hem	Enc / L / Par	Mat	3.44	-1.10	.992	.68	-0.26
	Enc / R / Par	Mat	3.44	-1.42	.932	.67	-0.34
	Enc / L / Fro	Mat	3.44	-0.93	.999	.62	-0.21
	Enc / R / Fro	Mat	3.44	-0.78	.999	.61	-0.18
	Rtv / L / Par	Mat	3.44	1.27	.971	.42	0.27
	Rtv / R / Par	Mat	3.44	1.53	.894	.48	0.33
	Rtv / L / Fro	Mat	3.44	0.82	.999	.53	0.18
	Rtv / R / Fro	Mat	3.44	0.51	.999	.53	0.11
	Ver / L / Par	Pro	3.44	-1.90	.689	.18	-0.41
	Non / L / Par	Pro	3.44	0.05	.999	.08	0.01
	Ver / L / Fro	Pro	3.44	-2.23	.469	.16	-0.51
	Non / L / Fro	Pro	3.44	-0.67	.999	.29	-0.16
	Ver / R / Par	Pro	3.44	-2.76	.203	.30	-0.63
	Non / R / Par	Pro	3.44	-0.13	.999	.21	-0.03
	Ver / R / Fro	Pro	3.44	-1.79	.764	.15	-0.39
	Non / R / Fro	Pro	3.44	-0.42	.999	.05	-0.10
	Ver / Enc / Par	Hem	3.44	2.36	.392	.87	0.51
	Non / Enc / Par	Hem	3.44	1.54	.889	.97	0.35
	Ver / Enc / Fro	Hem	3.44	-2.15	.524	.97	-0.50
	Non / Enc / Fro	Hem	3.44	-1.26	.974	.97	-0.27
	Ver / Rtv / Par	Hem	3.44	1.09	.992	.78	0.25
	Non / Rtv / Par	Hem	3.44	0.95	.998	.80	0.22
	Ver / Rtv / Fro	Hem	3.44	-0.02	.999	.88	0.00
	Non / Rtv / Fro	Hem	3.44	-0.52	.999	.88	-0.11
	Enc / Par	Mat * Hem	3.44	0.92	.999	.88	0.20
	Rtv / Par	Mat * Hem	3.44	-0.34	.999	.95	-0.07
	Enc / Fro	Mat * Hem	3.44	0.29	.999	.75	0.07
	Rtv / Fro	Mat * Hem	3.44	0.33	.999	.70	0.07
	Par / L	Pro * Hem	3.44	-1.86	.716	.67	-0.43
	Par / R	Pro * Hem	3.44	-1.33	.961	.59	-0.29
	Fro / L	Pro * Hem	3.44	-1.96	.652	.59	-0.46

	Fro / R	Pro * Hem	3.44	-0.99	.997	.62	-0.23

Mat = Material (Verbal - Nonverbal); Repetition (Old - New); Reg = Region (Parietal - Frontal); Hem = Hemisphere (Left - Right); Ver = Verbal; Non = Nonverbal; Par = Parietal; Fro = Frontal; L = Left; R = Right.

Supplementary Table 9a.

Descriptive and test statistics for mean alpha power change (0 to 500 ms)

Mat	Pro	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Enc	Par	L	-22.43	-31.09	-13.77
			R	-26.98	-36.98	-16.98
		Fro	L	-22.69	-31.82	-13.57
			R	-20.38	-29.28	-11.47
	Rtv	Par	L	-5.65	-14.67	3.37
			R	-6.31	-14.73	2.11
		Fro	L	-5.21	-12.06	1.64
			R	-7.84	-15.45	-0.22
Non	Enc	Par	L	-22.22	-30.82	-13.62
			R	-25.44	-36.03	-14.86
		Fro	L	-20.24	-29.29	-11.20
			R	-20.88	-29.19	-12.57
	Rtv	Par	L	-10.73	-20.32	-1.15
			R	-15.28	-23.70	-6.86
		Fro	L	-10.62	-18.23	-3.01
			R	-10.32	-18.41	-2.22

9b.

ANOVA Factor	$F(1,21)$	*p*	η_p^2
Mat	0.66	.425	.03
Pro	10.65	.004	.34
Reg	5.75	.026	.22
Hem	6.80	.016	.25
Mat * Pro	3.22	.087	.13
Mat * Reg	1.62	.216	.07
Mat * Hem	0.38	.542	.02
Pro * Hem	0.26	.616	.01
Reg * Hem	1.86	.187	.08
Pro * Reg	5.24	.033	.20
Mat * Pro * Hem	0.07	.798	.00
Mat * Reg * Hem	0.18	.680	.01
Mat * Pro * Reg	2.66	.118	.11
Pro * Reg * Hem	1.31	.265	.06
Mat * Pro * Reg * Hem	6.55	.018	.24

9c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mat * Pro	Enc	Mat	2.72	-0.30	.993	.74	-0.06
	Rtv	Mat	2.72	1.55	.432	.56	0.33
	Ver	Pro	2.72	-3.93	.004	.43	-0.85
	Non	Pro	2.72	-2.18	.154	.31	-0.47
		Mat * Pro	2.72	-1.79	.306	.43	-0.38
Mat * Reg	Par	Mat	2.48	1.03	.571	.65	0.22
	Fro	Mat	2.48	0.54	.856	.63	0.11
		Mat * Reg	2.48	1.27	.429	.91	0.27

Mat * Hem	L	Mat	2.68	0.68	.906	.61	0.15
	R	Mat	2.68	0.92	.801	.67	0.20
	Ver	Hem	2.68	1.78	.299	.98	0.39
	Non	Hem	2.68	2.28	.116	.97	0.51
		Mat * Hem	2.68	-0.62	.929	.93	-0.13
Pro * Hem	L	Pro	2.63	-3.21	.012	.29	-0.69
	R	Pro	2.63	-3.30	.010	.42	-0.71
	Enc	Hem	2.63	2.50	.068	.99	0.60
	Rtv	Hem	2.63	2.21	.121	.97	0.47
		Pro * Hem	2.63	-0.51	.940	.99	-0.11
Reg * Hem	Par	Hem	2.39	1.96	.119	.88	0.43
	Fro	Hem	2.39	0.19	.973	.96	0.04
		Reg * Hem	2.39	1.36	.317	-.62	0.29
Pro * Reg	Par	Pro	2.42	-3.36	.006	.37	-0.72
	Fro	Pro	2.42	-3.12	.010	.35	-0.67
		Pro * Reg	2.42	-2.29	.063	.98	-0.53
Mat * Pro * Hem	Enc / L	Mat	3.11	-0.43	.999	.72	-0.09
	Enc / R	Mat	3.11	-0.16	.999	.74	-0.03
	Rtv / L	Mat	3.11	1.43	.798	.54	0.31
	Rtv / R	Mat	3.11	1.63	.674	.57	0.35
	Ver / L	Pro	3.11	-3.98	.007	.41	-0.85
	Ver / R	Pro	3.11	-3.85	.009	.46	-0.83
	Non / L	Pro	3.11	-2.10	.370	.24	-0.45
	Non / R	Pro	3.11	-2.24	.294	.38	-0.48
	Ver / Enc	Hem	3.11	1.82	.543	.99	0.43
	Ver / Rec	Hem	3.11	1.54	.730	.96	0.33
	Non / Enc	Hem	3.11	1.94	.465	.98	0.43
	Non / Rec	Hem	3.11	1.95	.460	.96	0.42
	Enc	Mat * Hem	3.11	-0.72	.995	.94	-0.15
	Rtv	Mat * Hem	3.11	-0.36	.999	.93	-0.08
	Ver	Pro * Hem	3.11	-0.67	.997	.98	-0.14
	Non	Pro * Hem	3.11	-0.17	.999	.98	-0.04
Mat * Reg * Hem	Par / L	Mat	3.02	0.74	.973	.56	0.16
	Par / R	Mat	3.02	1.20	.818	.68	0.26
	Fro / L	Mat	3.02	0.51	.995	.60	0.11
	Fro / R	Mat	3.02	0.54	.993	.64	0.11
	Ver / Par	Hem	3.02	1.43	.683	.88	0.31
	Non / Par	Hem	3.02	1.76	.481	.82	0.38
	Ver / Fro	Hem	3.02	0.16	.999	.95	0.03
	Non / Fro	Hem	3.02	0.16	.999	.95	0.04
	Par	Mat * Hem	3.02	-0.55	.993	.73	-0.12
	Fro	Mat * Hem	3.02	-0.01	.999	.92	0.00
Mat * Pro * Reg	Enc / Par	Mat	2.89	-0.29	.999	.77	-0.06
	Rtv / Par	Mat	2.89	1.82	.368	.55	0.39
	Enc / Fro	Mat	2.89	-0.29	.999	.68	-0.06
	Rtv / Fro	Mat	2.89	1.19	.737	.57	0.26
	Par / Par	Pro	2.89	-4.23	.003	.45	-0.90
	Fro / Par	Pro	2.89	-2.14	.219	.31	-0.46
	Par / Fro	Pro	2.89	-3.52	.011	.41	-0.76
	Fro / Fro	Pro	2.89	-2.19	.198	.31	-0.47
	Par	Mat * Pro	2.89	-2.18	.204	.47	-0.47
	Fro	Mat * Pro	2.89	-1.31	.667	.37	-0.28

Pro * Reg * Hem	Par / L	Pro	2.94	-3.05	.040	.28	-0.65
	Par / R	Pro	2.94	-3.55	.012	.47	-0.78
	Fro / L	Pro	2.94	-3.29	.023	.34	-0.71
	Fro / R	Pro	2.94	-2.86	.056	.36	-0.61
	Enc / Par	Hem	2.94	2.47	.125	.95	0.61
	Rtv / Par	Hem	2.94	1.21	.752	.84	0.26
	Enc / Fro	Hem	2.94	-0.93	.899	.97	-0.20
	Rtv / Fro	Hem	2.94	0.96	.882	.93	0.21
	Par	Pro * Hem	2.94	0.71	.964	.92	0.15
	Fro	Pro * Hem	2.94	-1.49	.577	.95	-0.32
Mat * Pro * Reg * Hem	Enc / L / Par	Mat	3.44	-0.07	.999	.72	-0.01
	Enc / R / Par	Mat	3.44	-0.45	.999	.77	-0.10
	Enc / L / Fro	Mat	3.44	-0.69	.999	.67	-0.15
	Enc / R / Fro	Mat	3.44	0.15	.999	.66	0.03
	Rtv / L / Par	Mat	3.44	1.13	.988	.50	0.24
	Rtv / R / Par	Mat	3.44	2.34	.410	.55	0.50
	Rtv / L / Fro	Mat	3.44	1.65	.850	.56	0.35
	Rtv / R / Fro	Mat	3.44	0.71	.999	.58	0.15
	Ver / L / Par	Pro	3.44	-3.59	.034	.40	-0.77
	Non / L / Par	Pro	3.44	-2.12	.566	.23	-0.45
	Ver / L / Fro	Pro	3.44	-4.17	.009	.43	-0.91
	Non / L / Fro	Pro	3.44	-2.00	.636	.29	-0.43
	Ver / R / Par	Pro	3.44	-4.58	.003	.49	-0.99
	Non / R / Par	Pro	3.44	-2.06	.597	.44	-0.45
	Ver / R / Fro	Pro	3.44	-2.80	.186	.37	-0.60
	Non / R / Fro	Pro	3.44	-2.31	.435	.33	-0.49
	Ver / Enc / Par	Hem	3.44	2.96	.138	.95	0.69
	Non / Enc / Par	Hem	3.44	1.41	.941	.90	0.33
	Ver / Enc / Fro	Hem	3.44	-2.25	.474	.97	-0.48
	Non / Enc / Fro	Hem	3.44	0.47	.999	.95	0.10
	Ver / Rtv / Par	Hem	3.44	0.25	.999	.80	0.05
	Non / Rtv / Par	Hem	3.44	1.71	.819	.82	0.37
	Ver / Rtv / Fro	Hem	3.44	1.81	.764	.92	0.40
	Non / Rtv / Fro	Hem	3.44	-0.23	.999	.94	-0.05
	Enc / Par	Mat * Hem	3.44	0.58	.999	.75	0.12
	Rtv / Par	Mat * Hem	3.44	-1.86	.733	.90	-0.40
	Enc / Fro	Mat * Hem	3.44	-1.24	.976	.73	-0.27
	Rtv / Fro	Mat * Hem	3.44	2.01	.630	.91	0.43
	Par / L	Pro * Hem	3.44	-1.29	.966	.68	-0.28
	Par / R	Pro * Hem	3.44	-2.14	.549	.67	-0.46
	Fro / L	Pro * Hem	3.44	-2.82	.178	.69	-0.60
	Fro / R	Pro * Hem	3.44	-0.48	.999	.59	-0.10

Mat = Material (Verbal - Nonverbal); Repetition (Old - New); Reg = Region (Parietal - Frontal); Hem = Hemi sphere (Left - Right); Ver = Verbal; Non = Nonverbal; Par = Parietal; Fro = Frontal; L = Left; R = Right.

Supplementary Table 10a.

Descriptive and test statistics for mean alpha power change (0 to 500 ms) - Repetition effect

Mat	Rep	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Old	Par	L	10.10	3.36	16.84
			R	10.72	2.77	18.66
		Fro	L	6.28	-0.79	13.36
			R	4.86	-1.64	11.35

	New	Par	L	6.78	-3.61	17.16
			R	2.73	-2.95	8.42
		Fro	L	2.91	-2.55	8.38
			R	3.00	-4.42	10.42
Non	Old	Par	L	5.94	0.36	11.51
			R	4.67	-2.61	11.95
		Fro	L	3.40	-4.01	10.80
			R	4.78	-1.58	11.13
	New	Par	L	2.62	-6.34	11.58
			R	0.31	-5.26	5.87
		Fro	L	0.03	-7.09	7.14
			R	0.52	-5.21	6.24

10b.

ANOVA Factor	$F(1,21)$	p	η_p^2
Mat	1.50	.235	.07
Rep	5.76	.026	.22
Reg	4.71	.042	.18
Hem	1.31	.266	.06
Mat * Rep	0.01	.933	.00
Mat * Reg	1.89	.183	.08
Mat * Hem	0.43	.520	.02
Rep * Hem	1.20	.286	.05
Reg * Hem	0.55	.465	.03
Rep * Reg	1.10	.306	.05
Mat * Rep * Hem	0.13	.719	.01
Mat * Reg * Hem	0.18	.680	.01
Mat * Rep * Reg	1.18	.289	.05
Rep * Reg * Hem	0.51	.483	.02
Mat * Rep * Reg * Hem	0.53	.474	.03

10c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mat * Rep	Old	Mat	2.72	1.04	.707	.47	0.22
	New	Mat	2.72	0.96	.749	.49	0.21
	Ver	Rep	2.72	1.51	.431	.64	0.32
	Non	Rep	2.72	1.81	.276	.73	0.39
		Mat * Rep	2.72	0.09	.999	.34	0.02
Mat * Reg	Par	Mat	2.50	1.41	.338	.52	0.30
	Fro	Mat	2.50	0.88	.634	.63	0.19
		Mat * Reg	2.50	1.38	.358	.86	0.32
Mat * Hem	L	Mat	2.72	1.29	.582	.57	0.27
	R	Mat	2.72	1.09	.700	.57	0.23
	Ver	Hem	2.72	1.41	.504	.96	0.31
	Non	Hem	2.72	0.43	.971	.94	0.10
		Mat * Hem	2.72	0.65	.913	.90	0.14
Rep * Hem	L	Rep	2.77	1.76	.322	.77	0.38
	R	Rep	2.77	2.88	.039	.81	0.63
	Old	Hem	2.77	0.22	.997	.96	0.05
	New	Hem	2.77	1.42	.508	.95	0.38
		Rep * Hem	2.77	-1.09	.699	.79	-0.24
Reg * Hem	Par	Hem	2.41	1.03	.505	.82	0.23
	Fro	Hem	2.41	-0.11	.992	.90	-0.02
		Reg * Hem	2.41	0.74	.690	-.56	0.16

Rep * Reg	Par	Rep	2.57	2.52	.055	.77	0.54
	Fro	Rep	2.57	1.85	.188	.78	0.40
		Rep * Reg	2.57	1.05	.564	.68	0.22
Mat * Rep * Hem	Old / L	Mat	3.20	1.18	.916	.51	0.25
	Old / R	Mat	3.20	0.87	.983	.41	0.19
	New / L	Mat	3.20	1.02	.960	.49	0.22
	New / R	Mat	3.20	0.85	.985	.46	0.18
	Ver / L	Rep	3.20	1.17	.922	.64	0.25
	Ver / R	Rep	3.20	1.81	.586	.63	0.39
	Non / L	Rep	3.20	1.53	.755	.76	0.33
	Non / R	Rep	3.20	1.83	.576	.67	0.40
	Ver / Old	Hem	3.20	0.40	.999	.95	0.09
	Ver / Rec	Hem	3.20	1.93	.509	.97	0.49
	Non / Old	Hem	3.20	-0.05	.999	.93	-0.01
	Non / Rec	Hem	3.20	0.64	.997	.92	0.17
	Old	Mat * Hem	3.20	0.32	.999	.91	0.07
	New	Mat * Hem	3.20	0.76	.991	.92	0.18
	Ver	Rep * Hem	3.20	-1.38	.834	.92	-0.30
	Non	Rep * Hem	3.20	-0.58	.999	.73	-0.12
Mat * Reg * Hem	Par / L	Mat	3.01	1.13	.841	.46	0.24
	Par / R	Mat	3.01	1.59	.579	.56	0.34
	Fro / L	Mat	3.01	1.16	.828	.62	0.25
	Fro / R	Mat	3.01	0.47	.996	.55	0.10
	Ver / Par	Hem	3.01	0.75	.968	.79	0.17
	Non / Par	Hem	3.01	0.96	.910	.82	0.22
	Ver / Fro	Hem	3.01	0.52	.994	.90	0.11
	Non / Fro	Hem	3.01	-0.50	.995	.80	-0.11
	Par	Mat * Hem	3.01	-0.03	.999	.75	-0.01
	Fro	Mat * Hem	3.01	0.73	.971	.64	0.16
Mat * Rep * Reg	Old / Par	Mat	2.99	1.65	.490	.51	0.36
	New / Par	Mat	2.99	0.86	.921	.39	0.19
	Old / Fro	Mat	2.99	0.42	.997	.40	0.09
	New / Fro	Mat	2.99	1.01	.859	.57	0.22
	Par / Par	Rep	2.99	1.92	.343	.66	0.41
	Fro / Par	Rep	2.99	1.73	.443	.73	0.37
	Par / Fro	Rep	2.99	0.90	.906	.56	0.19
	Fro / Fro	Rep	2.99	1.57	.541	.68	0.34
	Par	Mat * Rep	2.99	0.50	.991	.47	0.11
	Fro	Mat * Rep	2.99	-0.30	.999	.15	-0.06
Rep * Reg * Hem	Par / L	Rep	3.10	1.17	.829	.69	0.28
	Par / R	Rep	3.10	3.11	.049	.77	0.73
	Fro / L	Rep	3.10	1.64	.549	.72	0.35
	Fro / R	Rep	3.10	1.72	.500	.78	0.37
	Old / Par	Hem	3.10	0.17	.999	.80	0.04
	New / Par	Hem	3.10	1.19	.819	.76	0.32
	Old / Fro	Hem	3.10	0.02	.999	.92	0.00
	New / Fro	Hem	3.10	-0.17	.999	.80	-0.04
	Par	Rep * Hem	3.10	-0.91	.937	.20	-0.20
	Fro	Rep * Hem	3.10	0.19	.999	.64	0.04
Mat * Rep * Reg * Hem	Old / L / Par	Mat	3.48	1.41	.934	.52	0.31
	Old / R / Par	Mat	3.48	1.53	.897	.42	0.33
	Old / L / Fro	Mat	3.48	0.74	.999	.37	0.16

Old / R / Fro	Mat	3.48	0.02	.999	.44	0.01
New / L / Par	Mat	3.48	0.82	.999	.41	0.18
New / R / Par	Mat	3.48	0.76	.999	.31	0.16
New / L / Fro	Mat	3.48	0.92	.998	.48	0.20
New / R / Fro	Mat	3.48	0.74	.999	.46	0.16
Ver / L / Par	Rep	3.48	0.88	.999	.65	0.21
Non / L / Par	Rep	3.48	1.07	.992	.70	0.26
Ver / L / Fro	Rep	3.48	1.11	.988	.52	0.24
Non / L / Fro	Rep	3.48	0.97	.997	.50	0.21
Ver / R / Par	Rep	3.48	2.92	.160	.70	0.67
Non / R / Par	Rep	3.48	1.26	.969	.40	0.28
Ver / R / Fro	Rep	3.48	0.61	.999	.59	0.13
Non / R / Fro	Rep	3.48	2.03	.617	.74	0.44
Ver / Old / Par	Hem	3.48	-0.26	.999	.78	-0.06
Non / Old / Par	Hem	3.48	0.49	.999	.69	0.11
Ver / Old / Fro	Hem	3.48	1.00	.996	.91	0.22
Non / Old / Fro	Hem	3.48	-1.04	.995	.93	-0.24
Ver / New / Par	Hem	3.48	1.33	.957	.85	0.40
Non / New / Par	Hem	3.48	0.67	.999	.60	0.16
Ver / New / Fro	Hem	3.48	-0.05	.999	.89	-0.01
Non / New / Fro	Hem	3.48	-0.16	.999	.50	-0.03
Old / Par	Mat * Hem	3.48	-0.58	.999	.59	-0.13
New / Par	Mat * Hem	3.48	1.70	.815	.91	0.39
Old / Fro	Mat * Hem	3.48	0.47	.999	.69	0.11
New / Fro	Mat * Hem	3.48	0.11	.999	.32	0.02
Par / L	Rep * Hem	3.48	0.00	.999	.36	0.00
Par / R	Rep * Hem	3.48	0.00	.999	-.21	0.00
Fro / L	Rep * Hem	3.48	0.75	.999	-.19	0.16
Fro / R	Rep * Hem	3.48	-0.63	.999	-.08	-0.14

Ver = Verbal; Non = Nonverbal; Par = Parietal; Fro = Frontal; L = Left; R = Right.

Supplementary Table 11a.

Descriptive and test statistics for mean alpha power change (500 to 1500 ms) - Repetition effect

Mat	Rep	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Old	Par	L	-4.81	-13.56	3.95
			R	-3.75	-13.40	5.90
		Fro	L	-4.45	-12.02	3.12
			R	-6.76	-14.22	0.71
	New	Par	L	-8.43	-16.79	-0.07
			R	-8.95	-17.59	-0.30
		Fro	L	-6.78	-13.61	0.05
			R	-10.39	-17.55	-3.22
Non	Old	Par	L	-7.40	-18.85	4.04
			R	-12.75	-22.83	-2.66
		Fro	L	-9.11	-18.83	0.62
			R	-6.77	-17.22	3.67
	New	Par	L	-12.92	-22.67	-3.18
			R	-17.23	-25.78	-8.68
		Fro	L	-11.38	-19.17	-3.59
			R	-12.67	-20.56	-4.78

11b.

ANOVA Factor	$F(1,21)$	p	η_p^2
Mat	1.78	.197	.08
Rep	2.35	.140	.10
Reg	1.01	.325	.05
Hem	4.98	.037	.19
Mat * Rep	0.04	.836	.00
Mat * Reg	4.82	.040	.19
Mat * Hem	0.38	.545	.02
Rep * Hem	3.19	.089	.13
Reg * Hem	0.15	.699	.01
Rep * Reg	1.29	.269	.06
Mat * Rep * Hem	0.01	.924	.00
Mat * Reg * Hem	4.70	.042	.18
Mat * Rep * Reg	0.04	.841	.00
Rep * Reg * Hem	0.58	.454	.03
Mat * Rep * Reg * Hem	1.13	.300	.05

11c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mat * Rep	Old	Mat	2.74	0.87	.833	.44	0.19
	New	Mat	2.74	1.65	.374	.68	0.35
	Ver	Rep	2.74	1.31	.570	.71	0.28
	Non	Rep	2.74	1.19	.650	.63	0.26
		Mat * Rep	2.74	-0.21	.997	.52	-0.05
Mat * Reg	Par	Mat	2.53	1.66	.228	.57	0.36
	Fro	Mat	2.53	0.90	.626	.59	0.20
		Mat * Reg	2.53	2.20	.093	.92	0.49
Mat * Hem	L	Mat	2.62	1.17	.664	.57	0.25
	R	Mat	2.62	1.46	.477	.59	0.31
	Ver	Hem	2.62	1.35	.546	.96	0.30
	Non	Hem	2.62	2.05	.178	.97	0.45
		Mat * Hem	2.62	-0.62	.935	.93	-0.13
Rep * Hem	L	Rep	2.61	1.27	.544	.71	0.27
	R	Rep	2.61	1.76	.281	.71	0.38
	Old	Hem	2.61	1.42	.453	.98	0.30
	New	Hem	2.61	2.49	.067	.96	0.53
		Rep * Hem	2.61	-1.78	.269	.96	-0.38
Reg * Hem	Par	Hem	2.49	1.20	.426	.86	0.26
	Fro	Hem	2.49	1.08	.494	.94	0.23
		Reg * Hem	2.49	0.39	.911	-.57	0.08
Rep * Reg	Par	Rep	2.48	1.61	.243	.70	0.34
	Fro	Rep	2.48	1.40	.333	.72	0.30
		Rep * Reg	2.48	1.14	.475	.94	0.26
Mat * Rep * Hem	Old / L	Mat	3.14	0.79	.993	.46	0.17
	Old / R	Mat	3.14	0.92	.980	.40	0.20
	New / L	Mat	3.14	1.39	.837	.63	0.30
	New / R	Mat	3.14	1.83	.567	.71	0.39
	Ver / L	Rep	3.14	1.05	.961	.69	0.22
	Ver / R	Rep	3.14	1.52	.773	.72	0.32
	Non / L	Rep	3.14	1.05	.960	.67	0.23
	Non / R	Rep	3.14	1.30	.880	.59	0.28
	Ver / Old	Hem	3.14	0.59	.999	.96	0.13
	Ver / Rec	Hem	3.14	1.64	.699	.94	0.36

	Non / Old	Hem	3.14	1.38	.843	.98	0.30
	Non / Rec	Hem	3.14	2.36	.259	.96	0.51
	Old	Mat * Hem	3.14	-0.57	.999	.95	-0.12
	New	Mat * Hem	3.14	-0.50	.999	.89	-0.11
	Ver	Rep * Hem	3.14	-1.18	.924	.91	-0.25
	Non	Rep * Hem	3.14	-1.46	.807	.98	-0.33
Mat * Reg * Hem	Par / L	Mat	3.02	0.85	.952	.53	0.19
	Par / R	Mat	3.02	2.29	.216	.56	0.49
	Fro / L	Mat	3.02	1.40	.707	.56	0.30
	Fro / R	Mat	3.02	0.35	.999	.61	0.08
	Ver / Par	Hem	3.02	-0.12	.999	.83	-0.03
	Non / Par	Hem	3.02	1.87	.412	.84	0.41
	Ver / Fro	Hem	3.02	2.27	.224	.92	0.48
	Non / Fro	Hem	3.02	-0.39	.999	.94	-0.08
	Par	Mat * Hem	3.02	-1.66	.544	.71	-0.36
	Fro	Mat * Hem	3.02	2.52	.141	.91	0.54
Mat * Rep * Reg	Old / Par	Mat	2.96	1.16	.789	.42	0.25
	New / Par	Mat	2.96	1.92	.345	.66	0.41
	Old / Fro	Mat	2.96	0.51	.989	.43	0.11
	New / Fro	Mat	2.96	1.20	.766	.66	0.26
	Par / Par	Rep	2.96	1.36	.671	.68	0.29
	Fro / Par	Rep	2.96	1.25	.735	.63	0.27
	Par / Fro	Rep	2.96	1.14	.796	.71	0.24
	Fro / Fro	Rep	2.96	1.07	.829	.62	0.24
	Par	Mat * Rep	2.96	-0.14	.999	.53	-0.03
	Fro	Mat * Rep	2.96	-0.27	.999	.46	-0.06
Rep * Reg * Hem	Par / L	Rep	2.98	1.46	.635	.70	0.31
	Par / R	Rep	2.98	1.62	.537	.70	0.35
	Fro / L	Rep	2.98	0.88	.926	.69	0.19
	Fro / R	Rep	2.98	1.80	.425	.72	0.39
	Old / Par	Hem	2.98	1.17	.808	.90	0.25
	New / Par	Hem	2.98	1.03	.867	.81	0.22
	Old / Fro	Hem	2.98	-0.01	.999	.94	0.00
	New / Fro	Hem	2.98	1.73	.467	.91	0.37
	Par	Rep * Hem	2.98	-0.15	.999	.83	-0.03
	Fro	Rep * Hem	2.98	-1.68	.496	.85	-0.36
Mat * Rep * Reg * Hem	Old / L / Par	Mat	3.44	0.51	.999	.47	0.11
	Old / R / Par	Mat	3.44	1.62	.875	.32	0.35
	Old / L / Fro	Mat	3.44	0.98	.996	.37	0.21
	Old / R / Fro	Mat	3.44	0.00	.999	.47	0.00
	New / L / Par	Mat	3.44	1.06	.994	.54	0.23
	New / R / Par	Mat	3.44	2.68	.249	.72	0.57
	New / L / Fro	Mat	3.44	1.57	.894	.66	0.34
	New / R / Fro	Mat	3.44	0.76	.999	.66	0.16
	Ver / L / Par	Rep	3.44	1.02	.995	.63	0.22
	Non / L / Par	Rep	3.44	1.36	.956	.69	0.29
	Ver / L / Fro	Rep	3.44	0.80	.999	.65	0.17
	Non / L / Fro	Rep	3.44	0.60	.999	.61	0.13
	Ver / R / Par	Rep	3.44	1.48	.924	.69	0.32
	Non / R / Par	Rep	3.44	1.08	.993	.58	0.23
	Ver / R / Fro	Rep	3.44	1.38	.951	.72	0.29
	Non / R / Fro	Rep	3.44	1.48	.928	.62	0.33

Ver / Old / Par	Hem	3.44	-0.44	.999	.86	-0.10
Non / Old / Par	Hem	3.44	1.90	.725	.86	0.42
Ver / Old / Fro	Hem	3.44	1.39	.949	.90	0.30
Non / Old / Fro	Hem	3.44	-1.43	.940	.95	-0.31
Ver / New / Par	Hem	3.44	0.17	.999	.74	0.04
Non / New / Par	Hem	3.44	1.59	.887	.82	0.35
Ver / New / Fro	Hem	3.44	2.33	.440	.90	0.50
Non / New / Fro	Hem	3.44	0.82	.999	.91	0.17
Old / Par	Mat * Hem	3.44	-1.73	.822	.76	-0.37
New / Par	Mat * Hem	3.44	2.21	.517	.90	0.47
Old / Fro	Mat * Hem	3.44	-1.18	.985	.65	-0.27
New / Fro	Mat * Hem	3.44	1.75	.812	.90	0.37
Par / L	Rep * Hem	3.44	-0.44	.999	.35	-0.09
Par / R	Rep * Hem	3.44	0.01	.999	.20	0.00
Fro / L	Rep * Hem	3.44	0.15	.999	.21	0.03
Fro / R	Rep * Hem	3.44	-0.54	.999	.24	-0.12

Mat = Material (Verbal - Nonverbal); Repetition (Old - New); Reg = Region (Parietal - Frontal); Hem = Hemisphere (Left - Right); Ver = Verbal; Non = Nonverbal; Par = Parietal; Fro = Frontal; L = Left; R = Right.

Supplementary Table 11a.

Descriptive and test statistics for mean alpha power change (500 to 1500 ms) - Repetition effect

Mat	Rep	Reg	Hem	*M*	CI_{low}	CI_{upp}
Ver	Old	Par	L	-4.81	-13.56	3.95
			R	-3.75	-13.40	5.90
		Fro	L	-4.45	-12.02	3.12
			R	-6.76	-14.22	0.71
	New	Par	L	-8.43	-16.79	-0.07
			R	-8.95	-17.59	-0.30
		Fro	L	-6.78	-13.61	0.05
			R	-10.39	-17.55	-3.22
Non	Old	Par	L	-7.40	-18.85	4.04
			R	-12.75	-22.83	-2.66
		Fro	L	-9.11	-18.83	0.62
			R	-6.77	-17.22	3.67
	New	Par	L	-12.92	-22.67	-3.18
			R	-17.23	-25.78	-8.68
		Fro	L	-11.38	-19.17	-3.59
			R	-12.67	-20.56	-4.78

11b.

ANOVA Factor	$F(1,21)$	p	η_p^2
Mat	1.78	.197	.08
Rep	2.35	.140	.10
Reg	1.01	.325	.05
Hem	4.98	.037	.19
Mat * Rep	0.04	.836	.00
Mat * Reg	4.82	.040	.19
Mat * Hem	0.38	.545	.02
Rep * Hem	3.19	.089	.13
Reg * Hem	0.15	.699	.01
Rep * Reg	1.29	.269	.06
Mat * Rep * Hem	0.01	.924	.00

Mat * Reg * Hem	4.70	.042	.18
Mat * Rep * Reg	0.04	.841	.00
Rep * Reg * Hem	0.58	.454	.03
Mat * Rep * Reg * Hem	1.13	.300	.05

11c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mat * Rep	Old	Mat	2.74	0.87	.833	.44	0.19
	New	Mat	2.74	1.65	.374	.68	0.35
	Ver	Rep	2.74	1.31	.570	.71	0.28
	Non	Rep	2.74	1.19	.650	.63	0.26
		Mat * Rep	2.74	-0.21	.997	.52	-0.05
Mat * Reg	Par	Mat	2.53	1.66	.228	.57	0.36
	Fro	Mat	2.53	0.90	.626	.59	0.20
		Mat * Reg	2.53	2.20	.093	.92	0.49
Mat * Hem	L	Mat	2.62	1.17	.664	.57	0.25
	R	Mat	2.62	1.46	.477	.59	0.31
	Ver	Hem	2.62	1.35	.546	.96	0.30
	Non	Hem	2.62	2.05	.178	.97	0.45
		Mat * Hem	2.62	-0.62	.935	.93	-0.13
Rep * Hem	L	Rep	2.61	1.27	.544	.71	0.27
	R	Rep	2.61	1.76	.281	.71	0.38
	Old	Hem	2.61	1.42	.453	.98	0.30
	New	Hem	2.61	2.49	.067	.96	0.53
		Rep * Hem	2.61	-1.78	.269	.96	-0.38
Reg * Hem	Par	Hem	2.49	1.20	.426	.86	0.26
	Fro	Hem	2.49	1.08	.494	.94	0.23
		Reg * Hem	2.49	0.39	.911	-.57	0.08
Rep * Reg	Par	Rep	2.48	1.61	.243	.70	0.34
	Fro	Rep	2.48	1.40	.333	.72	0.30
		Rep * Reg	2.48	1.14	.475	.94	0.26
Mat * Rep * Hem	Old / L	Mat	3.14	0.79	.993	.46	0.17
	Old / R	Mat	3.14	0.92	.980	.40	0.20
	New / L	Mat	3.14	1.39	.837	.63	0.30
	New / R	Mat	3.14	1.83	.567	.71	0.39
	Ver / L	Rep	3.14	1.05	.961	.69	0.22
	Ver / R	Rep	3.14	1.52	.773	.72	0.32
	Non / L	Rep	3.14	1.05	.960	.67	0.23
	Non / R	Rep	3.14	1.30	.880	.59	0.28
	Ver / Old	Hem	3.14	0.59	.999	.96	0.13
	Ver / Rec	Hem	3.14	1.64	.699	.94	0.36
	Non / Old	Hem	3.14	1.38	.843	.98	0.30
	Non / Rec	Hem	3.14	2.36	.259	.96	0.51
	Old	Mat * Hem	3.14	-0.57	.999	.95	-0.12
	New	Mat * Hem	3.14	-0.50	.999	.89	-0.11
	Ver	Rep * Hem	3.14	-1.18	.924	.91	-0.25
	Non	Rep * Hem	3.14	-1.46	.807	.98	-0.33
Mat * Reg * Hem	Par / L	Mat	3.02	0.85	.952	.53	0.19
	Par / R	Mat	3.02	2.29	.216	.56	0.49
	Fro / L	Mat	3.02	1.40	.707	.56	0.30
	Fro / R	Mat	3.02	0.35	.999	.61	0.08
	Ver / Par	Hem	3.02	-0.12	.999	.83	-0.03
	Non / Par	Hem	3.02	1.87	.412	.84	0.41

	Ver / Fro	Hem	3.02	2.27	.224	.92	0.48
	Non / Fro	Hem	3.02	-0.39	.999	.94	-0.08
	Par	Mat * Hem	3.02	-1.66	.544	.71	-0.36
	Fro	Mat * Hem	3.02	2.52	.141	.91	0.54
Mat * Rep * Reg	Old / Par	Mat	2.96	1.16	.789	.42	0.25
	New / Par	Mat	2.96	1.92	.345	.66	0.41
	Old / Fro	Mat	2.96	0.51	.989	.43	0.11
	New / Fro	Mat	2.96	1.20	.766	.66	0.26
	Par / Par	Rep	2.96	1.36	.671	.68	0.29
	Fro / Par	Rep	2.96	1.25	.735	.63	0.27
	Par / Fro	Rep	2.96	1.14	.796	.71	0.24
	Fro / Fro	Rep	2.96	1.07	.829	.62	0.24
	Par	Mat * Rep	2.96	-0.14	.999	.53	-0.03
	Fro	Mat * Rep	2.96	-0.27	.999	.46	-0.06
Rep * Reg * Hem	Par / L	Rep	2.98	1.46	.635	.70	0.31
	Par / R	Rep	2.98	1.62	.537	.70	0.35
	Fro / L	Rep	2.98	0.88	.926	.69	0.19
	Fro / R	Rep	2.98	1.80	.425	.72	0.39
	Old / Par	Hem	2.98	1.17	.808	.90	0.25
	New / Par	Hem	2.98	1.03	.867	.81	0.22
	Old / Fro	Hem	2.98	-0.01	.999	.94	0.00
	New / Fro	Hem	2.98	1.73	.467	.91	0.37
	Par	Rep * Hem	2.98	-0.15	.999	.83	-0.03
	Fro	Rep * Hem	2.98	-1.68	.496	.85	-0.36
Mat * Rep * Reg * Hem	Old / L / Par	Mat	3.44	0.51	.999	.47	0.11
	Old / R / Par	Mat	3.44	1.62	.875	.32	0.35
	Old / L / Fro	Mat	3.44	0.98	.996	.37	0.21
	Old / R / Fro	Mat	3.44	0.00	.999	.47	0.00
	New / L / Par	Mat	3.44	1.06	.994	.54	0.23
	New / R / Par	Mat	3.44	2.68	.249	.72	0.57
	New / L / Fro	Mat	3.44	1.57	.894	.66	0.34
	New / R / Fro	Mat	3.44	0.76	.999	.66	0.16
	Ver / L / Par	Rep	3.44	1.02	.995	.63	0.22
	Non / L / Par	Rep	3.44	1.36	.956	.69	0.29
	Ver / L / Fro	Rep	3.44	0.80	.999	.65	0.17
	Non / L / Fro	Rep	3.44	0.60	.999	.61	0.13
	Ver / R / Par	Rep	3.44	1.48	.924	.69	0.32
	Non / R / Par	Rep	3.44	1.08	.993	.58	0.23
	Ver / R / Fro	Rep	3.44	1.38	.951	.72	0.29
	Non / R / Fro	Rep	3.44	1.48	.928	.62	0.33
	Ver / Old / Par	Hem	3.44	-0.44	.999	.86	-0.10
	Non / Old / Par	Hem	3.44	1.90	.725	.86	0.42
	Ver / Old / Fro	Hem	3.44	1.39	.949	.90	0.30
	Non / Old / Fro	Hem	3.44	-1.43	.940	.95	-0.31
	Ver / New / Par	Hem	3.44	0.17	.999	.74	0.04
	Non / New / Par	Hem	3.44	1.59	.887	.82	0.35
	Ver / New / Fro	Hem	3.44	2.33	.440	.90	0.50
	Non / New / Fro	Hem	3.44	0.82	.999	.91	0.17
	Old / Par	Mat * Hem	3.44	-1.73	.822	.76	-0.37
	New / Par	Mat * Hem	3.44	2.21	.517	.90	0.47
	Old / Fro	Mat * Hem	3.44	-1.18	.985	.65	-0.27
	New / Fro	Mat * Hem	3.44	1.75	.812	.90	0.37

Par / L	Rep * Hem	3.44	-0.44	.999	.35	-0.09
Par / R	Rep * Hem	3.44	0.01	.999	.20	0.00
Fro / L	Rep * Hem	3.44	0.15	.999	.21	0.03
Fro / R	Rep * Hem	3.44	-0.54	.999	.24	-0.12

Mat = Material (Verbal - Nonverbal); Repetition (Old - New); Reg = Region (Parietal - Frontal); Hem = Hemisphere (Left - Right); Ver = Verbal; Non = Nonverbal; Par = Parietal; Fro = Frontal; L = Left; R = Right.

Segue to Chapter 5

In Chapters 3 and 4 the relative effects of material type and processing type on hemispheric lateralisation were explored, with Chapter 3 using event-related potential (ERP) measures and Chapter 4 using measures of frequency-specific EEG power. In Chapters 5 and 6 the findings of the Chapters 3 and 4 were expanded with greater focus on the role of lower-level perceptual processing in material specific lateralisation. The potential confounding role of stimulus differences has been discussed in Chapter 1, including the confound that spatial stimuli are usually comprised of lower spatial frequencies than word stimuli. The primary aim of Chapters 5 and 6 was to test the validity of the material specificity hypothesis of lateralisation using different tasks that are matched in terms of lower-level stimulus attributes, including the number of pixels, size, and spatial frequency. Another aim of Chapters 5 and 6 was to assess the impact of stimulus verbalisability on hemispheric lateralisation. The testing of verbalisability when stimuli are completely controlled for lower-level perceptual attributes provides a more powerful means to determine the strength of this putative confound implicated in nonverbal memory tests.

Chapter 5: Separable effects of perceptual form and memory on material-specific lateralisation during memory tasks: An ERP study

Adam Bentvelzen[1,2], Nicholas A. Badcock[1,3], Genevieve McArthur[1,3], & Greg Savage[1,2]

[1] ARC Centre of Excellence in Cognition and its Disorders, Macquarie University, NSW, 2109, Australia;

[2] Department of Psychology, Macquarie University, NSW, 2109, Australia.

[3] Department of Cognitive Science, Macquarie University, NSW, 2109, Australia;

Keywords: memory; material specificity; perceptual form; hemispheric lateralisation; N170; P300.

Running title: Effects of perceptual form and memory on ERP lateralisation

Corresponding author: Adam Bentvelzen, ARC Centre of Excellence in Cognition and its Disorders, Department of Cognitive Science, Macquarie University, NSW, 2109, Australia. Phone: +61 2 9850 4127. Email: adam.bentvelzen@students.mq.edu.au

Acknowledgements

This work was funded by an Australian Postgraduate Award (APA) to Adam Bentvelzen and supported by the Australian Research Council Centre of Excellence for Cognition and its Disorders (CE110001021) http://www.ccd.edu.au

Abstract

There is abundant evidence that the medial temporal lobe plays a unique role in recent memory function. As such, *material specific* hemispheric differences in the medial temporal lobe (verbal: left; nonverbal: right) have been understood as being related primarily to memory. There have been surprisingly few attempts, however, to examine the contribution of perceptual processing to these putatively memory-related lateralisation effects, particularly considering that material type and perceptual form are typically confounded. Furthermore, while neuroimaging methods provide the most common means of investigating hemispheric lateralisation in healthy participants, their low temporal resolution means that they have poor ability to detect very early perceptual lateralisation effects. We investigated the separate and interactive effects of memory-related and stimulus-related processing on material specific lateralisation. Event-related potentials (ERPs) were measured in 20 healthy adults at parietal electrodes during recognition of previously learned verbal materials (letter triplets) and spatial materials (arrays of positions) that differed in task-irrelevant perceptual form (standard: verbal or spatial only; hybrid: verbal-spatial). The results showed that spatial memory and spatial form were independently associated with right-lateralisation of the N170 peak. The P300 peak was left-lateralised by verbal perceptual form, however this effect was interpreted cautiously due its origins in a complex interaction involving an old/new effect. Verbal memory did not show expected left-lateralisation. The main findings of this study concerned the N170 peak that showed right-lateralisation to spatial memory demands and spatial perceptual processing. The outcomes support previous findings of an association between right-lateralisation and spatial processing and additionally suggest that spatial memory tasks show right-lateralisation due to separable perceptual- and memory-related components.

1. Introduction

Classic studies on the type of memory deficits that are observed after unilateral temporal lobe resection led to the theory of material specificity: that the medial temporal lobe in the left hemisphere mediates memory for verbal material and its right hemisphere counterpart mediates memory for nonverbal material, assuming left hemisphere language dominance (Blakemore & Falconer, 1967; Kimura, 1963; Milner, 1970). Subsequent studies of unilateral temporal lobe epilepsy patients before and after temporal lobectomy reliably support the material specificity account for the effects of left-sided damage on verbal memory (e.g., Alpherts et al., 2006; Ojemann & Dodrill, 1985), however a correlation between right temporal lobe damage and nonverbal memory impairment has not been observed consistently (e.g., Vaz, 2004).

On reason for this inconsistency may lie in the frequent use of nonverbal memory tests with abstract design stimuli. The designs are often simple or contain features that are amenable to verbalisation (i.e., verbal encoding), resulting in unwanted involvement of left-hemispheric verbal processes (e.g., Barr, 1997). In contrast to memory for abstract designs, clinical or experimental tests that involve memory for unfamiliar faces or exact spatial information (e.g., position, distance) have shown greater specificity to right temporal lobe damage (Diaz-Asper, Dopkins, Potolicchio, & Caputy, 2006; Hampstead et al., 2010; Kessels, de Haan, Kappelle, & Postma, 2001; Kessels, Postma, de Haan, & Kappelle, 2002; Kessels et al., 2006; Sherman et al., 2011; Vaz, 2004). Studies in neurologically intact subjects have supported these neuropsychological findings, with a meta-analysis of neuroimaging studies showing a specific role of the right hippocampus in the retrieval of navigational information compared with other forms of episodic memory (Kuhn & Gallinat, 2014). Other neuroimaging findings have linked the greater right-lateralisation of highly spatial materials to their greater resistance to verbalisation (Golby et al., 2001). In short, the right-lateralising capacity of nonverbal memory tasks could be improved by requiring participants to remember novel, exact spatial information.

Another important issue relating to interpretation of material effects, particularly when neuroimaging is involved, is the potential role of low-level stimulus characteristics. In the visual modality, the material specificity hypothesis is most commonly tested using printed words as verbal stimuli and images of pictures, faces, or textures as nonverbal stimuli (e.g., Golby et al., 2001; Kelley et al., 1998). However, while the categories of these stimuli are clearly different they also typically differ with respect to low-level stimulus characteristics such as their contrast, colour, size or spatial frequency. For example, words are typically small in size and change in contrast very frequently within this small area of space; that is, they are made up of high spatial frequencies. By comparison, faces are typically presented as larger stimuli and the arrangement of facial features, such as the outline of the head or the exact distance between the eyes, change in contrast less frequently within this area and hence have lower spatial frequency. Therefore, when comparing printed words with faces, both size and spatial frequency are confounded with material type.

These stimulus confounds are very relevant to studies of lateralisation as both larger size and lower spatial frequency have been associated with right-lateralisation of early neural activity within 250 ms after stimulus onset (e.g., Martinez et al., 2001; Sergent, 1982; van der Ham, Postma, & Laeng, 2014). Neuroimaging methods such as PET or fMRI have temporal resolutions of 5 seconds or lower, which is not sufficiently sensitive to separate these early lateralised effects from later neural activity related to task performance. To completely rule out the effects of size and spatial frequency in nonverbal memory tasks, the use of methods with higher temporal resolution is required to measure the lateralisation of neural activity, such as electroencephalography (EEG), along with an appropriate design to control the effects of size and spatial frequency.

In line with this approach, the current study asked 20 healthy adults to learn four types of verbal and spatial stimuli while the lateralisation of brain activity was measured using EEG. For each type of material to be remembered (verbal: letter triplets, spatial: spatial positions), the materials were presented in two types of visual forms. For “standard” stimulus

forms, the form of the stimulus was consistent with that usually expected with that type of material: the stimuli in the verbal memory task were letter strings arranged horizontally like a word (i.e., pronounceable CVCs or non-pronounceable CCCs that could not be rearranged to form a real word), and the stimuli in the spatial memory task were spatially arranged nonsense symbols (made of letters that were fragmented then rearranged). In contrast to the standard forms, "hybrid" stimulus forms were letter triplets (again, pronounceable CVCs or non-pronounceable CCCs) of which each individual letter was distributed in space, and hence consisted of both verbal and spatial elements. Hereafter the four conditions are denoted firstly by the type of material to-be-remembered and secondly by the type of stimulus form, separated by a hyphen as follows: 1) verbal-standard, 2) spatial-standard, 3) verbal-hybrid, and 4) spatial-hybrid. See Figure 1(a) for a depiction of these stimuli.

The "pure" effect of material-specific memory was tested by comparing verbal-hybrid to spatial-hybrid as these tasks were perceptually equivalent. The effect of verbal perceptual processing was tested by comparing the two spatial memory tasks as they only differed by the additional letters in the spatial-hybrid task (which had verbal-spatial stimulus form) versus the spatial-standard task (which only had spatial stimulus form). Conversely, the effect of spatial perceptual processing was tested via comparing the two verbal memory tasks as they only differed by the additional spatial stimulus elements in the verbal-hybrid task (letters were spatially distributed) versus the verbal-standard task (letters were in string form). Using this method ensured no overlap between memory-related and stimulus-related lateralisation effects, as there was an inverse correlation between the type of memory being tested and the type of perceptual processing compared. Following the four memory tasks, participants performed a rating task to report if they used verbal labels to help them remember the items, what the labels were, and how frequently they were used. The ratings were used to determine if the verbal memory tasks had a higher degree of verbalisation than the spatial memory tasks, as expected, and whether any difference in verbalisation correlated with the degree of lateralisation.

We measured hemispheric lateralisation due to these manipulations using event-related potentials (ERPs) during memory testing at parietal scalp locations. Based on previous research, we were interested in ERP peaks that appear during two time windows of theoretical interest from approximately 100 to 400 ms post-stimulus. The N170 is maximal from 140 to 230 ms and shows perception-related hemispheric lateralisation for visual stimuli (left: words; right: pictures, faces, or spatial locations; Baker & Holroyd, 2013; Bentin et al., 1999; Cohen et al., 2000; Curran & Dien, 2003; Maillard et al., 2011; Martinez, Di Russo, Anllo-Vento, & Hillyard, 2001). The second peak of interest, the P300 (300 to 500 ms, also termed 'P3b') is involved with attentional processes related to memory encoding and has also been associated with novelty-related changes originating from the hippocampus (Azizian & Polich, 2007; Friedman, Cycowicz, & Gaeta, 2001; Polich, 2007; Shucard, Tekok-Kilic, Shiels, & Shucard, 2009).

In summary, we measured ERPs in the parietal region to investigate the relative effects of memory task (verbal, spatial) and perceptual processing of stimuli (verbal, spatial) on lateralisation during recognition memory. We predicted relative left hemispheric lateralisation for verbal memory and relative right hemispheric lateralisation for nonverbal memory, whether stimulus forms were controlled or not. We also predicted left-lateralisation for verbal perceptual processing and right-lateralisation for spatial perceptual processing, given that the memory task was controlled in both cases.

2. Materials and Methods

2.1 Participants

Twenty students (mean age = 24.20 years, *SD* = 4.82, range 18 to 33; eleven males) were paid to participate in the experiment. Data from eight additional participants were excluded prior to analysis due to significant electroencephalography (EEG) artefacts (i.e., more than 40% of epochs rejected). All participants reported normal or corrected-to-normal vision and were right-handed according to the Edinburgh Handedness Inventory (*M* = 88.67, *SD* = 13.91, range 66 to 100). The experimental methods were approved by the Macquarie

University Human Research Ethics Committee in accordance with the Declaration of Helsinki. Informed consent was obtained from all participants.

2.2 Apparatus

Testing occurred in a dimly lit room, with participants sitting 60 cm away from an 18" Sony Trinitron CRT monitor (resolution 1024 x 768 pixels, 32 bit, 96 dpi, 100 Hz refresh rate) showing a light grey background colour. Task instructions for both conditions were displayed onscreen. Stimuli were controlled using Presentation (Neurobehavioral Systems Inc, Version 10.3) and EEG data were recorded with NeuroScan Synamps2 software. Participants responded with a Cedrus® RB830 button box, pressing one of two buttons that were positioned to the immediate left and right of the box's midline.

2.3 Stimuli and procedure

See Figure 1(a) for examples of the learned target stimuli, correct recognition stimuli, and incorrect foils for all four stimulus types. The memory tasks involved six Encoding blocks each followed by a Recognition block as shown in Figure 1(d). During Encoding blocks, participants learned the Target stimuli while Recognition blocks involved discriminating between Correct (equivalent to Target) and Foil (incorrect) stimuli (i.e., old/new judgements).

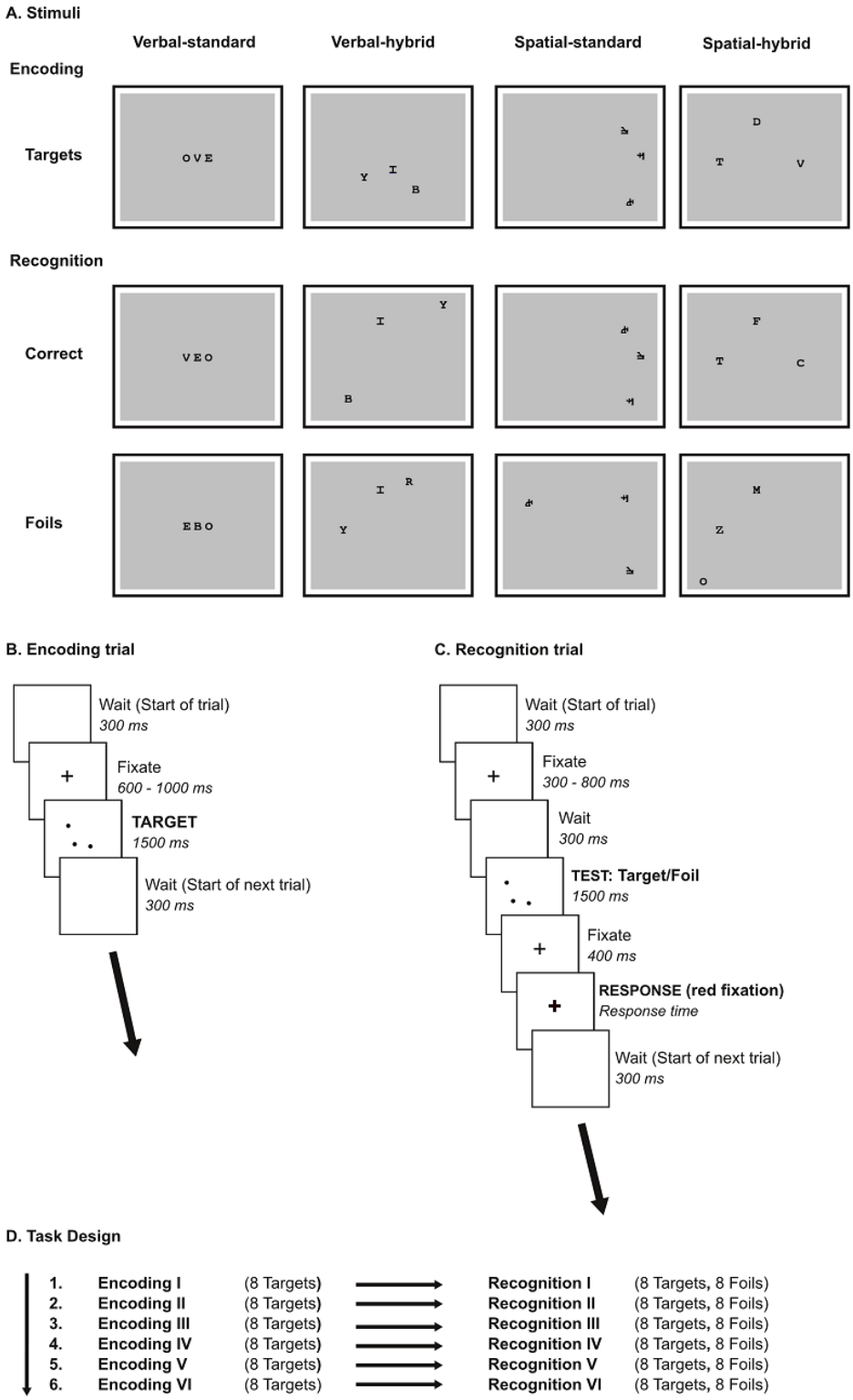

Fig 1. Experimental design. (A) Experimental stimuli - examples of targets and related foils for both material types. (B) Procedure, Encoding phase - target stimulus presentation preceded by interval of randomised duration; (C) Procedure, Recognition phase - test stimulus presentation (intermixed sequence of targets and foils) preceded by interval of randomised duration and followed by response screen. (D) Task Phases 1 to 6 – sequence of phases (Encoding followed by Recognition within each phase) including number of targets and foils per phase.

2.3.1 *Verbal-standard stimuli*

Target stimuli for the six Encoding blocks of the verbal-standard condition were a set of eight letter triplets (i.e., *G-M-T*, *E-O-V*, *A-X-Z*, *D-I-U*, *C-S-Y*, *F-K-L*, *B-J-N*, *H-P-R*). The triplets were chosen so that no mental rearrangement of the letters could form a real word. Across the six encoding blocks the letters of each triplet were pre-randomised to have different orders within the string (e.g., *G-M-T*, *G-T-M*, *M-G-T, M-T-G, T-G-M,* or *T-M-G* for the Target *G-M-T*) to prevent the formation of letter-position associations. Twenty-four letters of the alphabet were used with no letters repeated within the set. Letters were capitalised, modified from Courier New font to each fit a square space subtending 0.53^0 visual angle vertically and horizontally. Triplets were placed at the centre of the screen, with each letter separated by 0.29^0 of visual angle.

Stimuli for the six Recognition blocks were comprised of Correct stimuli that corresponded to re-presented Target stimuli, and six unique Foil items (one for each Recognition block) per Target (48 in total). Foil items were created for each Target by varying one letter of the Target (e.g., *D-M-T*, *G-M-R*, *G-T-U, J-M-T, G-N-T*, and *H-M-T* for the Target *G-M-T)*. Both Correct and Foil stimuli used the same set of 24 letters as for Target stimuli. There were no restrictions on whether foils could be phonologically, orthographically or visually confusable with their respective Targets. As for the set of Target stimuli, for Correct and Foil the order of the letters within each triplet was pre-randomised (e.g., *MGT, GTM, MTG, MTG, TMG, MTG* for Correct stimuli, and *TMD*, *RMG, UTG, TMJ, GTL, MTH* for Foil stimuli). The pre-randomisation of letters was fixed for all stimulus sets (Target, Correct, Foil) so that each participant experienced exactly the same stimuli across the task.

2.3.2 *Spatial-standard stimuli*

Each of the eight Target stimuli in the spatial-standard condition consisted of three spatially distributed positions marked by symbols as shown in Figure 1(a). Each Target stimulus was formed by selection of three positions from an irregular, asymmetric array of

twenty-four positions within a maximum two-dimensional range of 11.23^0 x 9.31^0 visual angle, centred on the screen without a grid or outer boundary. The positions were distributed approximately evenly across and within each quadrant of this range. Adjacent positions were separated by a minimum of 1.71^0 visual angle between the nearest outer edges of adjacent letters (i.e., designed to be greater than twice the width/height of a symbol to reduce perceptual grouping). Within the set of Target stimuli, all twenty-four positions were exhausted per set (i.e., no position was used twice), analogously to the method used for the verbal-standard stimuli.

The irregular design of the positional array meant that no pairs of positions could be completely aligned along any horizontal or vertical axis, and no triplet of positions could be aligned along a diagonal axis. In addition, no stimuli could "point" directly toward a corner, and no array configuration (i.e., the specific combination of angles between letters) could be exactly repeated in a transposed or rotated form. This particular array, and the restrictions, were applied to discourage verbalisation or perceptual grouping of different positions into one larger position, and instead promote encoding of the exact locations of and distances between the positions.

Three unique symbols were created in order to match this condition with the verbal-standard condition in terms of the variability of the non-mnemonic attribute (i.e., three possible horizontal locations in the case of verbal-standard stimuli, see Section 2.3.1). The symbols were constructed by dividing up the letter stimuli (used for verbal-standard stimuli) into fragments using a graphics editor and then re-pasting them together. This method meant that the average number of black pixels across the set of twenty-four letters (M = 555 pixels/letter, SD = 71.87) was statistically matched to the average for the symbols (M = 553 pixels/letter, SD = 32.36; $t(46) = 0.13$; $p = .90$). The three unique symbols were always used in each stimulus and were randomly pre-assigned to each of the three positions per stimulus, matching the use of letter order in the verbal-standard stimuli.

Spatial-standard stimuli for the Recognition blocks were comprised of six Correct

stimuli per Target per block (48 in total) and six unique Foil items per Target per block (48 in total). Foil items were created for each Target by varying one position of the Target. Correct and Foil stimuli used the same set of 24 positions as Targets, and any position in a Target could be re-used as part of a Foil (as for the letters in the verbal-standard stimuli).

2.3.3 Verbal-hybrid stimuli

For verbal-hybrid stimuli a set of eight, three-letter triplets were created as the set of to-be-remembered Target stimuli (i.e., as for the verbal-standard stimuli). In contrast to verbal-standard stimuli, the letters were not horizontally aligned as a string but distributed in positions within the same array used for spatial-standard stimuli. In addition, Target stimuli (and Correct and Foil stimuli accordingly) were composed of different combinations of the same 24 letters used for verbal-standard stimuli. In this condition the relative position of the letters within the array was pre-randomised in order to prevent letter-position associations (i.e., corresponding to the pre-randomisation of the letter order in the strings in the verbal-standard condition). Otherwise the stimuli, foil creation, and task conditions were identical to verbal-standard stimuli.

2.3.4 Spatial-hybrid stimuli

For spatial-hybrid Target stimuli, the set of positions was fixed across blocks while the letters were pre-randomised (i.e., in the opposite manner to the verbal-hybrid stimuli for which the sets of spatial positions were instead pre-randomised). The three-position combinations to be learned were different to those used in the spatial-standard stimuli. Otherwise, all other aspects of the stimulus creation, randomisation and control were the same as for spatial-standard stimuli.

2.3.5 Stimulus control – bigram frequency

Using the Windows program *N-Watch,* letter bigram frequency (e.g. of *G-M* combination within *G-M-T*) was statistically controlled between verbal-standard, verbal-hybrid, and spatial-hybrid stimuli and also between the Target, Correct, and Foil stimuli

within each stimulus type. Trigram frequency (e.g., *G-M-T*) was always zero as none of the triplets could be arranged to spell real words.

2.3.6 Stimulus control – spatial area

Foil items for spatial-standard and spatial-hybrid stimuli were created to be sufficiently distinguishable from targets. In addition, the spatial area subtended by sets of array positions was statistically controlled between spatial-standard, spatial-hybrid, and verbal-hybrid stimuli. Area (A) was calculated within the triangle created by the lines connecting the centres of each position using the formula for a scalene triangle: $A^2 = s.(s - a).(s - b).(s - c)$, where $s = (a + b + c)/2$. Area was chosen as an efficient summary measure that captures many spatial attributes simultaneously such as total size and horizontal/vertical distance.

2.4 Recognition memory task design

The format of the memory task, depicted in Figure 1(b, c), was equivalent for all four stimulus types and involved six phases, each of which consisted of i) an Encoding block (Targets) followed by ii) a Recognition block (Correct and Foils). In each of the six Encoding blocks, participants were instructed to learn the eight Target stimuli, with no instructions to categorise or label the stimuli. Target stimuli were presented sequentially in pseudorandom order. The same eight Encoding stimuli were shown during each of the six Encoding blocks, with constant memory-related attributes and pre-randomised stimulus-related attributes as described in Sections 2.3.1 to 2.3.4. Each Encoding block was followed by a Recognition block in which each Target stimulus was presented intermixed with eight Foil stimuli in a pseudorandom order.

For each Recognition block, participants pressed one button on a button box to indicate a match to a Target stimulus (“yes—seen before”) and a second button to indicate a new item (“no—unseen”). To account for any response-hand-related hemispheric lateralisation in ERP peaks, response instructions were counterbalanced between participants so that half were instructed to press the right button for “yes” and the left for “no” for both

tasks, and response instructions were reversed for the other half of the sample. Stimuli were always presented for 1500 ms. To enhance sustained attention to the task, the duration of pre- and post-stimulus intervals was jittered randomly between 600 and 1000 ms during Encoding blocks and 300 to 800 ms during Recognition blocks, as shown in Figure 1(b, c). Participants performed each of the four recognition tasks to completion before commencing a subsequent stimulus type, and the recognition tasks were presented in counterbalanced order between participants such that a verbal condition was always followed by a spatial condition and vice versa.

2.4.1 Verbalisation rating task

Following the four memory tasks involving the four different stimulus sets participants completed a surprise verbalisation rating task on the computer. One task combined the two verbal memory conditions and one combined the two spatial memory conditions. The tasks were administered in the same order that the memory tasks were completed (e.g., verbal rating task administered first if a verbal memory task had been first). Prior to task onset, participants were instructed to rate each stimulus by button press (i.e., "How often did you use a verbal label to help you remember the item during the task", on a scale: "0" ("never or don't remember the item"), "1" ("occasionally"), "2" ("often") and "3" ("always"). For each of the four memory tasks, all eight Learning stimuli (24 total) were presented one at a time (1500 ms duration) in an intermixed, pre-randomised order that was the same for every participant. Following the stimulus, a response screen was presented showing the four rating options and the button press required for each as described above. Although there was no time limit for the response participants were encouraged to respond as quickly as possible. It was heavily emphasised that this was a rating of how often they had used the verbal label *during* the task, rather than a test of their ability to think of appropriate verbal labels following their experience on the task. Following their rating, participants were asked by the experimenter what verbal label(s) they had used, if any. This was repeated for all items, and then followed by the remaining rating task. Response data for this task was saved

by the computer and the spoken responses were transcribed in full by the experimenter.

2.5 EEG recording and offline analysis

EEG was recorded during the Recognition Phase using sintered Ag-AgCl electrodes mounted in an Easy-Cap according to the 10-20 system (FP1, FP2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz, and O2). The ground electrode was positioned between FPz and Fz. Activity from both mastoids was recorded and the left mastoid served as the online reference. Vertical eye movements (VEOG) were measured with electrodes placed above and below the left eye. Horizontal eye movements (HEOG) were measured with electrodes on the outer canthi of each eye. Electrode impedance was kept below 5 kΩ. The signal was amplified 20,000 times (SynAmps2 amplifier, Compumedics Limited), sampled at 500 Hz, low-pass filtered at 100 Hz online and saved to the computer's hard disk.

Offline analysis was conducted using BESA Research software (version 6.0, BESA GMbH, Grafelfing, Germany). First, portions of the EEG containing large movement-related artefacts were manually rejected. The EEG was then set to reference-free and filtered (highpass 0.53Hz, forward, 6 db/octave; lowpass 8Hz, zero phase, 24 db/octave roll-off) for artefact correction, which was carried out using the adaptive method of the automatic artefact correction tool in BESA. This method applied a predefined source model to the data, combining three topographies accounting for EOG activities (HEOG, VEOG, blink) with a set of 12 regional sources modelling the different brain regions. If the EOG signals exceeded set thresholds (HEOG amplitude 150μV, VEOG/Blink threshold 250μV), then the current EEG topography was accumulated and averaged over the whole EEG. The first principle component of this averaged EOG signal served as the artifact topography that was used for artifact correction, which was performed using an adaptive method (see Ille, Berg, & Scherg, 2002, for further details).

The EEG was then divided into 1450 ms epochs with a 200 ms pre-stimulus interval

and 1250 ms post-stimulus interval. These epochs were then re-referenced to the average of the left and right mastoids, band pass filtered (highpass 0.30 Hz, forward phase, 6 dB/octave roll-off; lowpass 40 Hz, zero phase, 24 dB/octave roll-off) and baseline corrected using the mean pre-stimulus amplitude for the epoch. EEG artefacts, including blinks and eye-movements, were rejected using the BESA artefact scan tool, which rejects trials based on abnormally high amplitudes (120 μV), abrupt gradients in amplitude exceeding 75 μV, or unusually low signal (below 0.01 μV). The mean percentage of epochs rejected was low (verbal-standard: 2.86%; verbal-hybrid: 3.86%; spatial-standard: 2.55%; spatial-hybrid: 2.19%). Epochs associated with incorrect responses were also excluded from further analysis (average percentage of trials accepted - verbal-standard: 84.48%; verbal-hybrid: 80.05%; spatial-standard: 73.65%; spatial-hybrid: 75.00%).

2.5.1 ERPs

Accepted epochs were used to create 16 ERPs per participant: four hemispherically lateralised sites (P3, P4, P7, P8) by two to-be-remembered materials (verbal, nonverbal) by two task-irrelevant visual forms (standard, hybrid). Visual inspection of the grand average and individual average waveforms showed there was a positive-going peak from 80 to 120ms (P100), a large negative-going peak (N170) from 140 to 230 ms, and a large positive-going peak from 230 to 380 ms (P300).

The mean amplitude was calculated for each peak and then corrected for the mean amplitude of the previous peak (i.e., corrected N170 = N170- P100; corrected P300 = P300 - N170). These corrections an extra precaution to ensure that any hemispheric differences measured occurred uniquely in the time window of interest, rather than as an artefact of earlier hemispheric differences or an increase in background noise (for more on the general effects of the baseline on mean amplitude measures see e.g., Clayson, Baldwin, & Larson, 2012). Henceforth these corrected mean amplitudes are referred to as N170 and P300. Region-wide measures were then obtained by averaging the corrected mean amplitudes of left parietal (P3 and P7) and right parietal (P4 and P8) sites, resulting in 16 total measures used

for analysis per participant (2 peaks x 2 materials x 2 forms x 2 hemispheres).

2.6 Statistical analysis

2.6.1 Behavioural performance

Mean percentage correct responses to targets and foils were calculated during the Recognition Phase, from which mean percentage correct and sensitivity (*d'*) values for target/foil discrimination were calculated to ensure the different kinds of stimuli in each condition were adequately learned. *d'* is based on z-score transformations and takes into account both hits and false alarms, hence controlling for response biases (McNicol, 1972). Mean response times (latency to respond following response screen) were also calculated for each participant for the four memory tasks. Response times (RTs) were calculated by subtracting the time of response from the onset time of the response screen (see Figure 1), and mean RTs were calculated for each participant. For analysis response times were inverse transformed (i.e, 1/RT) to reduce the impact of outliers.

2.6.2 Verbalisation ratings

Mean verbalisation ratings were calculated for each stimulus type for each participant. After rating data were collected for all participants, the experimenter checked the validity of the verbal labels provided by participants. To be valid as "verbalised," a response had to contain semantic information, such as a real word, the name of a person, place, company, a well-known object or shape, meaningful initials, or an acronym. The response also had to be unique to that item. Examples of valid responses for the two verbal memory conditions include: for *F-A-C* using the word "face"; for *C-S-Y* using "CSI the TV show but with a Y"; or for *R-K-T* a made-up but meaningful label such as "Red Kitten's Telephone". Examples of valid "verbalised" responses for the two spatial memory conditions could include: "person lying on the beach", "right angle triangle on the left", or "equilateral triangle". Responses with no clearly defined strategy (e.g., "I just remembered them"), or that involved memory for superficial physical attributes such as a specific order of letters (with no assigned meaning or

association with a real word) or that were repetitions of earlier responses (e.g., repeating "right angle triangle") were considered as not validly verbalised and the rated verbalisation frequency was re-scored as 0.

2.6.3 ERP hemispheric lateralisation

Using SPSS, the key predictions of material and form effects on hemispheric differences were tested by comparing mean amplitudes using three-way (2 x 2 x 2) repeated measures ANOVA with factors memory (verbal, nonverbal), form (standard, hybrid), and hemisphere (left, right). Separate ANOVAs were run for each peak. We analysed main effects and interactions between these factors as well as planned contrasts. A grand average of Repetition (old – new) was calculated for each peak across stimulus types and analysed with a two-tailed one-sample *t*-test to determine if there was an overall repetition effect (e.g., old > new). Repetition (old – new) was also analysed in a Memory x Form x Hemisphere ANOVA for each peak.

2.6.4 Data treatment, effect size and correction for multiple comparisons

To ensure that analyses were robust to the effect of outliers, extreme values within all ERP, recognition accuracy and response time measures were subjected to a winsorisation procedure where values greater than the 95th or less than the 5th percentiles were adjusted to these cut-off values. Extreme values accounted for less than 5% of the data across variables. Verbalisation ratings were corrected for recognition accuracy (i.e., corrected ratings = ratings/proportion correct) as appropriate to each stimulus type.

Effect size for all ANOVAs was reported as partial eta-squared (η_p^2), the proportion of variance explained controlling for other effects (interpreted as small: .01 to .09, medium: .09 to .25, or large: > .25; Kenny, 1987). Cohen's *d* adjusted for repeated measures (Morris & DeShon, 2002), was reported for tests of simple main effects and appraised according to the review of Lipsey and Wilson (2001; i.e., small: < 0.3, medium: 0.3 to 0.7, large: > 0.7).

For simple main effects analyses, *p* values were adjusted for multiple comparisons

(reported as p_p) using a permutation testing procedure designed for repeated measures (10000 permutations, MATLAB function "mult_comp_perm_t1" by Groppe, Urbach, & Kutas, 2011). Like Bonferroni correction, this method adjusts *p* values in a way that controls the family-wise error rate. However, for ERP data the permutation method is more powerful than Bonferroni correction due to high within-subject correlations between sites and conditions (Blair & Karniski, 1993; Burgess & Gruzelier, 2000; Good, 1994; Manly, 1997).

3. Results

3.1 Behavioural performance

Figure 2 shows learning curves of memory performance across the six learning blocks for verbal-standard, verbal-hybrid, spatial-standard, and spatial-hybrid conditions. Mean recognition accuracy (*d'*) across the six learning trials was significantly higher for verbal material, $M = 2.35$ (mean 86% correct), than spatial material, $M = 1.57$ (77% correct), $p < .001$, $\eta_p^2 = .66$. In contrast, *d'* did not significantly differ between the standard (82%) and hybrid forms (81%), $p = .21$. The Material x Form interaction was not significant, $p = .08$, and planned contrasts showed the material effect (verbal > spatial) was significant for both forms (standard, $p_p < .001$; hybrid, $p_p = .02$) while the effect of form was not significant for either material, p_ps > .28.

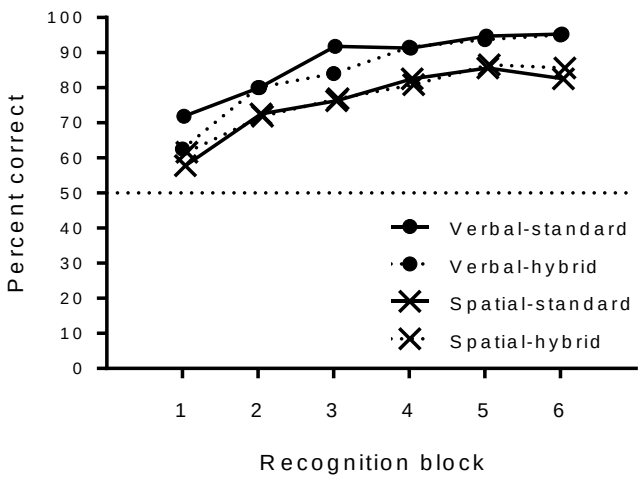

Fig 2. Mean recognition accuracy (percent correct for display purposes) across Recognition blocks 1 to 6 for all stimulus types.

In contrast to the difference in *d'* in favour of verbal memory, response times (RTs) were quicker for spatial memory, M = 459 ms [CI_{95}: 375 592], than verbal memory tasks, M = 532 ms [451 648], $F(1,19) = 6.35$, $p = .02$, $\eta_p^2 = .25$, and for stimuli with standard form, M = 463 ms [379 596], than hybrid form, M = 525 ms [444 643], $F(1,19) = 5.20$, $p = .03$, $\eta_p^2 = .22$. There was also a significant interaction between material and form, $F(1,19) = 5.00$, $p = .21$, $\eta_p^2 = .21$. with contrasts showing RTs for verbal-hybrid stimuli were significantly slower than for spatial-hybrid, $p_p = .03$, or for verbal-standard stimuli, $p_p = .02$. Mean RTs for all stimulus types are shown in Supplementary Table 1. In sum, recognition accuracy was superior for verbal memory versus spatial memory, while perceptual form did not affect accuracy. For response speed spatial memory was superior to verbal memory, while spatial form was related to slower response times compared with no spatial form.

3.2 Correlations between performance and ERP measures

Despite these significant differences in *d'* and RT as a function of memory task and visual form, there were no significant correlations between differences in *d*' as a function of either the type of memory task or the type of visual form and equivalent differences in ERP measures, *p*s > .43. Equivalent comparisons for RT differences also did not show any significant correlations, *p*s >.17. Taken together, the impact of recognition accuracy and response speed on lateralisation of EEG measures was negligible. See Supplementary Tables 2 and 3 in the Appendix for complete inferential statistics for *d'* and RT, respectively.

3.3 Verbalisation ratings

Figure 3(a) shows that verbalisation frequency ratings and recognition accuracy were strongly correlated when averaged across all four stimulus types. This correlation was also significant within verbal-standard, $r(18) = .61$, $p = .004$, verbal-hybrid, $r(18) = .51$, $p = .02$ and spatial-hybrid stimuli, $r(18) = .54$, $p = .01$, but not for spatial-standard stimuli, $r(18) = .36$, $p = .12$.

Figure 3(b) shows mean verbalisation frequency ratings corrected for accuracy (i.e.,

only verbalisation ratings for correct items were included) for all stimulus types. The ANOVA showed the main effect of material (verbal > spatial) on verbalisation frequency was significant, $p < .001$, while the main effect of Form was not significant, $p = .58$. The material x Form interaction was significant, $p = .04$, and explained by a significant effect of material for standard form only (i.e., verbal-standard > spatial-standard, $p_p < .001$). Together these results show that the verbalisation ratings clearly distinguished encoding strategies of verbal and spatial memory tasks, while also suggesting that equalising the perceptual form mildly reduced the difference in the degree of verbalisation between the material types.

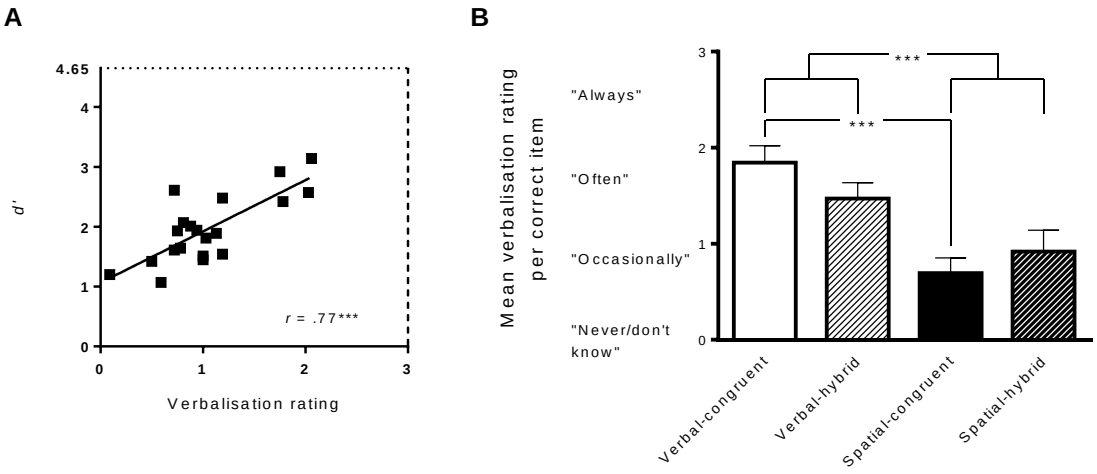

Fig. 3. Verbalisation ratings. (a). Correlation between verbalisation rating and *d'*, both averaged across conditions, with regression line of best fit. Dotted line indicates maximum possible *d'* and dashed line indicates maximum verbalisation frequency rating. (b). Mean verbalisation frequency ratings, corrected for recognition accuracy, for all four stimulus types. *** $p < .001$.

3.4 ERP hemispheric lateralisation: memory, form, and old/new effects

Figure 4 shows grand average ERPs separated by material (verbal, spatial), form (standard, hybrid) and hemisphere (left, right), with peaks labelled. Mean amplitudes of the negative N170 peak was transformed to absolute (i.e., positive) values to simplify reporting of results. Therefore, positive means, *t*, and *d* values always corresponded to differences in the following directions: verbal > spatial (memory), standard > hybrid (form), and left > right (hemisphere), with negative values indicating the respective opposite effects (e.g., spatial >

verbal for memory). For brevity, in-text reporting of contrasts is restricted to comparisons of direct theoretical relevance using p_p values.

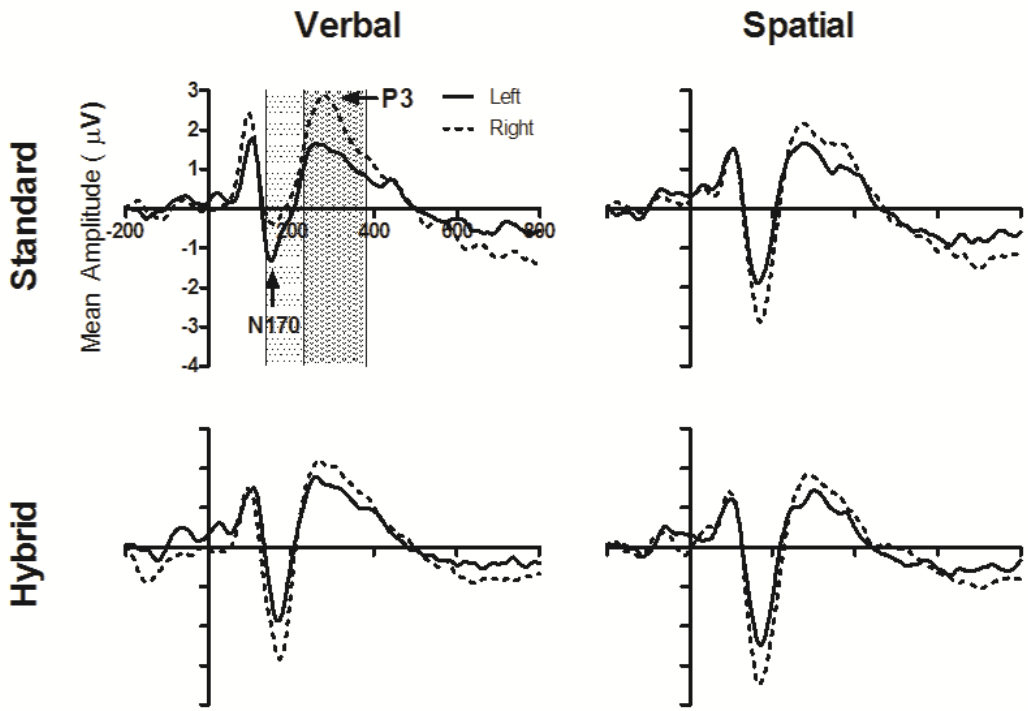

Fig. 4. Grand average ERP waveforms of all four stimulus types with electrodes in the left (average of P3 and P7) and right (average of P4 and P8) parietal sites. Shaded areas show time intervals that mean amplitude was calculated for N170 (140 to 230 ms), and P300 (230 to 380 ms).

3.4.1 N170 mean amplitude

The ANOVA revealed significant main effects of memory (spatial > verbal), $p < .001$, and form (hybrid > standard), $p = .004$, and significant interactions for Memory x Form, $p = .002$, Memory x Hemisphere, $p = .049$, and Form x Hemisphere, $p = .037$. Figure 5 shows the overall effects of memory and form on lateralisation. Planned contrasts showed spatial memory was right-lateralised, $p_p = .049$, consistent with the material hypothesis, but verbal memory was not left-lateralised, $p_p = .59$. The Form x Hemisphere interaction showed that hybrid stimuli produced larger peaks in the right hemisphere than standard stimuli, $p_p = .009$, and Figure 6 shows that the right-lateralising effect of hybrid form was significant for spatial perceptual form, $p_p = .002$ (i.e., left: $p_p = .02$, versus right: $p_p = .004$), but not for verbal perceptual form, $p_p = .99$. This indicates that the main effect of perceptual form was explained

solely by the right-lateralisation of spatial perceptual form.

Contrasts from the three-way interaction showed that spatial memory was right-lateralised relative to verbal memory for hybrid stimuli (left: p_p = .12; right: p_p = .03) but not for standard stimuli (left: p_p = .002; right: p_p = .001). The N170 peak did not show a significant main effect of repetition overall, indicating that the size of the peaks after repeated targets was not larger than after non-repeated foils (i.e., old > new, hereafter referred to as the "old/new effect"), p = .83, nor were there any significant main effects, interactions or planned contrasts from the ANOVA, ps > .17.

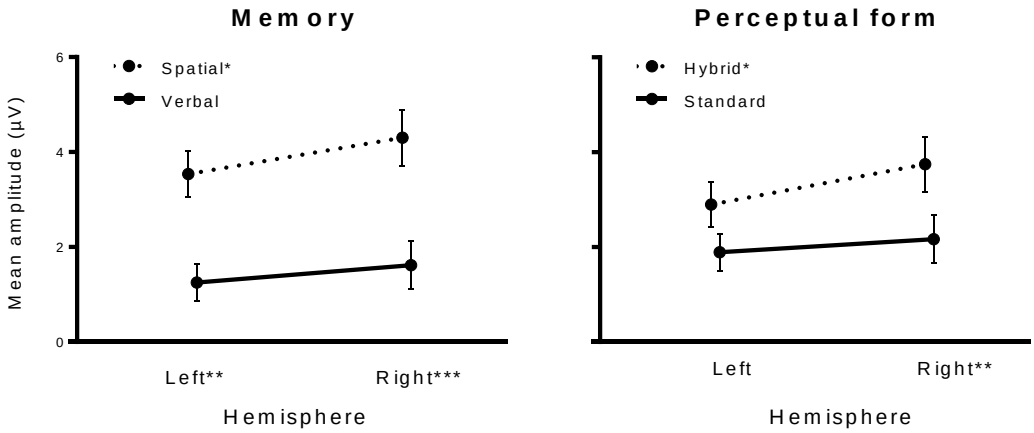

Fig. 5. Mean amplitude of the N170 peak (140 to 230 ms, corrected and standardised, with standard error bars) in both hemispheres. Left: memory effect; Right: perceptual form effect. Asterisks by x-axis labels refer to significant contrasts (i.e., memory: spatial > verbal; perception: hybrid > standard) and those by figure legend labels refer to significant lateralisation (right > left). * p_p < .05, ** p_p < .01, *** p_p < .001.

In summary, the N170 peak showed mild right-lateralisation due to a "pure" effect of spatial memory relative to verbal memory (i.e., when the stimuli were perceptually identical and the only source of difference was the type of to-be-remembered material), but this material-specific lateralisation effect was not significant when stimuli were in "standard" form. Spatial perceptual form showed right-lateralisation but verbal perceptual form did not show left-lateralisation. Consistent with expectations, N170 showed no significant old/new effects. Complete inferential statistics for the N170 peak are reported in the Appendix in

Supplementary Tables 4 and 5.

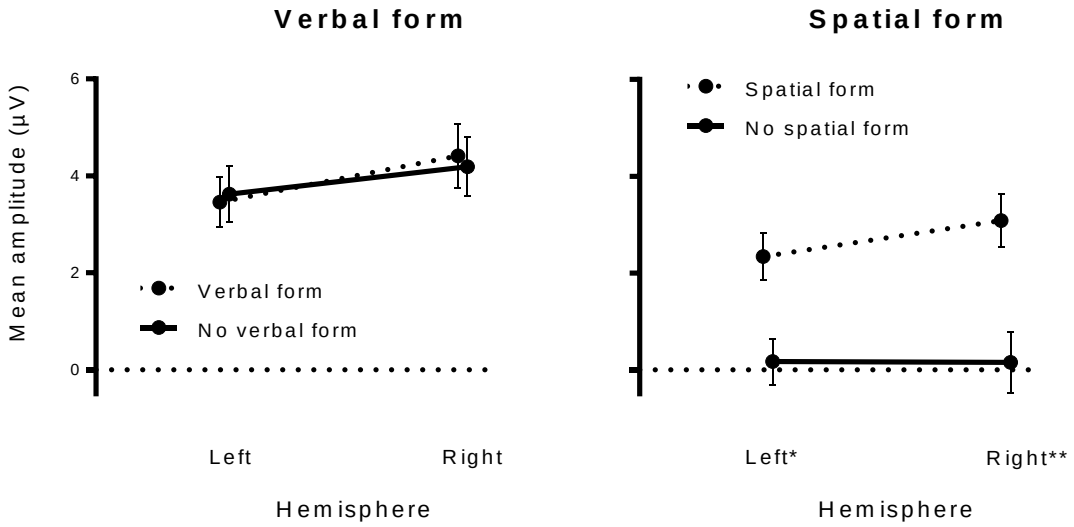

Fig. 6. Mean amplitude of the N170 peak (140 to 230 ms, corrected and standardised, with standard error bars) in both hemispheres. Left: effect of verbal perceptual form (verbal form [spatial-hybrid] versus no verbal form [spatial-standard]). right: effect of spatial perceptual form (spatial form [verbal-hybrid] versus no spatial form [verbal-standard]). Asterisks by x-axis labels refer to significant contrasts (spatial form > No spatial form; by x-axis labels). Hemispheric lateralisation was not significant for any of the four stimulus types within the Material x Form x Hemisphere interaction.

* $p_p < .05$, ** $p_p < .01$.

3.4.2 P300 mean amplitude

The ANOVA revealed significant main effects of Memory (spatial > verbal), $p < .001$, Form (hybrid > standard), $p < .001$, Hemisphere (right > left), $p = .007$, and a significant Memory x Form interaction, $p < .001$. The significant Memory x Form interaction was explained by smaller peaks for verbal-standard stimuli compared with verbal-hybrid stimuli, $p_p < .001$, and spatial-standard stimuli, $p_p < 001$. Planned contrasts revealed the P300 was consistently right-lateralised: verbal memory, $p_p = .048$, spatial memory, $p_p = .03$, hybrid form, $p_p = .03$, standard form, $p_p = .07$ (see Figure 7), with no significant differences in lateralisation due to Memory or Form. However, the pattern of contrasts from the near-significant Memory x Form x Hemisphere effect, $p = .07$, showing that verbal-standard

stimuli represented the only condition not showing a trend to right-lateralisation, p_p = .71 (with p_ps from .10 to .14 for the remaining tasks). While tentative, this suggests that right-lateralisation of the P300 peak was associated with the presence of spatial attributes, whether perceptual-only or related to the memory task.

In contrast to the lack of differences in lateralisation, the P300 peak showed a significant old/new effect, $p < .001$, which was significantly affected by Memory (spatial > verbal), $p = .01$, Form (hybrid > standard), $p = .045$, and a Memory x Form interaction, $p = .02$. Planned contrasts revealed the significant Material x Form interaction was attributable to larger old/new effect for spatial-hybrid stimuli compared with verbal-hybrid stimuli, $p_p = .01$, and spatial-standard stimuli, $p_p = .03$. This interaction effect also showed mild left-lateralisation (see Figure 8). Altogether these results suggest a right-lateralisation of the P300 related to shared spatially-related processing (i.e., regardless of memory and perceptual manipulations), and also suggest that verbal perception contributed to a mild left-lateralisation of the old/new effect. Complete inferential statistics for the P300 peak are reported in Supplementary Tables 6 and 7 (Appendix).

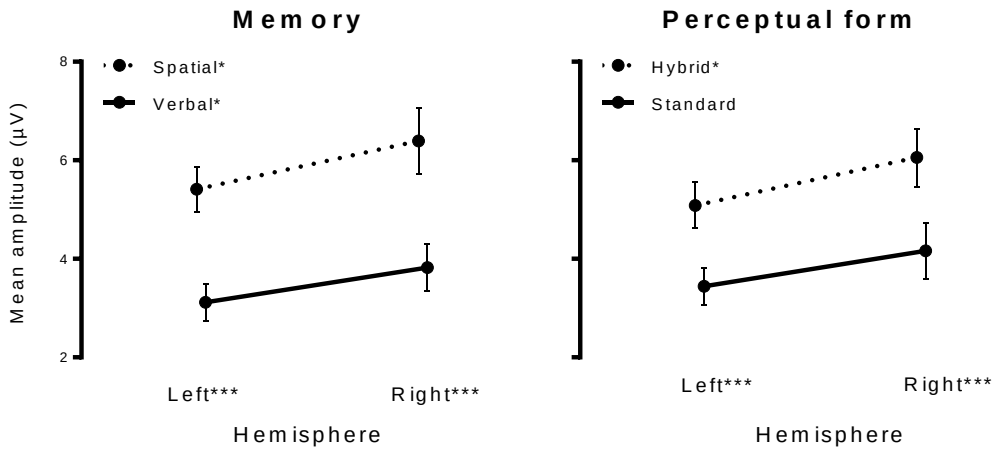

Fig. 7. Mean amplitude of the P300 peak (230 to 380 ms, corrected and standardised, with standard error bars) in both hemispheres. Left: memory effect; Right: perceptual form effect. Asterisks by x-axis labels refer to significant contrasts (verbal perception: hybrid > standard) and asterisks by figure legend labels refer to significant lateralisation (right > left). * $p_p < .05$, *** $p_p < .001$.

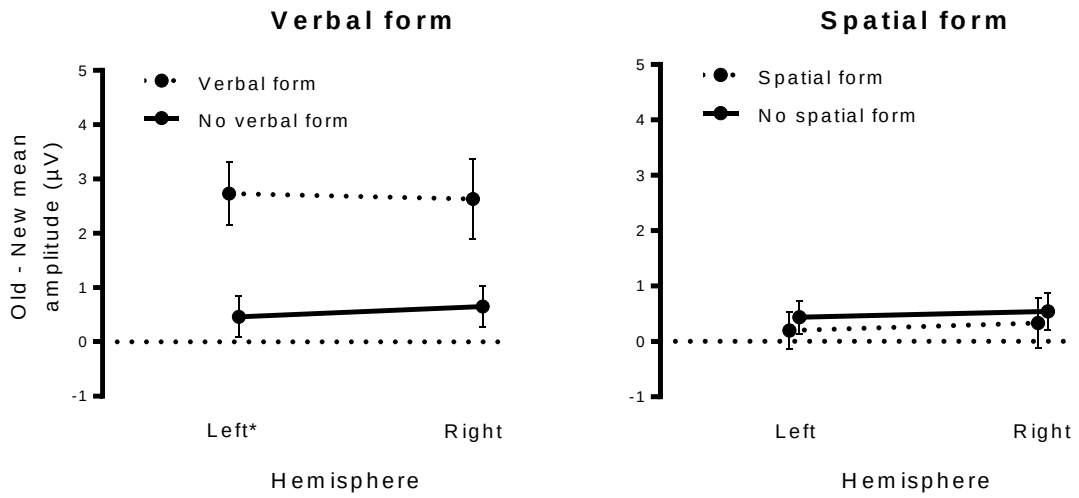

Fig. 8. Mean amplitude of the repetition effect (old – new) for the P300 peak (230 to 380 ms, corrected and standardised, with standard error bars) in both hemispheres. Left: effect of verbal perceptual form (Verbal form [spatial-hybrid] versus No verbal form [spatial-standard]). Right: effect of spatial perceptual form (Spatial form [verbal-hybrid] versus No spatial form [verbal-standard]). Asterisk by x-axis labels refers to significant contrast (verbal perceptual form: verbal-spatial > spatial). * $p_p < .05$.

4. Discussion

4.1 Effects of memory and perceptual form on material specific lateralisation

The aim of this study was to investigate the relative effects of memory task and perceptual form in mediating material specific hemispheric lateralisation. This was conducted by experimentally separating the demands of memory and perceptual form and measuring EEG lateralisation in healthy participants. We predicted that there would be relative material specific hemispheric lateralisation effects associated with both: 1) the memory task and 2) task-irrelevant perceptual form. For the N170 peak there were effects of memory and perceptual form that generally supported our hypotheses, as spatial memory and spatial perceptual form showed right-lateralisation. The P300 peak was associated with an old/new effect that was left-lateralised by the presence of verbal perceptual form. However, verbal memory did not show the expected left-lateralisation. In summary, the main findings of this study concerned the N170 peak, which showed right-lateralisation to spatial memory demands

and spatial perceptual processing, and the P300 peak, which showed left-lateralisation to verbal perceptual processing.

Our findings of an association between spatial memory and the right-lateralised N170 peak complement studies showing an association between right-lateralised N170 and spatial memory performance (Baker & Holroyd, 2013), and between increases in early theta band power (4-7 Hz, within 200 ms after stimulus onset) and successful memory encoding (Klimesch, Doppelmayr, Schmike, & Ripper, 1997). While the N170 has more frequently been associated with perceptual rather than memory-related aspects of material-specific lateralisation (e.g., Beisteiner et al., 1996; Maillard et al., 2011), our pattern of results is inconsistent with a clear temporal distinction between memory and perceptually based lateralisation (cf. Maillard et al., 2011) but rather suggest a high degree of temporal overlap at the early stages of processing. Importantly, the right-lateralisation of the N170 peak did not depend on differences in spatial perceptual form, as the effect was significant whether the perceptual form of the stimuli was matched or not. This is of crucial importance as it suggests that previous findings showing early right-lateralisation to spatial memory were not merely due to task-irrelevant perceptual processing. More broadly, the findings validate previous evidence across neuropsychological, neuroimaging, and ERP methodologies of an association between spatial memory and the right medial temporal lobe (Baker & Holroyd, 2013; Bellgowan, Buffalo, Bodurka, & Martin, 2009; Bohbot et al., 1998; Diaz-Asper, Dopkins, Potolicchio, & Caputy, 2006; Kessels et al., 2002).

Spatial perceptual processing showed right-lateralisation of the N170 peak, consistent with many previous findings with nonverbal materials (e.g., Beisteiner et al., 1996; Maillard et al., 2011) and specifically to low spatial frequency components of stimuli (Martinez et al., 2001). This effect cannot be attributed to spatial memory as the contrast involved a comparison between the two verbal memory tasks. Instead the effect could be due to differences in either size and/or spatial frequency between the word-like verbal-standard stimuli and the spatially arranged verbal-hybrid stimuli. Further investigation is needed to

disentangle their relative effects on the lateralisation of the N170 peak, and many previous findings suggest that both could produce right-lateralisation (see reviews by Dien, 2008, and van der Ham, Postma, & Laeng, 2014).

For verbal memory, there was no outright left-lateralisation but there was a lack of right-lateralisation of the N170 peak in contrast to spatial memory, indirectly consistent with previous findings (e.g., Alpherts et al., 2006; Falk, Cole, & Glosser, 2002; Ojemann & Dodrill, 1985). The lack of outright left-lateralisation of the verbal memory task may be due to the difference in stimuli compared to the majority of previous studies, as the to-be-remembered stimuli were in the form of a combination of letters that could not form a word. In addition, stimulus foils for verbal memory tasks only differed from targets by one letter, and all stimuli were presented with the letters in any order or location. Thus there was no role for left-lateralised word-level orthographic-to-phonological and semantic processes but rather a dependence on processes that have been associated with right-lateralised brain activity such as letter-by-letter reading and spatial localisation and ordering of the letters (e.g., Bouma, 1987; Ellis et al., 2004; Gross, 1972; Pirozzolo & Rayner, 1977).

The experimental manipulation of verbal perceptual form showed left-lateralisation of the old/new effect for the P300 peak. This effect was measured by contrasting the spatial memory tasks, which differed with respect to the presence of letters or meaningless symbols, and this effect cannot be attributed to the size or spatial frequency of the stimuli as these were matched. As such, this result could be interpreted as reflecting a low-level effect of stimulus processing in which letters showed greater left-lateralisation than meaningless symbols, consistent with previous findings (e.g., Cohen et al., 2000; Dehaene, Cohen, Sigman, & Vinckier, 2005). However, while the design of the analysis did not involve a comparison of the spatial-hybrid stimuli to the remaining three conditions, the pattern of data clearly suggest these stimuli were the only type to show a clear old/new effect which was more left-lateralised than the other stimuli (see Figure 8). As a result, the left-lateralisation effect and the old/new effect per se appear to be related to the combination of verbal perceptual form

and spatial memory. We speculate that this may involve reduced use of material-specific processing resources for hybrid stimuli, which is also discussed with respect to verbalisation in Section 4.2 below.

4.2 Verbalisation

Participants rated their verbalisation of stimuli used in the verbal memory tasks as higher than their verbalisation of stimuli used in the spatial memory task, consistent with predictions. This comparison was made, corrected for performance accuracy, as verbal memory tasks were performed more accurately than spatial memory tasks, and as higher verbalisation ratings were strongly correlated with better memory performance, particularly for verbal memory. The finding that peaks for spatial memory tasks were more right-lateralised N170 than for verbal memory tasks is consistent with previous studies indicating a negative correlation between the degree of verbalisability and the degree of involvement of the right medial temporal lobe in the memory tasks (e.g., Golby et al., 2001; Hampstead et al., 2010). This is despite the use of alternative measures of verbalisation such as behavioural dual-task interference in such studies (e.g., Golby et al., 2001; Hampstead et al., 2010; Silverberg & Buchanan, 2005).

Interestingly, despite the overall material-specific pattern, there was no significant difference in verbalisation when stimulus form was equivalent. This suggests that the mere presence of a competing material type, even when completely irrelevant to the task, impacts on the type of encoding strategy employed. Conceivably, this is due to a greater dependence on central, rather than material-specific, working memory resources to help resolve the verbal-spatial conflict (e.g., Morey & Cowan, 2005). However, this lack of difference in verbalisation was not accompanied by a disappearance of material-specific lateralisation of the N170 peak between these tasks (if anything, this was stronger than for tasks without matched stimuli, as reported in Section 3.3.1), suggesting that lateralisation effects were related to material specific long-term memory processes rather than to central, working memory processes.

Altogether it appears that the effect of verbalisation on hemispheric lateralisation is relatively subtle as it was prone to interference by the type of perceptual form and greater verbalisation did not result in outright left-lateralisation of the verbal memory tasks. The findings suggest that the verbalisation rating method has good validity in gauging the relative verbalisability of memory tasks. As this was an exploratory component, further validation is needed to test whether ratings differ between different kinds of nonverbal stimuli such as faces, scenes, and designs (e.g., Golby et al., 2001), to different kinds of spatial memory tasks (e.g., navigational, object-location association; Kessels et al., 2001) and between clinical memory tests with different kinds of material in healthy participants and patients (e.g., designs in the Visual Reproduction subtest of the Wechsler Memory Scale: e.g., Wechsler, 1997; faces in the Warrington Recognition Memory Test: Warrington, 1984).

4.3 Conclusion

The results of this study suggest that processing related to spatial memory demands and to spatial perceptual form have independent effects on material-specific hemispheric lateralisation. Both of these right-lateralising influences affected the N170 peak, suggesting that memory effects may be detected earlier than previously reported. Taken together, the findings of our study suggest that processes related to memory and perceptual form can be separated but both contribute to the material-specific hemispheric lateralisation of memory tasks.

References

Alpherts, W. C. J., Vermeulen, J., van Rijen, P. C., da Silva, F. H. L., van Veelen, C. W. M., & Dutch Collaborative Epilepsy, S. (2006). Verbal memory decline after temporal epilepsy surgery? A 6-year multiple assessments follow-up study. *Neurology, 67*(4), 626-631. doi: 10.1212/01.wnl.0000230139.45304.eb

Azizian, A., & Polich, J. (2007). Evidence for attentional gradient in the serial position memory curve from event-related potentials. *Journal of Cognitive Neuroscience, 19*(12), 2071-2081. doi: 10.1162/jocn.2007.19.12.2071

Baker, T. E., & Holroyd, C. B. (2013). The topographical N170: Electrophysiological evidence of a neural mechanism for human spatial navigation. *Biological Psychology, 94*(1), 90-105.

Barr, W. B. (1997). Examining the right temporal lobe's role in nonverbal memory. *Brain and Cognition, 35*(1), 26-41.

Beisteiner, R., Huter, D., Edward, V., Koch, G., Franzen, P., Egkher, A., . . . Lang, W. (1996). Brain potentials with old/new distinction of non-words and geometric figures. *Electroencephalography and Clinical Neurophysiology, 99*(6), 517-526.

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience, 11*(3), 235-260.

Bellgowan, P. S. F., Buffalo, E. A., Bodurka, J., & Martin, A. (2009). Lateralized spatial and object memory encoding in entorhinal and perirhinal cortices. *Learning & Memory, 16*(7), 433-438. doi: 10.1101/lm.1357309

Blair, R. C., & Karniski, W. (1993). An alternative method for significance testing of waveform difference potentials. *Psychophysiology, 30*(5), 518-524.

Blakemore, C. B., & Falconer, M. A. (1967). Long-term effects of anterior temporal lobectomy on certain cognitive functions. *Journal of Neurology, Neurosurgery, and Psychiatry, 30*(4), 364-367.

Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia, 36*(11), 1217-1238. doi: 10.1016/s0028-3932(97)00161-9

Bouma, A. (1987). Effects of concurrent spatial and verbal memory loads on serial position functions of laterally presented letter strings. *Brain and Cognition, 6*(3), 295-320. doi:10.1016/0278-2626(87)90128-x

Brazdil, M., Roman, R., Daniel, P., & Rektor, I. (2003). Intracerebral somatosensory event-related potentials: effect of response type (button pressing versus mental counting) on P3-like potentials within the human brain. *Clinical Neurophysiology, 114*(8), 1489-1496. doi: 10.1016/s1388-2457(03)00135-4

Burgess, A. P., & Gruzelier, J. H. (2000). Short duration power changes in the EEG during recognition memory for words and faces. *Psychophysiology, 37*(5), 596-606.

Clayson, P. E., Baldwin, S. A., & Larson, M. J. (2013). How does noise affect amplitude and latency measurement of event-related potentials (ERPs)? A methodological critique and simulation study. *Psychophysiology, 50*(2), 174-186.

Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, 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*, 291-307.

Curran, T., & Dien, J. (2003). Differentiating amodal familiarity from modality-specific memory processes: An ERP study. *Psychophysiology, 40*(6), 979-988.

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: a proposal. *Trends in Cognitive Sciences, 9*(7), 335-341.

Diaz-Asper, C. M., Dopkins, S., Potolicchio, S. J., & Caputy, A. (2006). Spatial memory following temporal lobe resection. *Journal of Clinical and Experimental Neuropsychology, 28*(8), 1462-1481. doi: 10.1080/13803390500434359

Dien, J. (2008). Looking both ways through time: the Janus model of lateralized cognition. *Brain and Cognition, 67(*3), 292-323.

Ellis, N. C., Natsume, M., Stavropoulou, K., Hoxhallari, L., Daal, V. H., Polyzoe, N., . . . Petalas, M. (2004). The effects of orthographic depth on learning to read alphabetic, syllabic, and logographic scripts. *Reading Research Quarterly, 39*(4), 438-468.

Falk, M. C., Cole, L. C., & Glosser, G. (2002). Pseudoword and real word memory in unilateral temporal lobe epilepsy. *Journal of Clinical and Experimental Neuropsychology*, *24*(3), 327-334. doi: 10.1076/jcen.24.3.327.979

Friedman, D., Cycowicz, Y. M., & Gaeta, H. (2001). The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience and Biobehavioral Reviews*, *25*(4), 355-373. doi: 10.1016/S0149-7634(01)00019-7

Golby, A. J., Poldrack, R. A., Brewer, J. B., Spencer, D., Desmond, J. E., Aron, A. P., & Gabrieli, J. D. E. (2001). Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. *Brain*, *124*, 1841-1854. doi: 10.1093/brain/124.9.1841

Good, P. (1994). *Permutation Tests: A Practical Guide to Resampling Methods for Testing Hypotheses.* New York: Springer-Verlag.

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

Gross, M. M. (1972). Hemispheric specialization for processing of visually presented verbal and spatial stimuli. *Perception and Psychophysics, 12*(4), 357-363. doi:10.3758/bf03207222

Hampstead, B. M., Lacey, S., Ali, S., Phillips, P. A., Stringer, A. Y., & Sathian, K. (2010). Use of complex three-dimensional objects to assess visuospatial memory in healthy individuals and patients with unilateral amygdalohippocampectomy. *Epilepsy and Behavior, 18*(1-2), 54-60.

Ille, N., Berg, P., & Scherg, M. (2002). Artefact Correction of the Ongoing EEG Using Spatial Filters Based on Artefact and Brain Signal Topographies. *Journal of Clinical Neurophysiology, 19*(2), 113-124.

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., . . . Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron, 20*(5), 927-936. doi: 10.1016/s0896-6273(00)80474-2

Kenny, D. A. (1987). *Statistics for the social and behavioral sciences.* Boston: Little, Brown.

Kessels, R. P. C., de Haan, E. H. F., Kappelle, L. J., & Postma, A. (2001). Varieties of human spatial memory: a meta-analysis on the effects of hippocampal lesions. *Brain Research Reviews, 35*(3), 295-303.

Kessels, R. P. C., Kappelle, L. J., de Haan, E. H. F., & Postma, A. (2002). Lateralization of spatial-memory processes: evidence on spatial span, maze learning, and memory for object locations. *Neuropsychologia, 40*(8), 1465-1473.

Kessels, R. P. C., Nys, G. M. S., Brands, A. M. A., van den Berg, E., & Van Zandvoort, M. J. E. (2006). The modified Location Learning Test: Norms for the assessment of spatial memory function in neuropsychological patients. *Archives of Clinical Neuropsychology, 21*(8), 841-846. doi:10.1016/j.acn.2006.06.015

Kimura, D. (1963). Right temporal-lobe damage. *Archives of Neurology, 8*, 264-271.

Klimesch, W., Doppelmayr, M., Schimke, H., & Ripper, B. (1997). Theta synchronization and alpha desynchronization in a memory task. *Psychophysiology, 34*(2), 169-176. doi: 10.1111/j.1469-8986.1997.tb02128.x

Kuhn, S., & Gallinat, J. (2014). Segregating Cognitive Functions Within Hippocampal Formation: A Quantitative Meta-analysis on Spatial Navigation and Episodic Memory. *Human Brain Mapping, 35*(4), 1129-1142. doi: 10.1002/hbm.22239

Lipsey, M.W. and Wilson, D.B. (2001) *Practical Meta-analysis*. Thousand Oaks, CA: Sage

Maillard, L., Barbeau, E. J., Baumann, C., Koessler, L., Benar, C., Chauvel, P., & Liegeois-Chauvel, C. (2011). From Perception to Recognition Memory: Time Course and Lateralization of Neural Substrates of Word and Abstract Picture Processing. *Journal of Cognitive Neuroscience, 23*(4), 782-800. doi: 10.1162/jocn.2010.21434

Manly, B. F. J. (1997). *Randomization, Bootstrap, and Monte Carlo Methods in Biology* (2nd ed.). London: Chapman and Hall.

Martinez, A., Di Russo, F., Anllo-Vento, L., & Hillyard, S. A. (2001). Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clinical Neurophysiology, 112*(11), 1980-1998.

McNicol, D. (1972). *A primer of signal detection theory*. Sydney: Australasian Publishing Company.

Milner, B. (1970). Memory and the medial temporal regions of the brain. In B. Pribram K.H., D.E. (Ed.), *Biology of Memory*. New York: Academic Press.

Morey, C. C., & Cowan, N. (2005). When do visual and verbal memories conflict? The importance of working-memory load and retrieval. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31*(4), 703.

Ojemann, G. A., & Dodrill, C. B. (1985). Verbal memory deficits after left temporal lobectomy for epilepsy. Mechanism and intraoperative prediction. *Journal of Neurosurgery, 62*(1), 101-107.

Pirozzolo, F. J., & Rayner, K. (1977). Hemispheric specialization in reading and word recognition. *Brain and Language, 4*(2), 248-261. doi:10.1016/0093-934x(77)90021-9

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology, 118*(10), 2128-2148.

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

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation. *Journal of Experimental Psychology-Human Perception and Performance, 8*(2), 253-272. doi:10.1037/0096-1523.8.2.253

Sherman, E. M. S., Wiebe, S., Fay-McClymont, T. B., Tellez-Zenteno, J., Metcalfe, A., Hernandez-Ronquillo, L., . . . Jette, N. (2011). Neuropsychological outcomes after epilepsy surgery: Systematic review and pooled estimates. *Epilepsia, 52*(5), 857-869. doi:10.1111/j.1528-1167.2011.03022.x

Shucard, J. L., Tekok-Kilic, A., Shiels, K., & Shucard, D. W. (2009). Stage and load effects on ERP topography during verbal and spatial working memory. *Brain Research, 1254*, 49-62. doi: 10.1016/j.brainres.2008.11.063

Silverberg, N., & Buchanan, L. (2005). Verbal mediation and memory for novel figural designs: A dual interference study. *Brain and Cognition, 57*(2), 198-209.

van der Ham, I. J. M., Postma, A., & Laeng, B. (2014). Lateralized perception: The role of attention in spatial relation processing. *Neuroscience and Biobehavioral Reviews, 45*, 142-148. doi:10.1016/j.neubiorev.2014.05.006

Vaz, S. A. M. (2004). Nonverbal memory functioning following right anterior temporal lobectomy: a meta-analytic review. *Seizure-European Journal of Epilepsy, 13*(7), 446-452. doi: 10.1016/j.seizure.2003.12.004

Warrington, E. K. (1984). *Recognition Memory Test: Rmt.(Words). Test Booklet 1*: NFER-Nelson Publishing Company.

Wechsler, D. (1997). *Wechsler memory scale (WMS-III)*: Psychological Corporation.

Supplementary Table 1.

Mean response times (ms) for all stimulus types

Memory	Form	Memory*Form	*M*	CI_{low}	CI_{upp}
Verbal			532	648	451
Spatial			459	592	375
	Standard		463	596	379
	Hybrid		525	643	444
		Verbal-standard	476	599	395
		Verbal-hybrid	602	732	512
		Spatial-standard	451	600	362
		Spatial-hybrid	466	596	383

Supplementary Table 2

Correlations between differences in *d'* and differences in *ERP* measures, for Memory and Form comparisons.

Difference	ERP measure	*r*	CI_{low}	CI_{upp}	*p*
Mem(Std)	N170 – L	.01	-.47	.47	.98
Mem(Std)	N170 – R	.01	-.53	.47	.96
Mem(Std)	P300 – L	-.13	-.52	.23	.57
Mem(Std)	P300 – R	-.13	-.53	.27	.59
Mem(Hyb)	N170 – L	-.02	-.38	.34	.94
Mem(Hyb)	N170 – R	-.02	-.38	.30	.93
Mem(Hyb)	P300 – L	-.11	-.46	.24	.65
Mem(Hyb)	P300 – R	-.08	-.46	.31	.73
Frm(Ver)	N170 – L	.13	-.26	.54	.58
Frm(Ver)	N170 – R	.16	-.30	.58	.50
Frm(Ver)	P300 – L	.10	-.39	.57	.69
Frm(Ver)	P300 – R	.17	-.34	.64	.47
Frm(Non)	N170 – L	.15	-.32	.61	.53
Frm(Non)	N170 – R	.15	-.34	.60	.54
Frm(Non)	P300 – L	-.11	-.51	.38	.64
Frm(Non)	P300 – R	-.32	-.58	.06	.17

Mem = Memory (Verbal - Nonverbal); Frm = Form (Standard - Hybrid);

Ver = Verbal; Non = Nonverbal; L = Left; R = Right; Std = Standard; Hyb = Hybrid;

r = correlation coefficient;

CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval (1000x bootstrapped);

p_p = permutation significance test

Supplementary Table 3

Correlations between differences in *RT* and differences in *ERP* measures, for Memory and Form comparisons.

Difference	ERP measure	*r*	CI_{low}	CI_{upp}	*p*
Mem(Std)	N170 – L	-.21	-.81	.27	.37
Mem(Std)	N170 – R	-.10	-.76	.44	.67

Mem(Std)	P300 – L	.00	-.75	.64	.99
Mem(Std)	P300 – R	.25	-.54	.81	.28
Mem(Hyb)	N170 – L	-.08	-.61	.41	.72
Mem(Hyb)	N170 – R	.03	-.54	.46	.90
Mem(Hyb)	P300 – L	-.04	-.47	.47	.86
Mem(Hyb)	P300 – R	-.01	-.43	.42	.95
Frm(Ver)	N170 – L	.03	-.51	.54	.89
Frm(Ver)	N170 – R	.01	-.54	.54	.95
Frm(Ver)	P300 – L	-.07	-.61	.48	.77
Frm(Ver)	P300 – R	-.06	-.65	.50	.82
Frm(Non)	N170 – L	.15	-.28	.58	.53
Frm(Non)	N170 – R	.15	-.29	.60	.54
Frm(Non)	P300 – L	-.11	-.50	.37	.64
Frm(Non)	P300 – R	-.32	-.59	.09	.17

Mem = Memory (Verbal - Nonverbal); Frm = Form (Standard - Hybrid);

Ver = Verbal; Non = Nonverbal; L = Left; R = Right; Std = Standard; Hyb = Hybrid;

r = correlation coefficient;

CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval (1000x bootstrapped);

p_p = permutation significance test

Supplementary Table 4a.

Descriptive and test statistics for N170 mean amplitude

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			1.44	0.55	2.32
	Spa			3.92	2.83	5.01
Frm		Std		2.03	1.13	2.93
		Hyb		3.32	2.28	4.37
Hem			L	2.40	1.59	3.20
			R	2.96	1.91	4.01
Mem * Frm	Ver	Std		0.16	-0.96	1.28
		Hyb		2.71	1.68	3.75
	Spa	Std		3.91	2.72	5.10
		Hyb		3.94	2.74	5.13
Mem * Hem	Ver		L	1.26	0.44	2.07
			R	1.62	0.57	2.67
	Spa		L	3.54	2.52	4.56
			R	4.30	3.07	5.53
Frm * Hem		Std	L	1.90	1.08	2.71
			R	2.17	1.10	3.24
		Hyb	L	2.90	1.92	3.88
			R	3.75	2.54	4.96
Mem * Frm * Hem	Ver	Std	L	0.17	-0.83	1.16
			R	0.15	-1.18	1.48
		Hyb	L	2.34	1.31	3.38
			R	3.09	1.95	4.23
	Spa	Std	L	3.62	2.42	4.83
			R	4.19	2.92	5.46
		Hyb	L	3.46	2.37	4.54
			R	4.41	3.03	5.80

4b.

ANOVA Factor	$F(1,19)$	p	η_p^2

Mem	34.22	<.001	.64
Frm	11.05	.004	.37
Hem	4.35	.051	.19
Mem * Frm	13.08	.002	.41
Mem * Hem	4.41	.049	.19
Frm * Hem	5.04	.037	.21
Mem * Frm * Hem	0.69	.416	.04

4c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mem * Frm	Std	Mem	2.73	-5.45	<.001	0.22	-1.22
	Hyb	Mem	2.73	-3.37	.013	0.78	-0.77
	Ver	Frm	2.73	-4.36	.002	0.35	-0.98
	Spa	Frm	2.73	-0.06	.999	0.69	-0.01
		Mem * Frm	2.73	-3.62	.008	0.23	-0.87
Mem * Hem	L	Mem	2.77	-5.31	.001	0.54	-1.21
	R	Mem	2.77	-6.10	<.001	0.68	-1.39
	Ver	Hem	2.77	-1.22	.591	0.81	-0.29
	Spa	Hem	2.77	-2.78	.049	0.89	-0.67
		Mem * Hem	2.77	2.10	.168	0.91	0.47
Frm * Hem	L	Frm	2.77	-2.62	.068	0.61	-0.60
	R	Frm	2.77	-3.64	.009	0.69	-0.82
	Std	Hem	2.77	-0.94	.774	0.83	-0.23
	Hyb	Hem	2.77	-2.78	.049	0.85	-0.66
		Frm * Hem	2.77	2.24	.138	0.81	0.51
Mem *Frm * Hem	Std / L	Mem	3.29	-4.85	.002	0.09	-1.09
	Std / R	Mem	3.29	-5.75	.001	0.36	-1.29
	Hyb / L	Mem	3.29	-2.82	.119	0.70	-0.63
	Hyb / R	Mem	3.29	-3.59	.027	0.83	-0.84
	Ver / L	Frm	3.29	-3.74	.021	0.28	-0.84
	Ver / R	Frm	3.29	-4.65	.004	0.44	-1.05
	Spa / L	Frm	3.29	0.34	.999	0.59	0.08
	Spa / R	Frm	3.29	-0.48	.999	0.73	-0.11
	Ver / Std	Hem	3.29	0.05	.999	0.85	0.01
	Ver / Hyb	Hem	3.29	-2.28	.302	0.81	-0.52
	Spa / Std	Hem	3.29	-1.74	.612	0.85	-0.39
	Spa / Hyb	Hem	3.29	-2.86	.110	0.87	-0.70
	Std	Mem * Hem	3.29	1.76	.596	0.89	0.39
	Hyb	Mem * Hem	3.29	0.87	.983	0.79	0.19
	Ver	Frm * Hem	3.29	2.45	.228	0.87	0.56
	Spa	Frm * Hem	3.29	1.07	.944	0.72	0.24

Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); Hem = Hemisphere (Left - Right).
Ver = Verbal; Spa = Spatial; Std = Standard; Hyb = Hybrid; L = Left; R = Right.

Supplementary Table 5a.

Descriptive and test statistics for N170 mean amplitude of repetition effects (old - new)

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			-0.14	-0.85	0.57
	Spa			0.21	-0.28	0.70
Frm		Std		0.20	-0.32	0.73
		Hyb		-0.13	-0.67	0.42
Hem			L	0.11	-0.26	0.48
			R	-0.03	-0.46	0.39
Mem * Frm	Ver	Std		0.33	-0.55	1.21

		Hyb		-0.60	-1.66	0.45
	Spa	Std		0.07	-0.81	0.95
		Hyb		0.35	-0.17	0.87
Mem * Hem	Ver		L	-0.22	-0.84	0.40
			R	-0.05	-0.98	0.87
	Spa		L	0.44	0.06	0.81
			R	-0.02	-0.73	0.70
Frm * Hem		Std	L	0.18	-0.37	0.73
			R	0.23	-0.41	0.86
		Hyb	L	0.04	-0.45	0.53
			R	-0.29	-1.01	0.42
Mem * Frm * Hem	Ver	Std	L	0.15	-0.54	0.85
			R	0.51	-0.66	1.67
		Hyb	L	-0.59	-1.63	0.44
			R	-0.61	-1.89	0.67
	Spa	Std	L	0.20	-0.59	1.00
			R	-0.06	-1.22	1.10
		Hyb	L	0.67	0.23	1.12
			R	0.03	-0.71	0.76

5b.

ANOVA Factor	$F(1,19)$	p	η_p^2
Mem	0.54	.473	.03
Frm	0.72	.406	.04
Hem	0.63	.437	.03
Mem * Frm	2.04	.170	.10
Mem * Hem	1.67	.211	.08
Frm * Hem	0.95	.341	.05
Mem * Frm * Hem	0.00	.988	.00

5c.

	M	CI_{low}	CI_{upp}	t	p
Rep (grand average)	0.04	-0.31	0.39	0.22	.830

5d.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mem * Frm	Std	Mem	2.73	0.38	.981	-0.28	0.09
	Hyb	Mem	2.73	-1.59	.378	-0.17	-0.37
	Ver	Frm	2.73	1.48	.443	0.07	0.33
	Spa	Frm	2.73	-0.54	.946	-0.10	-0.12
		Mem * Frm	2.73	1.43	.474	0.11	0.32
Mem * Hem	L	Mem	2.74	-1.97	.201	0.06	-0.45
	R	Mem	2.74	-0.06	.999	-0.48	-0.01
	Ver	Hem	2.74	-0.52	.948	0.69	-0.13
	Spa	Hem	2.74	1.63	.346	0.57	0.42
		Mem * Hem	2.74	-1.29	.531	0.75	-0.39
Frm * Hem	L	Frm	2.72	0.40	.984	0.02	0.09
	R	Frm	2.72	1.03	.750	-0.21	0.23
	Std	Hem	2.72	-0.18	.998	0.58	-0.04
	Hyb	Hem	2.72	1.24	.618	0.62	0.30
		Frm * Hem	2.72	-0.98	.781	0.64	-0.23
Mem *Frm * Hem	Std / L	Mem	3.25	-0.10	.999	0.08	-0.02
	Std / R	Mem	3.25	0.61	.998	-0.40	0.14
	Hyb / L	Mem	3.25	-2.10	.415	-0.34	-0.49
	Hyb / R	Mem	3.25	-0.89	.983	-0.06	-0.20
	Ver / L	Frm	3.25	1.24	.907	-0.03	0.28
	Ver / R	Frm	3.25	1.46	.806	0.14	0.33
	Spa / L	Frm	3.25	-0.94	.976	-0.38	-0.21
	Spa / R	Frm	3.25	-0.13	.999	0.08	-0.03
	Ver / Std	Hem	3.25	-0.96	.973	0.77	-0.26

	Ver / Hyb	Hem	3.25	0.04	.999	0.66	0.01
	Spa / Std	Hem	3.25	0.59	.998	0.61	0.14
	Spa / Hyb	Hem	3.25	2.16	.388	0.52	0.53
	Std	Mem * Hem	3.25	-0.99	.969	0.79	-0.30
	Hyb	Mem * Hem	3.25	-1.09	.950	0.63	-0.25
	Ver	Frm * Hem	3.25	-0.68	.996	0.70	-0.16
	Spa	Frm * Hem	3.25	-0.76	.992	0.62	-0.18

Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); Hem = Hemisphere (Left - Right).
Ver = Verbal; Spa = Spatial; Std = Standard; Hyb = Hybrid; L = Left; R = Right.

Supplementary Table 6a.

Descriptive and test statistics for P300 mean amplitude

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			3.47	2.62	4.32
	Spa			5.90	4.75	7.06
Frm		Std		3.80	2.83	4.77
		Hyb		5.57	4.51	6.63
Hem			L	4.26	3.42	5.11
			R	5.11	3.95	6.27
Mem * Frm	Ver	Std		1.74	0.78	2.70
		Hyb		5.20	4.19	6.22
	Spa	Std		5.87	4.66	7.08
		Hyb		5.94	4.74	7.14
Mem * Hem	Ver		L	3.12	2.33	3.90
			R	3.82	2.83	4.81
	Spa		L	5.41	4.45	6.38
			R	6.39	4.99	7.80
Frm * Hem		Std	L	3.44	2.66	4.23
			R	4.16	2.96	5.36
		Hyb	L	5.08	4.11	6.06
			R	6.06	4.83	7.29
Mem * Frm * Hem	Ver	Std	L	1.55	0.73	2.36
			R	1.93	0.79	3.07
		Hyb	L	4.69	3.69	5.69
			R	5.72	4.56	6.88
	Spa	Std	L	5.34	4.38	6.30
			R	6.39	4.87	7.92
		Hyb	L	5.48	4.41	6.55
			R	6.39	5.00	7.79

6b.

ANOVA Factor	$F(1,19)$	p	η_p^2
Mem	74.46	<.001	.80
Frm	38.22	<.001	.67
Hem	9.32	.007	.33
Mem * Frm	34.71	<.001	.65
Mem * Hem	1.68	.210	.08
Frm * Hem	1.17	.292	.06
Mem * Frm * Hem	3.70	.070	.16

6c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mem * Frm	Std	Mem	2.66	-8.75	<.001	0.60	-2.01
	Hyb	Mem	2.66	-2.30	.101	0.83	-0.53
	Ver	Frm	2.66	-7.26	<.001	0.49	-1.63

	Spa	Frm	2.66	-0.22	.996	0.85	-0.05
		Mem * Frm	2.66	-5.89	<.001	-0.02	-1.34
Mem * Hem	L	Mem	2.70	-9.78	<.001	0.86	-2.34
	R	Mem	2.70	-7.23	<.001	0.86	-1.92
	Ver	Hem	2.70	-2.72	.048	0.84	-0.65
	Spa	Hem	2.70	-2.99	.028	0.90	-0.86
		Mem * Hem	2.70	1.30	.487	0.82	0.35
Frm * Hem	L	Frm	2.75	-6.40	<.001	0.84	-1.53
	R	Frm	2.75	-5.34	<.001	0.81	-1.20
	Std	Hem	2.75	-2.59	.073	0.92	-0.82
	Hyb	Hem	2.75	-3.01	.031	0.84	-0.72
		Frm * Hem	2.75	1.08	.667	0.74	0.26
Mem *Frm * Hem	Std / L	Mem	3.24	-9.38	<.001	0.55	-2.12
	Std / R	Mem	3.24	-7.62	<.001	0.61	-1.77
	Hyb / L	Mem	3.24	-2.39	.234	0.78	-0.54
	Hyb / R	Mem	3.24	-1.95	.459	0.86	-0.46
	Ver / L	Frm	3.24	-7.01	<.001	0.48	-1.59
	Ver / R	Frm	3.24	-6.78	<.001	0.48	-1.52
	Spa / L	Frm	3.24	-0.45	.999	0.81	-0.10
	Spa / R	Frm	3.24	0.00	.999	0.85	0.00
	Ver / Std	Hem	3.24	-1.54	.711	0.91	-0.44
	Ver / Hyb	Hem	3.24	-2.83	.106	0.76	-0.65
	Spa / Std	Hem	3.24	-2.68	.141	0.88	-0.81
	Spa / Hyb	Hem	3.24	-2.87	.099	0.89	-0.73
	Std	Mem * Hem	3.24	1.90	.489	0.81	0.49
	Hyb	Mem * Hem	3.24	-0.54	.999	0.78	-0.12
	Ver	Frm * Hem	3.24	1.90	.491	0.79	0.45
	Spa	Frm * Hem	3.24	-0.49	.999	0.69	-0.11

Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); Hem = Hemisphere (Left - Right).
Ver = Verbal; Spa = Spatial; Std = Standard; Hyb = Hybrid; L = Left; R = Right.

Supplementary Table 7a.

Descriptive and test statistics for P300 mean amplitude of repetition effects (old - new)

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			0.38	-0.10	0.85
	Spa			1.62	0.88	2.37
Frm		Std		0.53	0.07	0.98
		Hyb		1.47	0.74	2.21
Hem			L	0.96	0.55	1.37
			R	1.04	0.62	1.46
Mem * Frm	Ver	Std		0.49	-0.14	1.12
		Hyb		0.27	-0.49	1.03
	Spa	Std		0.56	-0.20	1.31
		Hyb		2.68	1.36	4.00
Mem * Hem	Ver		L	0.32	-0.13	0.76
			R	0.44	-0.13	1.01
	Spa		L	1.60	0.88	2.32
			R	1.64	0.81	2.47
Frm * Hem		Std	L	0.45	-0.01	0.91
			R	0.60	0.11	1.09
		Hyb	L	1.47	0.80	2.13

			R	1.48	0.60	2.37
Mem * Frm * Hem	Ver	Std	L	0.44	-0.19	1.07
			R	0.54	-0.15	1.24
		Hyb	L	0.20	-0.52	0.91
			R	0.33	-0.63	1.30
	Spa	Std	L	0.46	-0.31	1.24
			R	0.65	-0.14	1.44
		Hyb	L	2.73	1.54	3.93
			R	2.63	1.10	4.16

7b.

ANOVA Factor	$F(1,19)$	p	η_p^2
Mem	7.26	.014	.28
Frm	4.63	.045	.20
Hem	0.52	.481	.03
Mem * Frm	6.95	.016	.27
Mem * Hem	0.07	.802	.00
Frm * Hem	0.13	.719	.01
Mem * Frm * Hem	0.39	.538	.02

7c.

	M	CI_{low}	CI_{upp}	t	p
Rep (grand average)	1.00	0.64	1.36	5.26	<.001

7d.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mem * Frm	Std	Mem	2.71	-0.13	.999	-0.17	-0.03
	Hyb	Mem	2.71	-3.21	.014	-0.08	-0.74
	Ver	Frm	2.71	0.46	.964	-0.07	0.10
	Spa	Frm	2.71	-2.87	.034	-0.05	-0.66
		Mem * Frm	2.71	2.64	.056	0.04	0.60
Mem * Hem	L	Mem	2.75	-3.08	.026	-0.07	-0.70
	R	Mem	2.75	-2.20	.144	-0.32	-0.50
	Ver	Hem	2.75	-0.69	.884	0.76	-0.16
	Spa	Hem	2.75	-0.21	.995	0.86	-0.05
		Mem * Hem	2.75	-0.25	.991	0.83	-0.06
Frm * Hem	L	Frm	2.69	-2.65	.054	0.02	-0.60
	R	Frm	2.69	-1.60	.359	-0.36	-0.36
	Std	Hem	2.69	-0.99	.727	0.79	-0.22
	Hyb	Hem	2.69	-0.07	.999	0.79	-0.02
		Frm * Hem	2.69	-0.37	.980	0.77	-0.09
Mem *Frm * Hem	Std / L	Mem	3.25	-0.05	.999	-0.15	-0.01
	Std / R	Mem	3.25	-0.20	.999	-0.13	-0.05
	Hyb / L	Mem	3.25	-3.65	.022	-0.11	-0.84
	Hyb / R	Mem	3.25	-2.62	.173	-0.04	-0.60
	Ver / L	Frm	3.25	0.50	.999	-0.13	0.11
	Ver / R	Frm	3.25	0.36	.999	-0.08	0.08
	Spa / L	Frm	3.25	-3.35	.040	0.01	-0.77
	Spa / R	Frm	3.25	-2.32	.294	-0.09	-0.54
	Ver / Std	Hem	3.25	-0.55	.999	0.82	-0.12
	Ver / Hyb	Hem	3.25	-0.39	.999	0.64	-0.09
	Spa / Std	Hem	3.25	-0.92	.977	0.85	-0.21

Spa / Std	Hem	3.25	0.28	.999	0.87	0.07
Spa / Std	Mem * Hem	3.25	0.31	.999	0.88	0.07
Spa / Std	Mem * Hem	3.25	-0.48	.999	0.82	-0.11
Spa / Std	Frm * Hem	3.25	0.07	.999	0.66	0.02
Spa / Std	Frm * Hem	3.25	-0.68	.996	0.87	-0.17

Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); Hem = Hemisphere (Left - Right).

Ver = Verbal; Spa = Spatial; Std = Standard; Hyb = Hybrid; L = Left; R = Right.

Segue to Chapter 6

In Chapter 5 the effects of memory-related and perceptual processing on lateralisation were compared using event-related potential measures from healthy participants. In Chapter 6, the same effects were explored using measures of EEG power in the theta and alpha frequency bands. As a result, some sections of Chapter 6 are identical to those in Chapter 5, including Sections 2.1 to 2.4 and Section 2.6 of the Materials and Methods, and Section 3.1 of the Results which pertain to behavioural measures of participant accuracy and response time, and Section 3.3 which pertains to the verbalisability ratings.

As discussed earlier in 'Segue to Chapter 4' and in Chapter 4, EEG oscillations index aspects of neural activity that ERPs filter out, including recurrent and reciprocal changes between cortical regions. Event-related EEG is also particularly well-suited to measure longer-lasting cognitive processes (up to many seconds after the stimulus), whilst ERPs predominantly index activity within 0 to 500 ms. For short periods after a stimulus (e.g., 0 to 500 ms), event-related EEG is partially correlated with and partially independent of ERP measures. In sum, EEG is a temporally and qualitatively different measure of neural activity than ERPs that usefully complements ERP measures.

There is a considerable evidence that power in the theta (4 to 7 Hz) and alpha (8 to 13 Hz) EEG rhythms are linked to memory processing. The alpha rhythm has long been known to be involved in visual processing but it has also been linked to a specific "gating" role for sensory information by changing depending on its relevance to a particular task. This general property of alpha power has also been found with respect to memory tasks, and there is also evidence that alpha power shows material-specific hemispheric lateralisation. Taken together, alpha power may be particularly well suited as an added and complementary measure to ERPs to compare the relative material specific lateralisation effects due to the processing of memory versus the processing of perceptual form.

Chapter 6: EEG power shows right hemisphere lateralisation during memory tasks regardless of material type remembered or perceptual processing

Adam Bentvelzen[1,2], Nicholas A. Badcock[1,3], Genevieve McArthur[1,3], & Greg Savage[1,2]

[1] ARC Centre of Excellence in Cognition and its Disorders, Macquarie University, NSW, 2109, Australia;

[2] Department of Psychology, Macquarie University, NSW, 2109, Australia.

[3] Department of Cognitive Science, Macquarie University, NSW, 2109, Australia;

Keywords: memory; material specificity; perceptual form; hemispheric lateralisation; theta; alpha.

Running title: EEG power shows right-lateralisation during memory tasks

Corresponding author: Adam Bentvelzen, ARC Centre of Excellence in Cognition and its Disorders, Department of Cognitive Science, Macquarie University, NSW, 2109, Australia. Phone: +61 2 9850 4127. Email: adam.bentvelzen@students.mq.edu.au

Acknowledgements

This work was funded by an Australian Postgraduate Award (APA) to Adam Bentvelzen and supported by the Australian Research Council Centre of Excellence for Cognition and its Disorders (CE110001021) http://www.ccd.edu.au

Abstract

Material specific hemispheric differences involving the medial temporal region of the brain (verbal: left; nonverbal: right) have been linked to differences in memory processing, regardless of differences in lower-level stimulus attributes. In contrast, alternative accounts of hemispheric lateralisation have emphasised the central importance of lower-level perceptual and attentional processes, such as those related to the spatial frequency of stimuli. Considering that material type and perceptual form are typically confounded between verbal and nonverbal memory tasks, there have been surprisingly few attempts to systematically examine the contribution of perceptual processing to memory-related lateralisation. In addition, little is known of the time-frequency dimensions of such effects, despite the precise temporal resolution of theta (4-7 Hz) and alpha (8-13 Hz) oscillations and their demonstrated involvement in memory-related processing. In the current study, event-related power change in the theta and alpha frequency bands were measured in 20 healthy adults during recognition of novel verbal material (letter triplets) and spatial material (arrays of positions) that differed in task-irrelevant perceptual form (standard: verbal or spatial only; hybrid: verbal-spatial). Results showed that both types of material, whether relevant or irrelevant to the memory task, were associated with right-lateralisation of power in the theta and alpha frequency bands. In contrast, ratings of stimulus verbalisation were sensitive to both the to-be-remembered material type and to task-irrelevant perceptual form. Taken together, the results are interpreted as reflecting an overshadowing of transient material-specific effects in the EEG by general, right-lateralised visual-spatial attention processes that were common to all tasks. Further research is needed to cast light on more precise localisation and functional characteristics of the right-lateralised EEG observed in this study.

1. Introduction

The idea of material specificity has remained the predominant conceptual framework concerning the hemispheric lateralisation of memory function since its inception (Milner, 1968). Material specificity predicts that the medial temporal lobe (MTL) in the left hemisphere mediates memory for verbal material and the right MTL mediates memory for nonverbal material. Reviews of decades of research have revealed a consistent association between left MTL function and verbal memory, however right MTL function has not been associated with nonverbal memory reliably, particularly in the context of clinical assessment of right-sided temporal lobe epilepsy (TLE) patients using neuropsychological memory tests (Lee, Yip, & Jones-Gotman, 2002; Sherman et al., 2011; Vaz, 2004). This inconsistency is likely related to the dependence on visual designs as the to-be-remembered nonverbal material, which are shown to be unreliable predictors of right MTL function (e.g., Naugle, Chelune, Cheek, Luders, & Awad, 1993).

In contrast to memory for designs, there is evidence that experimental memory tasks using precise visual-spatial information, such as exact position and distance, have a superior ability to detect right MTL damage (Diaz-Asper, Dopkins, Potolicchio, & Caputy, 2006; Kessels, Kappelle, de Haan, & Postma, 2002). Memory for metric spatial information may show greater involvement of the right hippocampus than tasks involving associations between visual materials (e.g., objects and locations; Kessels, de Haan, Kappelle, & Postma, 2001). A meta-analysis of neuroimaging findings in healthy participants supports the hypothesis that the right MTL is involved in memory for metric spatial information, such as in navigational tasks (Kuhn & Gallinat, 2014). There is also evidence that the correlation between right MTL function and spatial memory is mediated by right-lateralised processing of lower-level stimulus attributes including spatial perception and attention (e.g., van der Ham, Postma, & Laeng, 2014). In addition, there is evidence that purely spatial materials are more difficult to describe verbally compared to other kinds of nonverbal stimuli such as scenes or faces, resulting in less contamination by left-sided “verbalisation” strategies (Barr, 1997; Hampstead

et al., 2010; Golby et al., 2001). Therefore, the likelihood that a memory task will detect right MTL pathology may be related to a joint and correlated contribution of the type of spatial perceptual processing and resistance to verbalisation.

An overlooked issue in research on material-specific lateralisation is that previous comparisons between material type (e.g., verbal and nonverbal) and between different nonverbal stimuli (e.g., faces, mazes, scenes) typically have not controlled for lower-level stimulus characteristics. For example, printed words are typically small in size, and their high level of detail means they frequently change in contrast within this small area of space; that is, they are comprised of high spatial frequencies. By comparison, a picture of a series of dots marking positions on a map involves less frequent and detailed changes in contrast over a larger area of space, and hence are composed of lower spatial frequencies (Sergent, 1982). Therefore, the dot patterns have lower spatial frequency and larger size than printed words, and material type and stimulus characteristics are confounded. Importantly, these stimulus confounds have both been associated with right-lateralisation of early neural activity within 250 ms after stimulus onset (e.g., Martinez et al., 2001; Sergent, 1982; van der Ham et al., 2014).

Further compounding the issue, many experimental designs use neuroimaging methods (PET, fMRI) for which the temporal resolution is 5 seconds or longer, meaning that rapid stimulus-based lateralisation effects may be obscured by longer-lasting processes of the memory task. By contrast, the use of electroencephalography (EEG) to measure brain activity and an appropriate design in which lower-level attributes are controlled allows for a clearer interpretation of material specific hemispheric lateralisation effects with respect to perceptual and memory-related processing. However, few studies have utilised such an approach for this purpose.

To help fill this gap, the current study asked healthy adults to learn four types of visual stimuli, between which, memory-related and stimulus-related aspects of material (verbal, spatial) were independently manipulated and compared in a subtraction design. For each type

of to-be-remembered material (verbal: letter triplets, spatial: sets of three spatial positions), the stimuli were presented in two visual forms. First, "standard" forms in which there was no conflict between the type of material remembered in the memory task and the task-irrelevant perceptual form (i.e., verbal memory: letters in string form; spatial memory: positions marked by nonsense symbols). Second, "hybrid" forms with equivalent verbal-spatial stimuli (i.e., letters in distributed positions) that induced a conflict between the to-be-remembered material type and the irrelevant material type. We denote the four tasks by their memory demands and then their type of visual form as follows: 1) verbal-standard, 2) verbal-hybrid, 3) spatial-standard, and 4) spatial-hybrid.

The "pure" effect of material-specific memory (i.e., independent of perceptual form) was tested by comparing the verbal-hybrid task to the perceptually equivalent spatial-hybrid task. The independent effect of verbal perceptual processing was tested by comparing the two spatial memory tasks to each other as they only differed by the additional verbal stimulus elements in the spatial-hybrid task. Conversely, the effect of spatial perceptual processing was tested via comparing the two verbal memory tasks as they only differed by the additional spatial stimulus elements in the verbal-hybrid task. Furthermore, using this method ensured no overlap between measurement of the memory-related and perceptual lateralisation effects, as verbal perception was tested during spatial memory tasks and spatial perceptual processing during verbal memory tasks. Following the four memory tasks there was a rating task in which participants reported what verbal labels they used to help them remember the items and how frequently they used these labels. The ratings were used to determine if the expected higher level of verbalisation for the verbal memory tasks correlated with the degree of left-lateralisation.

We measured hemispheric lateralisation during the four memory tasks using event-related theta and alpha power change at parietal scalp locations during memory testing. There is a considerable evidence that power in the theta (4 to 7 Hz) and alpha (8 to 13 Hz) EEG rhythms are linked to memory processing (Dujardin, Bourriez, & Guieu, 1994; Fell et al.,

2011; Guderian & Duzel, 2005; Klimesch, 1999; Klimesch et al., 2005). Episodic encoding success is associated with increased theta activity during the same "early" time period (100 to 250 ms post-stimulus) as the material and modality-specific N170 event-related potential (ERP) peak, suggesting that theta could also show such material specificity (Klimesch, Doppelmayr, Pachinger, & Russegger, 1997; Klimesch, Doppelmayr, Schwaiger, Winkler, & Gruber, 2000; Klimesch, Freunberger, Sauseng, & Gruber, 2008; Klimesch et al., 2001, 2004).

Beyond the well-known role of the alpha rhythm in visual processing (Berger, 1930), recent work suggests that alpha power plays a specific "gating" role for sensory information by decreasing during task-relevant processing and increasing during task-irrelevant processing (Pfurtscheller & da Silva, 1999). This general property of alpha power is found with respect to memory tasks (Klimesch, 1999), with additional evidence that such changes in "late" alpha power (750 to 1250 ms post-stimulus) show material specificity with left-lateralisation during memory for words memory and right-lateralisation during memory for faces (Burgess & Gruzelier, 2000). Taken together, alpha power may be particularly well suited to compare the relative material specific lateralisation effects due to the processing of memory versus processing related to perceptual form.

In summary, we measured event-related theta and alpha power at parietal electrodes to investigate the relative effects of memory-related and perceptual processing of different materials (verbal, spatial) on lateralisation of brain activity. While changes in theta power peak much more quickly after stimulus onset (0 to 500 ms) than do more prolonged changes in alpha power (500 to 1500 ms), we analysed data in both time windows as memory-related effects have been reported in both for each frequency band (Klimesch, Sauseng, & Hanslmayr, 2007; Mitchell, McNaughton, Flanagan, & Kirk, 2008). It was predicted that verbal memory tasks would show left-lateralisation and the spatial memory tasks would show right-lateralisation of theta and alpha power. It was also predicted that theta power would show left-lateralisation for verbal perceptual processing and right-lateralisation for spatial perceptual processing. As alpha power is known to decrease for memory-related processing

and increase for memory-irrelevant processing, it was predicted that alpha power would show a left-lateralised increase for verbal perceptual processing and a right-lateralised increase for spatial perceptual processing.

An additional exploratory hypothesis was that hybrid stimuli, which had conflicting memory and perceptual information affecting opposite hemispheres, would show a larger hemispheric difference in alpha power than standard stimuli. For example, as spatial-hybrid stimuli would show a right-lateralised decrease due to memory, and a left-lateralised *increase* due to verbal perceptual processing, this should result in a larger difference between the hemispheres than for spatial-standard stimuli, which should only show a right-lateralised decrease in alpha power due to the spatial memory task.

2. Materials and Methods

2.1 Participants

Twenty students (mean age = 24.20 years, *SD* = 4.82, range 18 to 33; eleven males) were paid to participate in the experiment. Data from eight additional participants were excluded prior to analysis due to significant electroencephalography (EEG) artefacts (i.e., more than 40% of epochs rejected). All participants reported normal or corrected-to-normal vision and were right-handed according to the Edinburgh Handedness Inventory (*M* = 88.67, *SD* = 13.91, range 66 to 100). The experimental methods were approved by the Macquarie University Human Research Ethics Committee in accordance with the Declaration of Helsinki. Informed consent was obtained from all participants.

2.2 Apparatus

Testing occurred in a dimly lit room, with participants sitting 60 cm away from an 18” Sony Trinitron CRT monitor (resolution 1024 x 768 pixels, 32 bit, 96 dpi, 100 Hz refresh rate) showing a light grey background colour. Task instructions for both conditions were displayed onscreen. Stimuli were controlled using Presentation (Neurobehavioral Systems Inc, Version 10.3) and EEG data were recorded with NeuroScan Synamps2 software. Participants

responded with a Cedrus® RB830 button box, pressing one of two buttons that were positioned to the immediate left and right of the box's midline.

2.3 Stimuli and procedure

See Figure 1(a) for examples of the learned target stimuli, correct recognition stimuli, and incorrect foils for all four stimulus types. The memory tasks involved six Encoding blocks each followed by a Recognition block as shown in Figure 1(d). During Encoding blocks, participants learned the Target stimuli while Recognition blocks involved discriminating between Correct (equivalent to Target) and Foil (incorrect) stimuli (i.e., old/new judgements).

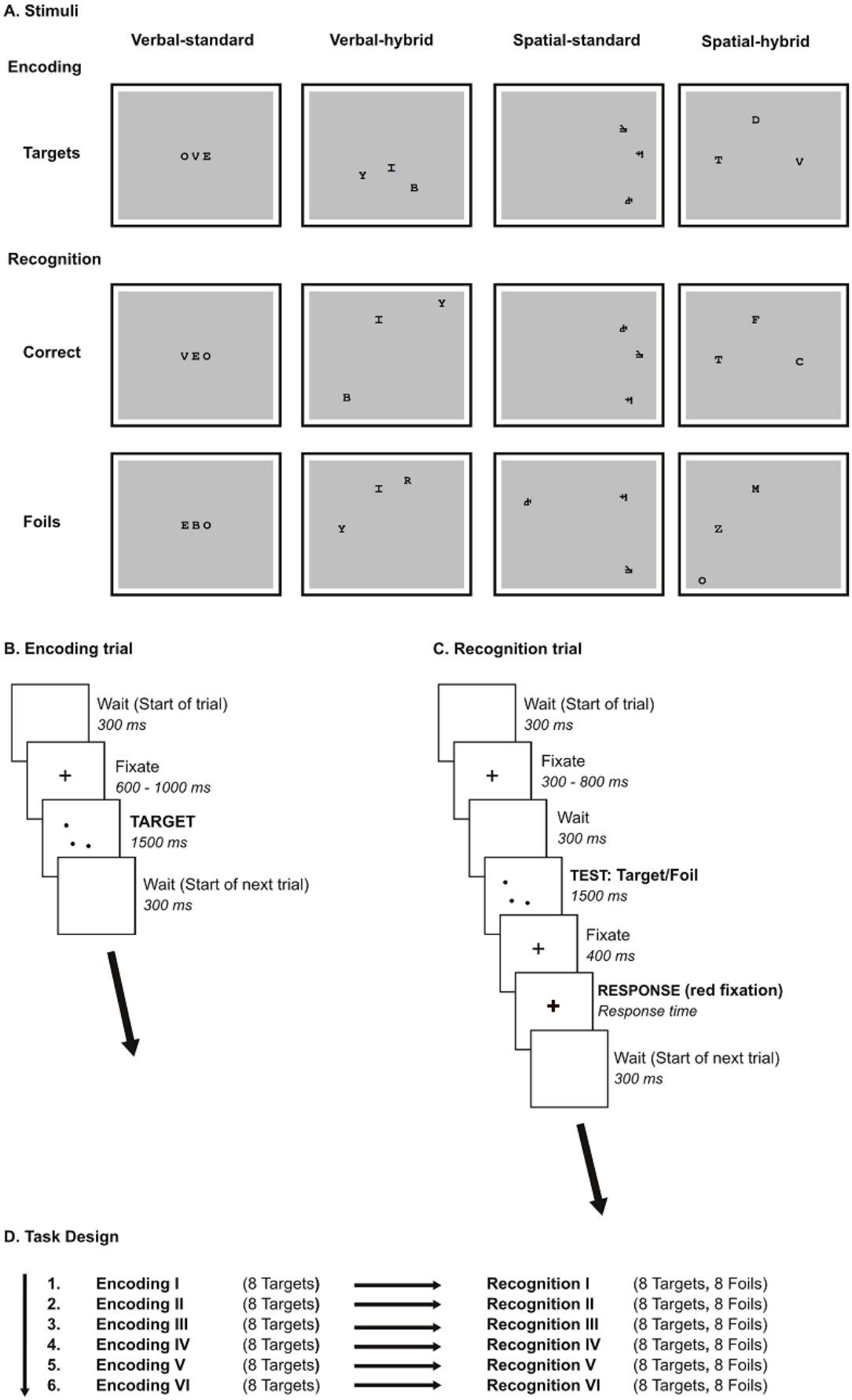

Fig 1. Experimental design. (A) Experimental stimuli - examples of targets and related foils for both material types. (B) Procedure, Encoding phase - target stimulus presentation preceded by interval of

randomised duration; (C) Procedure, Recognition phase - test stimulus presentation (intermixed sequence of targets and foils) preceded by interval of randomised duration and followed by response screen. (D) Task Phases 1 to 6 – sequence of phases (Encoding followed by Recognition within each phase) including number of targets and foils per phase.

2.3.1 Verbal-standard stimuli

Target stimuli for the six Encoding blocks of the verbal-standard condition were a set of eight letter triplets (i.e., *G-M-T*, *E-O-V*, *A-X-Z*, *D-I-U*, *C-S-Y*, *F-K-L*, *B-J-N*, *H-P-R*). The triplets were chosen so that no mental rearrangement of the letters could form a real word. Across the six encoding blocks the letters of each triplet were pre-randomised to have different orders within the string (e.g., *G-M-T*, *G-T-M*, *M-G-T, M-T-G, T-G-M,* or *T-M-G* for the Target *G-M-T*) to prevent the formation of letter-position associations. Twenty-four letters of the alphabet were used with no letters repeated within the set. Letters were capitalised, modified from Courier New font to each fit a square space subtending 0.53^0 visual angle vertically and horizontally. Triplets were placed at the centre of the screen, with each letter separated by 0.29^0 of visual angle.

Stimuli for the six Recognition blocks were comprised of Correct stimuli that corresponded to re-presented Target stimuli, and six unique Foil items (one for each Recognition block) per Target (48 in total). Foil items were created for each Target by varying one letter of the Target (e.g., *D-M-T*, *G-M-R*, *G-T-U, J-M-T, G-N-T*, and *H-M-T* for the Target *G-M-T)*. Both Correct and Foil stimuli used the same set of 24 letters as for Target stimuli. There were no restrictions on whether foils could be phonologically, orthographically or visually confusable with their respective Targets. As for the set of Target stimuli, for Correct and Foil the order of the letters within each triplet was pre-randomised (e.g., *MGT, GTM, MTG, MTG, TMG, MTG* for Correct stimuli, and *TMD*, *RMG, UTG, TMJ, GTL, MTH* for Foil stimuli). The pre-randomisation of letters was fixed for all stimulus sets (Target, Correct, Foil) so that each participant experienced exactly the same stimuli across the task.

2.3.2 Spatial-standard stimuli

Each of the eight Target stimuli in the spatial-standard condition consisted of three spatially distributed positions marked by symbols as shown in Figure 1(a). Each Target stimulus was formed by selection of three positions from an irregular, asymmetric array of twenty-four positions within a maximum two-dimensional range of 11.23^0 x 9.31^0 visual angle, centred on the screen without a grid or outer boundary. The positions were distributed approximately evenly across and within each quadrant of this range. Adjacent positions were separated by a minimum of 1.71^0 visual angle between the nearest outer edges of adjacent letters (i.e., designed to be greater than twice the width/height of a symbol to reduce perceptual grouping). Within the set of Target stimuli, all twenty-four positions were exhausted per set (i.e., no position was used twice), analogously to the method used for the verbal-standard stimuli.

The irregular design of the positional array meant that no pairs of positions could be completely aligned along any horizontal or vertical axis, and no triplet of positions could be aligned along a diagonal axis. In addition, no stimuli could "point" directly toward a corner, and no array configuration (i.e., the specific combination of angles between letters) could be exactly repeated in a transposed or rotated form. This particular array, and the restrictions, were applied to discourage verbalisation or perceptual grouping of different positions into one larger position, and instead promote encoding of the exact locations of and distances between the positions.

Three unique symbols were created in order to match this condition with the verbal-standard condition in terms of the variability of the non-mnemonic attribute (i.e., three possible horizontal locations in the case of verbal-standard stimuli, see Section 2.3.1). The symbols were constructed by dividing up the letter stimuli (used for verbal-standard stimuli) into fragments using a graphics editor and then re-pasting them together. This method meant that the average number of black pixels across the set of twenty-four letters (M = 555 pixels/letter, SD = 71.87) was statistically matched to the average for the symbols (M = 553

pixels/letter, *SD* = 32.36; $t(46) = 0.13$; $p = .90$). The three unique symbols were always used in each stimulus and were randomly pre-assigned to each of the three positions per stimulus, matching the use of letter order in the verbal-standard stimuli.

Spatial-standard stimuli for the Recognition blocks were comprised of six Correct stimuli per Target per block (48 in total) and six unique Foil items per Target per block (48 in total). Foil items were created for each Target by varying one position of the Target. Correct and Foil stimuli used the same set of 24 positions as Targets, and any position in a Target could be re-used as part of a Foil (as for the letters in the verbal-standard stimuli).

2.3.3 Verbal-hybrid stimuli

For verbal-hybrid stimuli a set of eight, three-letter triplets were created as the set of to-be-remembered Target stimuli (i.e., as for the verbal-standard stimuli). In contrast to verbal-standard stimuli, the letters were not horizontally aligned as a string but distributed in positions within the same array used for spatial-standard stimuli. In addition, Target stimuli (and Correct and Foil stimuli accordingly) were composed of different combinations of the same 24 letters used for verbal-standard stimuli. In this condition the relative position of the letters within the array was pre-randomised in order to prevent letter-position associations (i.e., corresponding to the pre-randomisation of the letter order in the strings in the verbal-standard condition). Otherwise the stimuli, foil creation, and task conditions were identical to verbal-standard stimuli.

2.3.4 Spatial-hybrid stimuli

For spatial-hybrid Target stimuli, the set of positions was fixed across blocks while the letters were pre-randomised (i.e., in the opposite manner to the verbal-hybrid stimuli for which the sets of spatial positions were instead pre-randomised). The three-position combinations to be learned were different to those used in the spatial-standard stimuli. Otherwise, all other aspects of the stimulus creation, randomisation and control were the same as for spatial-standard stimuli.

2.3.5 Stimulus control – bigram frequency

Using the Windows program *N-Watch,* letter bigram frequency (e.g. of *G-M* combination within *G-M-T*) was statistically controlled between verbal-standard, verbal-hybrid, and spatial-hybrid stimuli and also between the Target, Correct, and Foil stimuli within each stimulus type. Trigram frequency (e.g., *G-M-T*) was always zero as none of the triplets could be arranged to spell real words.

2.3.6 Stimulus control – spatial area

Foil items for spatial-standard and spatial-hybrid stimuli were created to be sufficiently distinguishable from targets. In addition, the spatial area subtended by sets of array positions was statistically controlled between spatial-standard, spatial-hybrid, and verbal-hybrid stimuli. Area (A) was calculated within the triangle created by the lines connecting the centres of each position using the formula for a scalene triangle: $A^2 = s.(s - a).(s - b).(s - c)$, where $s = (a + b + c)/2$. Area was chosen as an efficient summary measure that captures many spatial attributes simultaneously such as total size and horizontal/vertical distance.

2.4 Recognition memory task design

The format of the memory task, depicted in Figure 1(b, c), was equivalent for all four stimulus types and involved six phases, each of which consisted of i) an Encoding block (Targets) followed by ii) a Recognition block (Correct and Foils). In each of the six Encoding blocks, participants were instructed to learn the eight Target stimuli, with no instructions to categorise or label the stimuli. Target stimuli were presented sequentially in pseudorandom order. The same eight Encoding stimuli were shown during each of the six Encoding blocks, with constant memory-related attributes and pre-randomised stimulus-related attributes as described in Sections 2.3.1 to 2.3.4. Each Encoding block was followed by a Recognition block in which each Target stimulus was presented intermixed with eight Foil stimuli in a pseudorandom order.

For each Recognition block, participants pressed one button on a button box to indicate a match to a Target stimulus ("yes—seen before") and a second button to indicate a new item ("no—unseen"). To account for any response-hand-related hemispheric lateralisation in ERP peaks, response instructions were counterbalanced between participants so that half were instructed to press the right button for "yes" and the left for "no" for both tasks, and response instructions were reversed for the other half of the sample. Stimuli were always presented for 1500 ms. To enhance sustained attention to the task, the duration of pre- and post-stimulus intervals was jittered randomly between 600 and 1000 ms during Encoding blocks and 300 to 800 ms during Recognition blocks, as shown in Figure 1(b, c). Participants performed each of the four recognition tasks to completion before commencing a subsequent stimulus type, and the recognition tasks were presented in counterbalanced order between participants such that a verbal condition was always followed by a spatial condition and vice versa.

2.4.1 Verbalisation rating task

Following the four memory tasks involving the four different stimulus sets participants completed a surprise verbalisation rating task on the computer. One task combined the two verbal memory conditions and one combined the two spatial memory conditions. The tasks were administered in the same order that the memory tasks were completed (e.g., verbal rating task administered first if a verbal memory task had been first). Prior to task onset, participants were instructed to rate each stimulus by button press (i.e., "How often did you use a verbal label to help you remember the item during the task", on a scale: "0" ("never or don't remember the item"), "1" ("occasionally"), "2" ("often") and "3" ("always"). For each of the four memory tasks, all eight Learning stimuli (24 total) were presented one at a time (1500 ms duration) in an intermixed, pre-randomised order that was the same for every participant. Following the stimulus, a response screen was presented showing the four rating options and the button press required for each as described above. Although there was no time limit for the response participants were encouraged to respond as

quickly as possible. It was heavily emphasised that this was a rating of how often they had used the verbal label *during* the task, rather than a test of their ability to think of appropriate verbal labels following their experience on the task. Following their rating, participants were asked by the experimenter what verbal label(s) they had used, if any. This was repeated for all items, and then followed by the remaining rating task. Response data for this task was saved by the computer and the spoken responses were transcribed in full by the experimenter.

2.5 EEG recording and offline analysis

Each participant's EEG was recorded during the Recognition Phase using sintered Ag-AgCl electrodes mounted in an Easy-Cap according to the 10-20 system (FP1, FP2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz, and O2). The ground electrode was positioned between FPz and Fz. Activity from both mastoids was recorded and the left mastoid served as the online reference. Vertical eye movements (VEOG) were measured with electrodes placed above and below the left eye. Horizontal eye movements (HEOG) were measured with electrodes on the outer canthi of each eye. Electrode impedance was kept below 5 kΩ. The signal was amplified 20,000 times (SynAmps2 amplifier, Compumedics Limited), sampled at 500 Hz, low-pass filtered at 100 Hz online and saved to the computer's hard disk.

Offline analysis was conducted using BESA Research software (version 6.0, BESA GMbH, Grafelfing, Germany). First, portions of EEG containing large movement-related artefacts were manually rejected. EEG was then set to reference-free and filtered (highpass 0.53Hz, forward, 6 db/octave; lowpass 8Hz, zero phase, 24 db/octave roll-off), for artefact correction which was carried out using the adaptive method of the automatic artefact correction tool in BESA. This method applied a predefined source model to the data, combining three topographies accounting for EOG activities (HEOG, VEOG, blink) with a set of 12 regional sources modelling the different brain regions. If the EOG signals exceeded set thresholds (HEOG amplitude 150μV, VEOG/Blink threshold 250μV), then the current EEG topography was accumulated and averaged over the whole EEG. The first principle

component of this averaged EOG signal served as the artifact topography that was used for artifact correction, which was performed using an adaptive method (see Ille, Berg, & Scherg, 2002, for further details).

EEG data were then divided into 2500 ms epochs with a 1000 ms pre-stimulus interval and 1500 ms post-stimulus interval. These epochs were then re-referenced to the average of the left and right mastoids, band pass filtered (highpass 0.53 Hz, forward phase, 6 dB/octave roll-off; lowpass 200 Hz, zero phase, 24 dB/octave roll-off) and baseline corrected the using mean pre-stimulus amplitude for the epoch. EEG artefacts, including blinks and eye-movements, were rejected using the BESA artefact scan tool, which rejects trials based on abnormally high amplitudes (120 μV), abrupt gradients in amplitude exceeding 75 μV, or unusually low signal (below 0.01 μV). Mean percentage of epochs rejected was low (verbal-standard, 4.48%, verbal-hybrid, 6.60%, spatial-standard, 5.52%, spatial-hybrid, 5.42%). Epochs associated with incorrect responses were also excluded from further analysis, resulting in the following average percentage of trials accepted: (verbal-standard, 87.08%, verbal-hybrid, 82.67%, spatial-standard, 78.61%, spatial-hybrid, 79.38%).

2.5.1 Event-related power change

EEG amplitude for each accepted epoch and channel was squared in order to obtain simple power estimates and averaged separately for each experimental condition and participant. BESA was then used to conduct time-frequency analysis (frequency range 2 to 20 Hz, frequency/time sampling of 1 Hz/50 ms) resulting in 969 time-frequency measures (19 frequency samples x 51 time samples) per electrode. Based on these data, event-related power change (power) values were calculated as the percentage decrease or increase in band power during the test interval (stimulus onset to 1500 ms post-stimulus) compared with the reference interval (1000 ms pre-stimulus to stimulus onset; Pfurtscheller & da Silva, 1999). Positive power values indicated a mean power increase relative to baseline while negative values indicated a mean power decrease. These power measures were then averaged to create 64 frequency- and time-specific power measures per participant: four hemispherically lateralised

sites in the left (P3 and P7) and right parietal (P4 and P8) region by two memory tasks (verbal, nonverbal) by two forms (standard, hybrid) by two frequency bands (theta: 4 to 7 Hz; alpha: 8 to 13 Hz) by two time windows (early: 0 to 500 ms; late: 500 to 1500 ms). Region-wide measures were then obtained by averaging the mean power of P3 and P7 (left parietal), P4 and P8 (right parietal), resulting in 32 total measures used for analysis: Memory (2) x Form (2) x Frequency (2) x Time (2) x Hemisphere (2).

2.6 Statistical analysis

2.6.1 Behavioural performance

Mean percentage correct responses to targets and foils were calculated during the Recognition Phase, from which mean percentage correct and sensitivity (*d'*) values for target/foil discrimination were calculated to ensure the different kinds of stimuli in each condition were adequately learned. *d'* is based on z-score transformations and takes into account both hits and false alarms, controlling for response biases (McNicol, 1972). Response times (RTs) were calculated by subtracting the time of response from the onset time of the response screen (see Figure 1), and median RTs were calculated for each participant. For analysis response times were inverse transformed (i.e, 1/RT) to reduce the impact of outliers.

In order to determine whether task performance had a significant impact on EEG measures, accuracy/EEG correlational analyses were conducted, specifically between: 1) the difference in recognition accuracy (*d'*) between the materials (i.e. $d'_{\text{verbal}} - d'_{\text{nonverbal}}$), and 2) the difference in EEG measures between the materials (i.e. $power_{\text{verbal}} - power_{\text{nonverbal}}$), for the 32 relevant power measures (i.e., all frequency [theta, alpha] by form [standard, hybrid] by time [early, late] by hemisphere [left, right] combinations). Equivalent correlations were calculated for differences due to form (standard – hybrid), and also between (inverse transformed) response times and EEG measures. To calculate 95% confidence intervals for each correlation a bootstrap method was conducted with 1000 samples (IBM SPSS Statistics version 22).

2.6.2 EEG hemispheric lateralisation and memory (old/new) effects

Using SPSS, the key predictions of material and process effects on hemispheric differences were tested by comparing mean amplitudes using three-way repeated measures ANOVA with factors memory (verbal, nonverbal), form (standard, hybrid), and hemisphere (left, right). Separate ANOVAs were run for each of the four combinations of frequency band (theta, alpha) and time window (early, late). We analysed main effects and interactions between these factors as well as planned simple effects to compare memory and form effects.

As we used an experimental procedure with multiple repeated items and trials in order to maximise the proportion of correct responses, we did not compare mean power data between correct and incorrect responses due to the likely low proportion, and hence poor reliability, of the mean data associated incorrect responses. Instead, a grand average of Repetition (old – new) was calculated for each peak across stimulus types and analysed with a two-tailed one-sample *t*-test to determine if there was an overall repetition effect (e.g., old > new). Repetition (old – new) was also analysed in a Memory x Form x Hemisphere ANOVA for each frequency band and time window.

2.6.3 Data treatment, effect size and correction for multiple comparisons

To ensure that analyses were robust to the effect of outliers, extreme values within all EEG, recognition accuracy and response time measures were subjected to a winsorisation procedure where values greater than the 95th or less than the 5th percentiles were adjusted to these cut-off values. Extreme values accounted for less than 5% of the data across variables. Verbalisation ratings were corrected for recognition accuracy (i.e., corrected ratings = ratings/proportion correct) as appropriate to each stimulus type.

Effect size for all ANOVAs was reported as partial eta-squared (η_p^2), the proportion of variance explained controlling for other effects (interpreted as small: .01 to .09, medium: .09 to .25, or large: > .25; Kenny, 1987). Cohen's *d* adjusted for repeated measures (Morris & DeShon, 2002), was reported for tests of simple main effects and appraised according to the

review of Lipsey andWilson (2001), i.e., small: < 0.3, medium: 0.3 to 0.7, large: > 0.7).

The statistical significance of analyses involving *t*-tests was assessed using a bootstrapped *p* value with 1000 samples in SPSS (reported simply as *p*). For simple main effects analyses, *p* values were adjusted for multiple comparisons (reported as p_p) using a permutation testing procedure designed for repeated measures (10000 permutations, MATLAB function "mult_comp_perm_t1" by Groppe, Urbach, & Kutas, 2011). Like Bonferroni correction, this method adjusts *p* values in a way that controls the family-wise error rate. However, for EEG data the permutation method is more powerful than Bonferroni correction due to high within-subject correlations between sites and conditions (Blair & Karniski, 1993; Burgess & Gruzelier, 2000; Good, 1994; Manly, 1997).

3. Results

3.1 Behavioural performance

Figure 2 shows learning curves of memory performance across the six learning blocks for verbal-standard, verbal-hybrid, spatial-standard, and spatial-hybrid conditions. Mean recognition accuracy (*d'*) across the six learning trials was significantly higher for verbal material, $M = 2.35$ (mean 86% correct), than spatial material, $M = 1.57$ (77% correct), $p < .001$, $\eta_p^2 = .66$. In contrast, *d'* did not significantly differ between the standard (82%) and hybrid forms (81%), $p = .21$. The Material x Form interaction was not significant, $p = .08$, and planned contrasts showed the material effect (verbal > spatial) was significant for both forms (standard, $p_p < .001$; hybrid, $p_p = .02$) while the effect of form was not significant for either material, p_ps > .28.

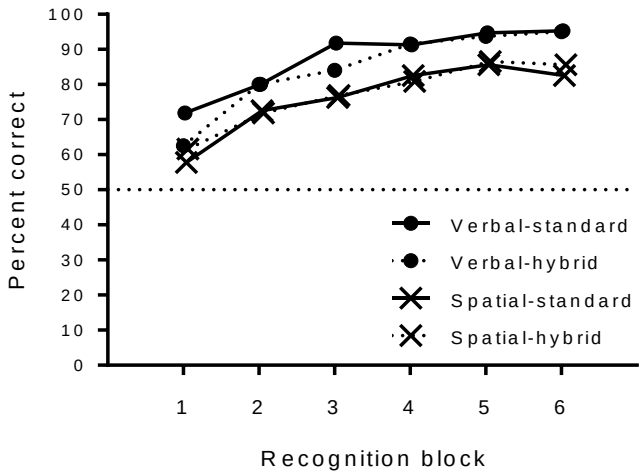

Fig 2. Mean recognition accuracy across recognition blocks 1 to 6 for all stimulus types (percent correct for display purposes).

In contrast to the difference in *d'* in favour of verbal memory, response times (RTs) were quicker for spatial memory, M = 459 ms [CI_{95}: 375 592], than verbal memory tasks, M = 532 ms [451 648], $F(1,19) = 6.35$, $p = .02$, $\eta_p^2 = .25$, and for stimuli with standard form, M = 463 ms [379 596], than hybrid form, M = 525 ms [444 643], $F(1,19) = 5.20$, $p = .03$, $\eta_p^2 = .22$. There was also a significant interaction between material and form, $F(1,19) = 5.00$, $p = .21$, $\eta_p^2 = .21$. with contrasts showing RTs for verbal-hybrid stimuli were significantly slower than for spatial-hybrid, $p_p = .03$, or for verbal-standard stimuli, $p_p = .02$. Mean RTs for all stimulus types are shown in Supplementary Table 1. In sum, recognition accuracy was superior for verbal memory versus spatial memory, while perceptual form did not affect accuracy. For response speed spatial memory was superior to verbal memory, while spatial form was related to slower response times compared with no spatial form.

3.2 Correlations between performance and EEG measures

Despite these significant differences in *d'* and RT as a function of memory task and visual form, the differences in *d*' between the materials (i.e., verbal – nonverbal) or forms (standard – hybrid) and equivalent differences in EEG measures were not significantly correlated with the exception of alpha (verbal-standard – verbal-hybrid), $r(20) = -.49$ [$CI_{95(bootstrap)}$: -.77 -.12], uncorrected $p = .03$, in the right hemisphere. Equivalent comparisons for RT differences did not show any significant correlations. In sum, the impact of recognition

accuracy or response speed on EEG measures appears to be low (in total only approximately 3% of correlations were significant). See Supplementary Tables 2 and 3 in the Appendix for complete inferential statistics for *d'* and RT, respectively.

3.3 Verbalisation ratings

Figure 3(a) shows a strong correlation between verbalisation frequency ratings and recognition accuracy averaged across all four stimulus types. This correlation was also significant within verbal-standard, $r(18) = .61$, $p = .004$, verbal-hybrid, $r(18) = .51$, $p = .02$ and spatial-hybrid stimuli, $r(18) = .54$, $p = .01$, but not for spatial-standard stimuli, $r(18) = .36$, $p = .12$.

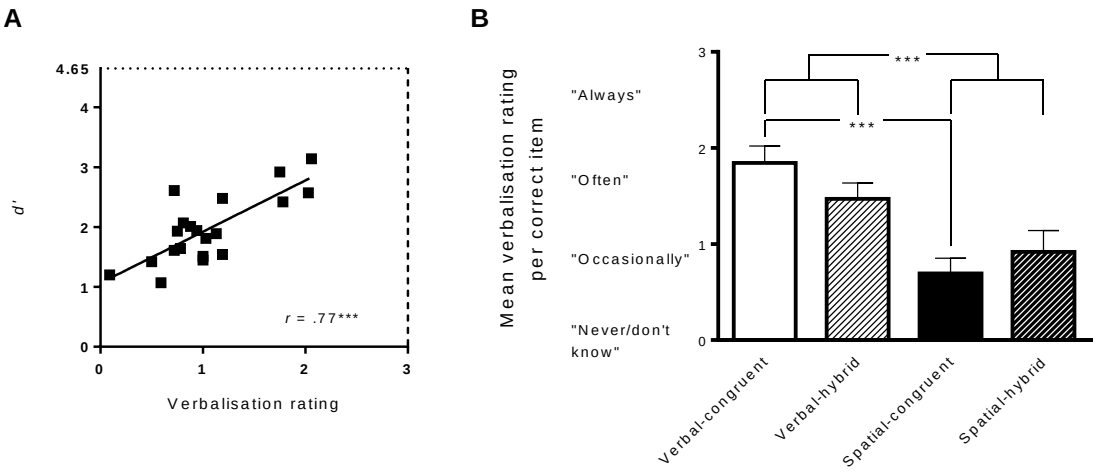

Fig. 3. Verbalisation ratings. (a). Correlation between verbalisation ratings and *d'*, both averaged across conditions, with regression line of best fit. Dotted line indicates maximum possible *d'* and dashed line indicates maximum verbalisation frequency rating. (b). Mean verbalisation frequency ratings, corrected for recognition accuracy, for all four stimulus types. *** $p < .001$.

Figure 3(b) shows corrected mean verbalisation frequency ratings (i.e. verbalisation rating per correct item), for all stimulus types. The ANOVA showed the main effect of Memory (verbal > spatial) on verbalisation frequency was significant, $p < .001$, while the main effect of Form was not significant, $p = .58$. The Memory x Form interaction was significant, $p = .04$, and explained by a significant effect of memory for standard form only (i.e., verbal-standard > spatial-standard, $p_p < .001$). Together these results show that the verbalisation ratings clearly distinguished encoding strategies of verbal and spatial memory

tasks, while also suggesting that equalising the perceptual form to a verbal-spatial hybrid reduced the difference in verbalisation strategy due to the to-be-remembered material type.

3.4 EEG lateralisation: memory, perceptual, and old/new effects

3.4.1 Early theta power, 0 to 500 ms

Figure 4 shows the left and right hemisphere mean event-related theta power change across all combinations of material and form. As expected, the theta response showed a rapid increase peaking at approximately 250 ms and subsequent decrease to baseline within approximately 500 ms post-stimulus (below the baseline in the case of spatial-hybrid). In-text reporting of contrasts is restricted to comparisons of direct theoretical relevance; for brevity, using p_p values only. Complete inferential statistics for theta analyses are reported in Supplementary Tables 4 to 7 in the Appendix.

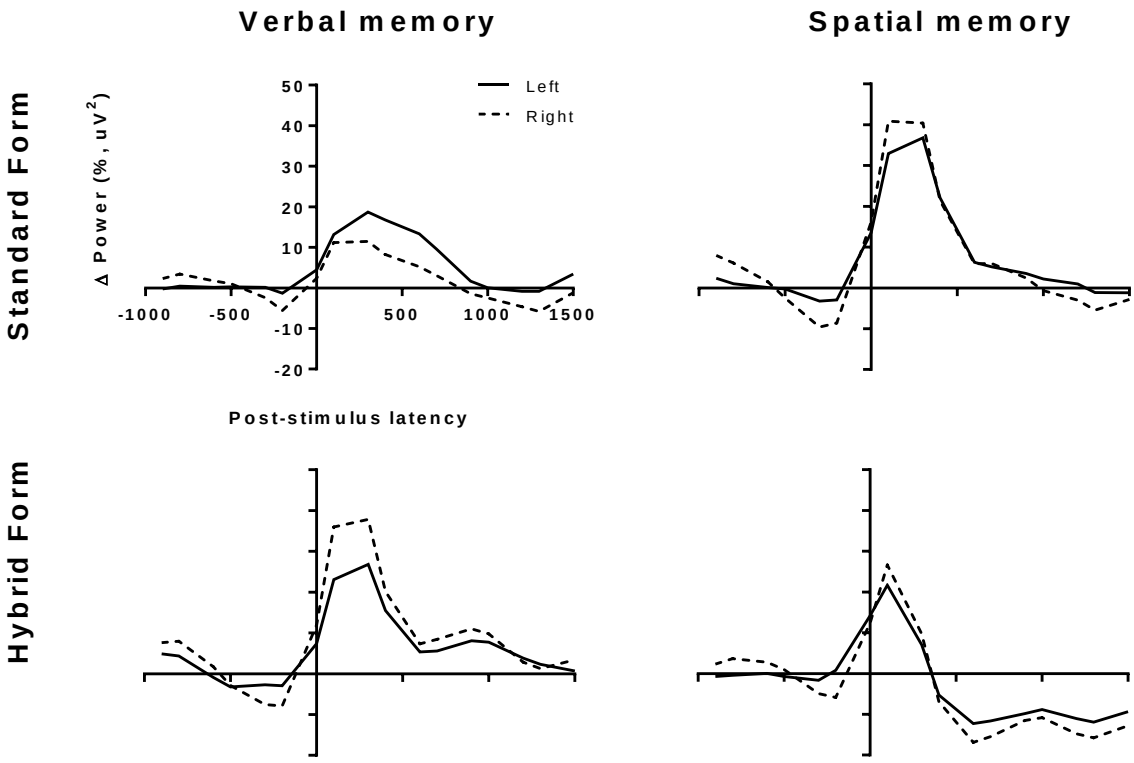

Fig. 4. Mean percent theta power change from -1000 ms pre-stimulus to 1500 ms post-stimulus for verbal and spatial materials with standard and hybrid forms at parietal sites in both hemispheres.

Early theta power revealed a significant main effect of memory (spatial > verbal), $p = .03$, and form (hybrid > standard), $p = .006$, while hemisphere was not significant, $p = .51$.

However, none of the ANOVA interaction effects testing for associations between material, form and lateralisation were significant. Interaction contrasts showed that the main effect of memory (spatial > verbal) reached significance in the left hemisphere, p_p = .046, but not in the right hemisphere, p_p = .19, which is opposite to the predicted pattern (see Figure 5). Hybrid stimuli showed a larger increase in theta power than standard stimuli in the right hemisphere, p_p = .01, but not in the left, p_p = .12.

Early theta did not show a significant main effect of Repetition overall (i.e., repeated targets did not differ from non-repeated foils; old > new, hereafter termed the "old/new effect"), p = .77, or interactions, although there were a number of marginally significant trends with ps ranging from .06 to .09. While contrasts showed no old/new effect per se there was a novelty effect (i.e., new > old) that was larger in the left hemisphere for hybrid than standard form, p_p = .02 (right, p_p = .87; see Figure 6). Overall, early theta power showed subtle signs of lateralisation that opposed our predictions for memory-related effects of material, and there was no consistent lateralisation effect associated specifically with verbal or spatial perceptual form.

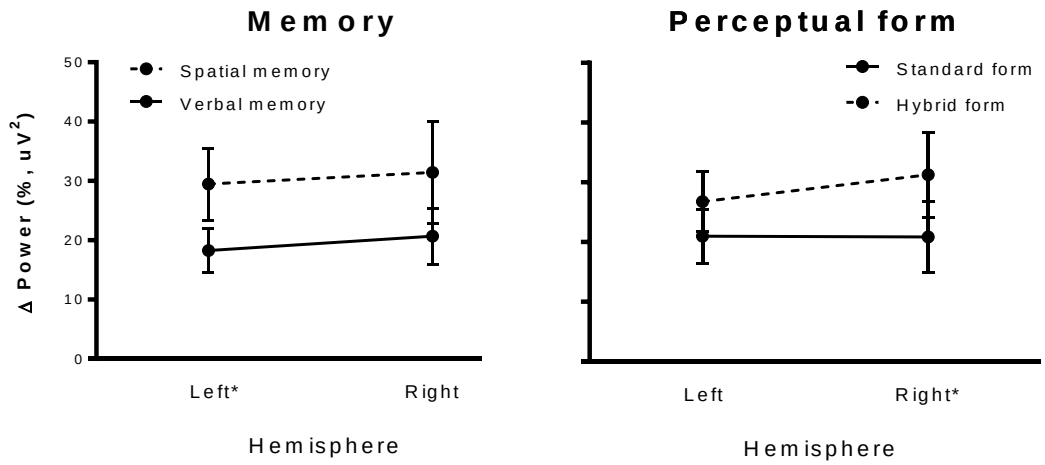

Fig. 5. Mean percent power change for early theta (0 to 500 ms post-stimulus, with standard error bars) for verbal and spatial memory in both hemispheres. Left: memory-related effect of material; Right: perceptual form effect. Asterisks by x-axis labels refer to significant contrasts (i.e., spatial > verbal memory; perception: hybrid > standard). * p_p < .05.

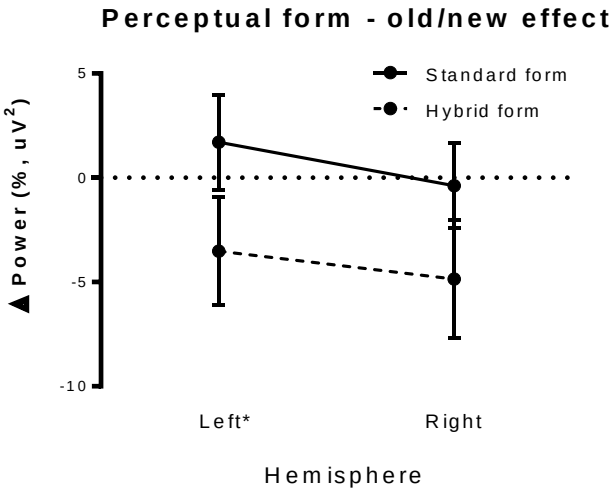

Fig. 6. Mean percent power change for early theta (0 to 500 ms post-stimulus, with standard error bars) for repetition effect (old – new) for standard and hybrid visual form in both hemispheres. Asterisks by x-axis labels refer to significant contrasts (i.e., perceptual form: standard > hybrid old/new effect). * $p_p < .05$.

3.4.2 Late theta power, 500 to 1500 ms

Late theta power revealed a significant main effect of memory (spatial > verbal decrease), $p = .02$, and hemisphere (right > left decrease) $p = .001$, but none of the ANOVA interactions were significant. However, interaction contrasts showed that right-lateralisation was significant for spatial memory, $p_p = .005$, but not verbal memory, $p_p = .13$ (see Figure 7). Right-lateralisation was significant for both spatial-standard form, $p_p = .003$, and spatial-hybrid form, $p_p = .045$, but was not significant for either verbal-standard, $p_p = .09$, or verbal-hybrid forms, $p_p = .80$.

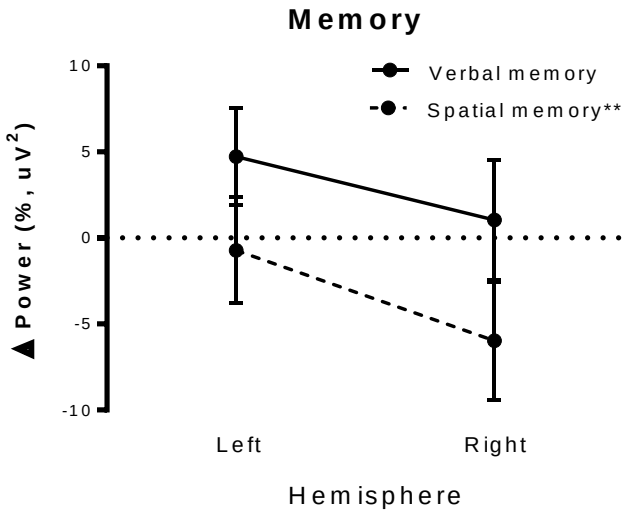

Fig. 7. Mean percent power change for late theta (500 to 1500 ms post-stimulus) for verbal and spatial memory in both hemispheres. Asterisks by x-axis labels refer to significant contrasts (i.e., memory: spatial > verbal) and those by figure legend labels refer to significant lateralisation (right > left). ** p_p < .01.

The main effect of repetition was not significant, p = .34, nor were any of the ANOVA interactions, ps > .08, and none of the interaction contrasts were significant. In sum, late theta showed slightly stronger right-lateralisation for spatial compared to verbal memory, but there was no effect of perceptual form of materials on lateralisation.

3.4.3 Early alpha power, 0 to 500 ms

Figure 8 shows alpha power has a small increase before the stimulus before declining rapidly below baseline levels with a minimum "peak" at approximately 500 ms post-stimulus, before slowly increasing from 500 to 1500 ms. Complete inferential statistics for alpha are reported in the Appendix (Supplementary Tables 8 to 11).

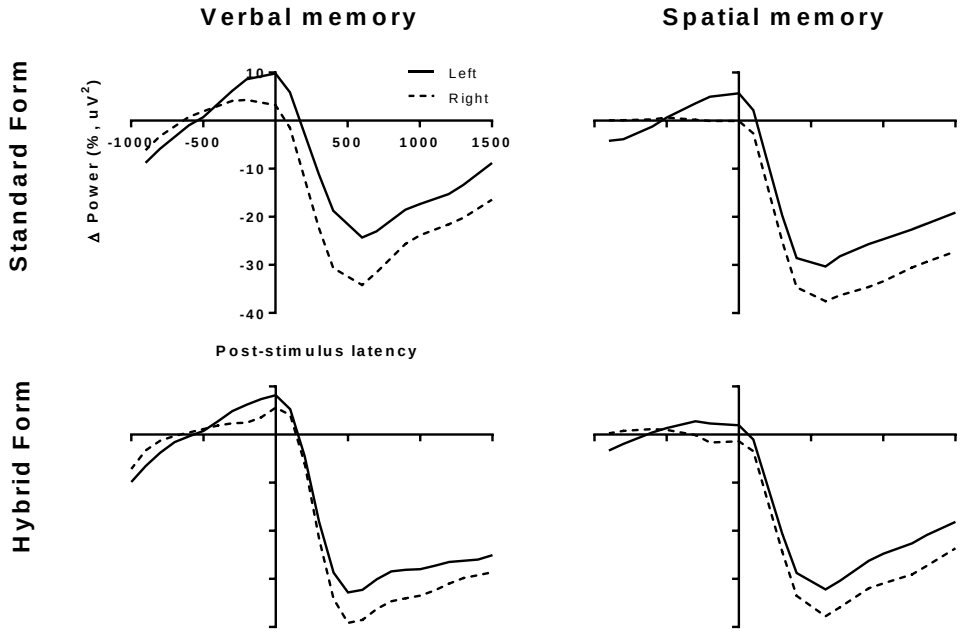

Fig. 8. Mean percent alpha power change from -1000 ms pre-stimulus to 1500 ms post-stimulus for verbal and spatial materials with standard and hybrid forms at parietal sites in both hemispheres.

For early alpha power the main effect of hemisphere (right > left) was significant, p = .002, but there were no other significant main effects or interactions from the ANOVA. Interaction contrasts showed that all four combinations of memory task and visual form were significantly right-lateralised to a similar degree, with p_ps ranging from .017 to .027 (see Figure 9). For the old/new effect there were no significant main effects, interactions, or contrasts. In summary, early alpha showed strong right hemispheric lateralisation but was not sensitive to the type of material, whether memory-related or not.

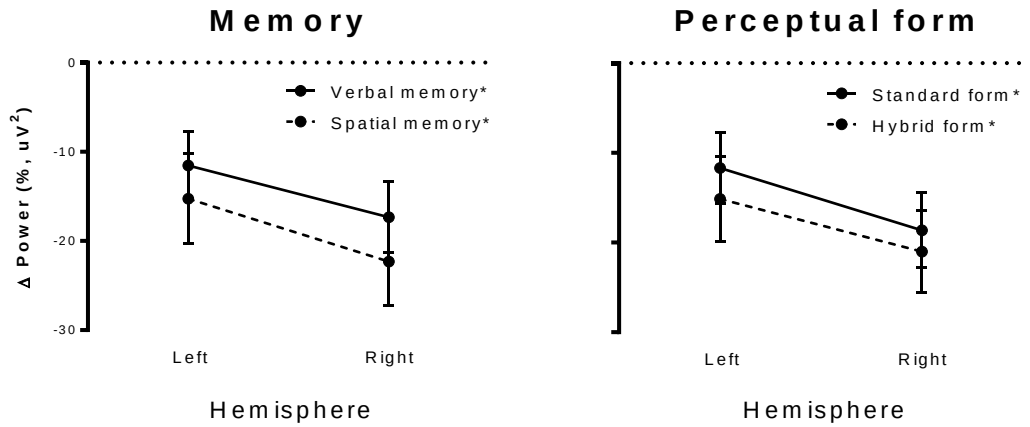

Fig. 9. Mean percent power change for early alpha (0 to 500 ms post-stimulus, with standard error bars) for verbal and spatial memory in both hemispheres. Left: memory effect; Right: perceptual form

effect. Asterisks by x-axis labels refer to significant contrasts (i.e., spatial > verbal memory; perception: hybrid > standard) * $p_p < .05$.

3.4.4 Late alpha power, 500 to 1500 ms

For late alpha power there was a significant main effect of form (hybrid > standard decrease), $p = .01$, and hemisphere (right > left), $p = .001$. The Memory x Form interaction was significant, $p = .01$, but the remaining interactions were not significant. Interaction contrasts showed the effect of form (hybrid > standard) was larger for verbal memory, $p_p = .01$, than for spatial memory, $p_p = .99$. For verbal memory this form effect was significant only in the left, $p_p = .03$ (right $p_p = .17$), suggesting that the lack of significance in the right hemisphere was due to spatial perceptual form *decreasing* alpha power in the right hemisphere, consistent with predictions (see Figure 10).

Right-lateralisation was significant for both verbal and spatial memory but was perhaps slightly more pronounced for spatial memory, $p_p = .001$, than verbal memory, $p_p = .03$. The old/new effect was significant overall, $p = .02$; however, none of the ANOVA interactions or contrasts were significant, p_ps > .06. In summary, late alpha showed strong right-lateralisation in general while spatial perceptual processing mildly reduced right-lateralisation, as predicted.

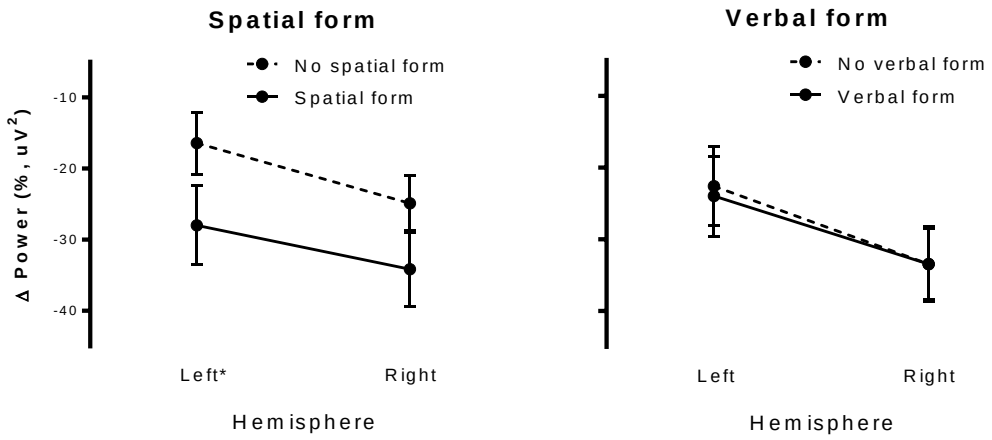

Fig. 10. Mean percent power change for late alpha (500 to 1500 ms post-stimulus, with standard error bars) for verbal and spatial memory in both hemispheres. Left: spatial perceptual form; Right: verbal perceptual form. Asterisks by x-axis labels refer to significant contrasts (i.e., spatial > no spatial form). * $p_p < .05$.

4. Discussion

4.1 Effects of memory and perceptual form on material specific lateralisation

The aim of this study was to investigate the relative effects of memory task and perceptual form in mediating material specific hemispheric lateralisation. This was conducted by experimentally separating the demands of memory and perceptual form and measuring EEG lateralisation in healthy participants. We predicted a pattern of relative left-lateralisation of theta band power due to both verbal memory and verbal perceptual form, and an opposing effect of right-lateralisation for spatial memory and spatial perceptual form. For alpha band power the predictions were the same as those for theta in terms of memory but were reversed for perceptual form, due to the known antagonistic nature of alpha power responses to memory-relevant versus memory-irrelevant processing. Overall, neither set of predictions were clearly supported. The secondary hypothesis predicting larger material specific lateralisation differences in alpha power between hybrid stimuli compared with standard stimuli, was also not supported overall.

While there was the expected association between spatial memory and right

hemispheric lateralisation for late theta, this pattern was reversed for early theta (i.e., spatial > verbal in left). For perceptual processing the pattern of lateralisation was also inconsistent. While spatial perceptual form was associated with a relative decrease in right hemisphere alpha power as predicted, the pattern for theta was more general and inconsistently lateralised, confounding a clear interpretation. Late alpha showed an overall old/new memory effect, consistent with some previous findings (e.g., Burgess & Gruzelier, 2000); however, again the lateralisation of this effect was not affected by memory task or visual form. The most striking effect in this study was a large-sized right-lateralisation effect in late theta, early alpha, and late alpha across all tasks (η_p^2s > .40). In summary, the results showed consistent and strong right-lateralisation in both theta and alpha, but with only minimal and inconsistent effects of our experimental manipulations of material-specific memory and perceptual form.

4.2 Verbalisation

Despite the lack of EEG evidence for material specific hemispheric lateralisation, overall spatial memory was associated with lower verbalisation ratings than verbal memory, suggesting the former was comparatively more difficult to verbalise. This finding is consistent with previous studies that used alternative measures of verbalisation (e.g., behavioural dual-task interference in Golby et al., 2001, and Hampstead et al., 2010), but the lack of associated material specific EEG lateralisation is inconsistent with previous findings that greater right-lateralisation is associated with lower stimulus verbalisability (e.g., Golby et al., 2001). Interestingly, despite this overall pattern (i.e., verbal > spatial verbalisation), there was no significant difference between spatial and verbal memory tasks with hybrid forms, suggesting that the mere presence of an irrelevant material type reduced or interfered with material-specific encoding strategies. Conceivably, managing the conflict between relevant and irrelevant materials could have resulted in poorer implicit encoding of verbalisation strategies and hence explain the lower reporting of such strategies following the memory tasks. This finding is arguably supported by slower response times for the verbal-hybrid task than for the verbal-standard task (see Section 3.1). Together, the results suggest that while the

verbalisation ratings appeared to validate our manipulations of memory and perceptual form, either this difference was not sufficiently large to elicit the expected EEG changes (cf. Burgess & Gruzelier, 2000), or the type of frequency measures used in this study were not sufficiently sensitive to detect the difference.

4.3 Limitations

It is possible that the width of the time windows used to measure EEG power were too large to detect the effects of interest in this study. This speculation is supported by successful findings with the same dataset using ERP measures within the first 350 ms after stimulus onset (Chapter 5). In addition, while previous investigations have found material-specific effects with EEG power measures in very similar time windows (e.g., Burgess & Gruzelier, 2000) or using fMRI (e.g., Kelley et al., 1998), these studies did not test stimulus-level characteristics as precisely as in this study. Putting aside the experimental manipulations, the tasks had many overlapping visual and spatial processing demands. Each task required attention to the precise visual and spatial characteristics of the stimuli and such general visual-spatial attentional processing could explain the near-universal pattern of right-lateralisation in this study (e.g., Corbetta & Shulman, 2011; Langner & Eickhoff, 2013; van der Ham et al., 2014). Alternatively, the design of the verbal memory tasks may have encouraged strategies similar to letter-by-letter reading which have been associated with the right hemisphere (e.g., see Ellis et al., 2004, for a review). Future studies could compare these potential causes of the pattern of right-lateralised EEG power observed in this study, as well as measuring EEG power within different time windows to determine if timing was a mediating factor.

4.4 Conclusion

The results of this study suggest that measures of EEG power in the theta and alpha frequency bands may not be sensitive to differences in material-specific processing when stimulus-related attributes are controlled or manipulated, unlike ERP measures (as shown in Chapter 5). These transient effects may have been overshadowed by general, ongoing visual and spatial attentional processes involving the right hemisphere common to all tasks. This

right-lateralisation was unrelated to verbalisation which differed in the expected manner according to the type of material remembered and by task-irrelevant perceptual processing. Further research is needed to cast light on the precise localisation and functional characteristics of the right-lateralised EEG observed in this study.

References

Barr, W. B. (1997). Examining the right temporal lobe's role in nonverbal memory. *Brain and Cognition, 35*(1), 26-41.

Berger, H. (1930). Uber das Elektroenkephalogramm des Menschen. II. *Jour Psychol U Neurol, 40*((5/6)), 160-179.

Blair, R. C., & Karniski, W. (1993). An alternative method for significance testing of waveform difference potentials. *Psychophysiology, 30*(5), 518-524.

Burgess, A. P., & Gruzelier, J. H. (2000). Short duration power changes in the EEG during recognition memory for words and faces. *Psychophysiology, 37*(5), 596-606.

Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. In S. E. Hyman, T. M. Jessell, C. J. Shatz, C. F. Stevens, & H. Y. Zoghbi (Eds.), *Annual Review of Neuroscience, Vol 34* (Vol. 34, pp. 569-599).

Diaz-Asper, C. M., Dopkins, S., Potolicchio, S. J., & Caputy, A. (2006). Spatial memory following temporal lobe resection. *Journal of Clinical and Experimental Neuropsychology, 28*(8), 1462-1481. doi: 10.1080/13803390500434359

Dujardin, K., Bourriez, J. L., & Guieu, J. D. (1994). Event-related desynchronization (ERD) patterns during verbal memory tasks: effect of age. *International Journal of Psychophysiology, 16*(1), 17-27. doi:10.1016/0167-8760(94)90038-8

Ellis, N. C., Natsume, M., Stavropoulou, K., Hoxhallari, L., Daal, V. H., Polyzoe, N., . . . Petalas, M. (2004). The effects of orthographic depth on learning to read alphabetic, syllabic, and logographic scripts. *Reading Research Quarterly, 39*(4), 438-468.

Falk, M. C., Cole, L. C., & Glosser, G. (2002). Pseudoword and real word memory in unilateral temporal lobe epilepsy. *Journal of Clinical and Experimental Neuropsychology, 24*(3), 327-334. doi: 10.1076/jcen.24.3.327.979

Fell, J., Ludowig, E., Staresina, B. P., Wagner, T., Kranz, T., Elger, C. E., & Axmacher, N. (2011). Medial Temporal Theta/Alpha Power Enhancement Precedes Successful

Memory Encoding: Evidence Based on Intracranial EEG. *Journal of Neuroscience, 31*(14), 5392-5397. doi:10.1523/jneurosci.3668-10.2011

Golby, A. J., Poldrack, R. A., Brewer, J. B., Spencer, D., Desmond, J. E., Aron, A. P., & Gabrieli, J. D. E. (2001). Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. *Brain, 124*, 1841-1854. doi: 10.1093/brain/124.9.1841

Good, P. (1994). *Permutation Tests: A Practical Guide to Resampling Methods for Testing Hypotheses.* New York: Springer-Verlag.

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

Gross, M. M. (1972). Hemispheric specialization for processing of visually presented verbal and spatial stimuli. *Perception and Psychophysics, 12*(4), 357-363. doi:10.3758/bf03207222

Guderian, S., & Duzel, E. (2005). Induced theta oscillations mediate large-scale synchrony with mediotemporal areas during recollection in humans. *Hippocampus, 15*(7), 901-912. doi:10.1002/hipo.20125

Hampstead, B. M., Lacey, S., Ali, S., Phillips, P. A., Stringer, A. Y., & Sathian, K. (2010). Use of complex three-dimensional objects to assess visuospatial memory in healthy individuals and patients with unilateral amygdalohippocampectomy. *Epilepsy and Behavior, 18*(1-2), 54-60.

Ille, N., Berg, P., & Scherg, M. (2002). Artefact Correction of the Ongoing EEG Using Spatial Filters Based on Artefact and Brain Signal Topographies. *Journal of Clinical Neurophysiology, 19*(2), 113-124.

Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., . . . Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal

cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron, 20*(5), 927-936. doi: 10.1016/s0896-6273(00)80474-2

Kenny, D. A. (1987). *Statistics for the social and behavioral sciences.* Boston: Little, Brown.

Kessels, R. P. C., de Haan, E. H. F., Kappelle, L. J., & Postma, A. (2001). Varieties of human spatial memory: a meta-analysis on the effects of hippocampal lesions. *Brain Research Reviews, 35*(3), 295-303.

Kessels, R. P. C., Kappelle, L. J., de Haan, E. H. F., & Postma, A. (2002). Lateralization of spatial-memory processes: evidence on spatial span, maze learning, and memory for object locations. *Neuropsychologia, 40*(8), 1465-1473.

Kessels, R. P. C., Nys, G. M. S., Brands, A. M. A., van den Berg, E., & Van Zandvoort, M. J. E. (2006). The modified Location Learning Test: Norms for the assessment of spatial memory function in neuropsychological patients. *Archives of Clinical Neuropsychology, 21*(8), 841-846. doi:10.1016/j.acn.2006.06.015

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews, 29*(2-3), 169-195. doi:10.1016/s0165-0173(98)00056-3

Klimesch, W., Doppelmayr, M., Pachinger, T., & Russegger, H. (1997). Event-related desynchronization in the alpha band and the processing of semantic information. *Cognitive Brain Research, 6*(2), 83-94. doi:10.1016/s0926-6410(97)00018-9

Klimesch, W., Doppelmayr, M., Schwaiger, J., Winkler, T., & Gruber, W. (2000). Theta oscillations and the ERP old/new effect: independent phenomena? *Clinical Neurophysiology, 111*(5), 781-793. doi:10.1016/s1388-2457(00)00254-6

Klimesch, W., Doppelmayr, M., Yonelinas, A., Kroll, N. E., Lazzara, M., Roehm, D., & Gruber, W. (2001). Theta synchronization during episodic retrieval: neural correlates of conscious awareness. *Cognitive Brain Research, 12*(1), 33-38.

Klimesch, W., Freunberger, R., Sauseng, P., & Gruber, W. (2008). A short review of slow phase synchronization and memory: Evidence for control processes in different memory systems? *Brain Research, 1235*, 31-44.

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews, 53*(1), 63-88. doi:10.1016/j.brainresrev.2006.06.003

Kuhn, S., & Gallinat, J. (2014). Segregating Cognitive Functions Within Hippocampal Formation: A Quantitative Meta-analysis on Spatial Navigation and Episodic Memory. *Human Brain Mapping, 35*(4), 1129-1142. doi: 10.1002/hbm.22239

Langner, R., & Eickhoff, S. B. (2013). Sustaining Attention to Simple Tasks: A Meta-Analytic Review of the Neural Mechanisms of Vigilant Attention. *Psychological Bulletin, 139*(4), 870-900. doi:10.1037/a0030694

Lee, T. M. C., Yip, J. T. H., & Jones-Gotman, M. (2002). Memory deficits after resection from left or right anterior temporal lobe in humans: A meta-analytic review. *Epilepsia, 43*(3), 283-291.

Lipsey, M.W. and Wilson, D.B. (2001) *Practical Meta-analysis*. Thousand Oaks, CA: Sage

Manly, B. F. J. (1997). *Randomization, Bootstrap, and Monte Carlo Methods in Biology* (2nd ed.). London: Chapman and Hall.

Martinez, A., Di Russo, F., Anllo-Vento, L., & Hillyard, S. A. (2001). Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clinical Neurophysiology, 112*(11), 1980-1998.

McNicol, D. (1972). *A primer of signal detection theory*. Sydney: Australasian Publishing Company.

Milner, B. (1968). Visual recognition and recall after right temporal-lobe excision in man. *Neuropsychologia, 6*(3), 191-209. doi:10.1016/0028-3932(68)90019-5

Naugle, R. I., Chelune, G. J., Cheek, R., Luders, H., & Awad, I. A. (1993). Detection of changes in material-specific memory following temporal lobectomy using the

Wechsler Memory Scale-Revised. *Archives of Clinical Neuropsychology, 8*(5), 381-395. doi:10.1016/0887-6177(93)90002-i

Pfurtscheller, G., & da Silva, F. H. L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical Neurophysiology, 110*(11), 1842-1857. doi:10.1016/s1388-2457(99)00141-8

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation. *Journal of Experimental Psychology-Human Perception and Performance, 8*(2), 253-272. doi:10.1037/0096-1523.8.2.253

Sherman, E. M. S., Wiebe, S., Fay-McClymont, T. B., Tellez-Zenteno, J., Metcalfe, A., Hernandez-Ronquillo, L., . . . Jette, N. (2011). Neuropsychological outcomes after epilepsy surgery: Systematic review and pooled estimates. *Epilepsia, 52*(5), 857-869. doi:10.1111/j.1528-1167.2011.03022.x

van der Ham, I. J. M., Postma, A., & Laeng, B. (2014). Lateralized perception: The role of attention in spatial relation processing. *Neuroscience and Biobehavioral Reviews, 45*, 142-148. doi:10.1016/j.neubiorev.2014.05.006

Vaz, S. A. M. (2004). Nonverbal memory functioning following right anterior temporal lobectomy: a meta-analytic review. *Seizure-European Journal of Epilepsy, 13*(7), 446-452. doi: 10.1016/j.seizure.2003.12.004

Supplementary Table 1.

Mean response times (*RT*; in milliseconds) for all stimulus types

Memory	Form	Memory*Form	*M*	CI_{low}	CI_{upp}
Verbal			532	648	451
Spatial			459	592	375
	Standard		463	596	379
	Hybrid		525	643	444
		Verbal-standard	476	599	395
		Verbal-hybrid	602	732	512
		Spatial-standard	451	600	362
		Spatial-hybrid	466	596	383

M = mean; CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval.

Supplementary Table 2.

Correlations between differences in *d'* and differences in *EEG* measures, for Memory and Form comparisons.

Difference	ERP measure	*r*	CI_{low}	CI_{upp}	*p*
Mem(Std)	Theta – L	.34	-.03	.66	.14
Mem(Std)	Theta – R	.19	-.15	.49	.43
Mem(Std)	Alpha – L	.29	-.08	.60	.21
Mem(Std)	Alpha – R	.35	-.04	.67	.14
Mem(Hyb)	Theta – L	.32	-.08	.59	.17
Mem(Hyb)	Theta – R	.27	-.08	.54	.24
Mem(Hyb)	Alpha – L	.12	-.35	.48	.61
Mem(Hyb)	Alpha – R	.07	-.47	.53	.76
Frm(Ver)	Theta – L	.13	-.25	.49	.60
Frm(Ver)	Theta – R	-.25	-.65	.37	.29
Frm(Ver)	Alpha – L	-.08	-.53	.28	.73
Frm(Ver)	Alpha – R	-.49	-.77	-.12	.03
Frm(Spa)	Theta – L	.23	-.10	.55	.33
Frm(Spa)	Theta – R	.19	-.12	.49	.41
Frm(Spa)	Alpha – L	-.20	-.50	.19	.41
Frm(Spa)	Alpha – R	-.20	-.58	.17	.39

Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); L = Left; R = Right; Std = Standard; Hyb = Hybrid; *r* = correlation coefficient; CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval (1000x bootstrapped); *p* = significance test (uncorrected).

Supplementary Table 3.

Correlations between differences in *RT* and differences in *EEG* measures, for Memory and Form comparisons.

Difference	ERP measure	*r*	CI_{low}	CI_{upp}	*p*
Mem(Std)	Theta – L	-.13	-.72	.38	.59
Mem(Std)	Theta – R	-.12	-.75	.43	.61
Mem(Std)	Alpha – L	-.20	-.52	.28	.39
Mem(Std)	Alpha – R	-.19	-.61	.19	.42
Mem(Hyb)	Theta – L	-.00	-.48	.48	.99
Mem(Hyb)	Theta – R	.01	-.36	.34	.98
Mem(Hyb)	Alpha – L	-.28	-.59	.19	.23
Mem(Hyb)	Alpha – R	-.09	-.47	.40	.71

Frm(Ver)	Theta – L	.09	-.37	.53	.69
Frm(Ver)	Theta – R	-.02	-.49	.46	.94
Frm(Ver)	Alpha – L	.24	-.23	.82	.32
Frm(Ver)	Alpha – R	.26	-.22	.72	.27
Frm(Non)	Theta – L	.04	-.44	.41	.86
Frm(Non)	Theta – R	.02	-.38	.35	.93
Frm(Non)	Alpha – L	.43	.11	.66	.06
Frm(Non)	Alpha – R	.29	-.06	.64	.21

Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); L = Left; R = Right; Std = Standard; Hyb = Hybrid; *r* = correlation coefficient; CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval (1000x bootstrapped); *p* = significance test (uncorrected).

Supplementary Table 4a.

Descriptive and test statistics for theta (0 to 500 ms) mean amplitude.

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			19.48	10.92	28.03
	Spa			30.44	15.59	45.28
Frm		Std		20.90	10.24	31.57
		Hyb		29.01	16.86	41.16
Hem			L	23.87	14.27	33.47
			R	26.04	12.75	39.34
Mem * Frm	Ver	Std		12.89	6.34	19.44
		Hyb		26.07	14.14	38.00
	Spa	Std		28.92	11.44	46.39
		Hyb		31.95	18.15	45.76
Mem * Hem	Ver		L	18.28	10.43	26.14
			R	20.67	10.79	30.55
	Spa		L	29.46	16.77	42.14
			R	31.42	13.51	49.32
Frm * Hem		Std	L	20.97	11.53	30.40
			R	20.84	8.46	33.21
		Hyb	L	26.77	16.27	37.27
			R	31.25	16.28	46.22
Mem * Frm * Hem	Ver	Std	L	13.34	7.26	19.42
			R	12.44	4.84	20.04
		Hyb	L	23.23	12.22	34.23
			R	28.91	14.86	42.95
	Spa	Std	L	28.60	13.03	44.16
			R	29.24	9.04	49.44
		Hyb	L	30.31	18.88	41.74
			R	33.59	16.13	51.05

4b.

ANOVA Factor	$F(1,19)$	*p*	η_p^2
Mem	5.60	.029	.23
Frm	9.60	.006	.34
Hem	0.46	.507	.02
Mem * Frm	1.75	.202	.08
Mem * Hem	0.02	.881	.00
Frm * Hem	2.77	.112	.13

Mem * Frm * Hem	0.72	.405	.04	

4c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mem * Frm	Std	Mem	2.75	-2.16	.148	0.47	-0.61
	Hyb	Mem	2.75	-1.42	.457	0.78	-0.32
	Ver	Frm	2.75	-3.13	.021	0.69	-0.85
	Spa	Frm	2.75	-0.60	.916	0.80	-0.14
		Mem * Frm	2.75	-1.32	.515	0.22	-0.31
Mem * Hem	L	Mem	2.64	-2.68	.046	0.73	-0.70
	R	Mem	2.64	-1.98	.192	0.82	-0.60
	Ver	Hem	2.64	-0.98	.723	0.86	-0.24
	Spa	Hem	2.64	-0.45	.959	0.88	-0.12
		Mem * Hem	2.64	-0.15	.999	0.86	-0.04
Frm * Hem	L	Frm	2.65	-2.23	.119	0.86	-0.51
	R	Frm	2.65	-3.18	.014	0.89	-0.76
	Std	Hem	2.65	0.05	.999	0.91	0.01
	Hyb	Hem	2.65	-1.06	.687	0.81	-0.27
		Frm * Hem	2.65	1.66	.342	0.58	0.38
Mem *Frm * Hem	Std / L	Mem	3.16	-2.24	.322	0.41	-0.60
	Std / R	Mem	3.16	-1.97	.478	0.48	-0.55
	Hyb / L	Mem	3.16	-1.88	.539	0.75	-0.42
	Hyb / R	Mem	3.16	-0.94	.970	0.80	-0.22
	Ver / L	Frm	3.16	-2.48	.211	0.66	-0.66
	Ver / R	Frm	3.16	-3.15	.051	0.63	-0.83
	Spa / L	Frm	3.16	-0.36	.999	0.76	-0.09
	Spa / R	Frm	3.16	-0.76	.992	0.81	-0.17
	Ver / Std	Hem	3.16	0.44	.999	0.83	0.11
	Ver / Hyb	Hem	3.16	-1.45	.799	0.81	-0.35
	Spa / Std	Hem	3.16	-0.15	.999	0.91	-0.04
	Spa / Hyb	Hem	3.16	-0.66	.996	0.82	-0.18
	Std	Mem * Hem	3.16	0.37	.999	0.87	0.09
	Hyb	Mem * Hem	3.16	-0.80	.989	0.80	-0.19
	Ver	Frm * Hem	3.16	1.68	.669	0.67	0.39
	Spa	Frm * Hem	3.16	0.81	.988	0.82	0.19

Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); L = Left; R = Right; Std = Standard; Hyb = Hybrid; *M* = mean; CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval; $t_{critical}$ = critical *t*-value derived from permutation method; *t* = observed *t*-statistic; p_p = permutation significance test (10000x repetitions); *r* = correlation coefficient between tested means; *d* = effect size.

Supplementary Table 5a.

Descriptive and test statistics for theta (0 to 500 ms) mean amplitude of repetition effects (old - new)

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			2.75	-2.18	7.69
	Spa			-3.79	-9.56	1.99
Frm		Std		3.21	-1.59	8.02
		Hyb		-4.25	-10.29	1.80
Hem			L	1.51	-3.17	6.19
			R	-2.54	-6.38	1.30
Mem * Frm	Ver	Std		7.77	1.10	14.45
		Hyb		-2.27	-8.18	3.65
	Spa	Std		-1.35	-8.90	6.21
		Hyb		-6.23	-16.01	3.56
Mem * Hem	Ver		L	6.12	-0.08	12.32

			R	-0.61	-6.08	4.85
	Spa		L	-3.10	-9.51	3.31
			R	-4.47	-11.11	2.17
Frm * Hem		Std	L	6.95	1.50	12.41
			R	-0.52	-7.07	6.02
		Hyb	L	-3.93	-10.08	2.22
			R	-4.56	-11.33	2.22
Mem * Frm * Hem	Ver	Std	L	11.01	2.99	19.03
			R	4.54	-3.59	12.66
		Hyb	L	1.23	-5.72	8.18
			R	-5.76	-12.50	0.97
	Spa	Std	L	2.90	-3.74	9.53
			R	-5.59	-16.24	5.07
		Hyb	L	-9.10	-19.04	0.84
			R	-3.35	-14.40	7.70

5b.

ANOVA Factor	$F(1,19)$	p	η_p^2
Mem	2.97	.101	.14
Frm	3.63	.072	.16
Hem	3.41	.080	.15
Mem * Frm	0.58	.454	.03
Mem * Hem	1.86	.189	.09
Frm * Hem	3.23	.088	.15
Mem * Frm * Hem	4.00	.060	.17

5c.

	M	CI_{low}	CI_{upp}	t	p
Rep (grand average)	-0.52	-3.58	2.98	-0.30	.770

5d.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mem * Frm	Std	Mem	2.82	1.81	.283	-0.09	0.41
	Hyb	Mem	2.82	0.77	.860	0.13	0.18
	Ver	Frm	2.82	2.68	.065	0.23	0.60
	Spa	Frm	2.82	0.78	.857	-0.13	0.18
		Mem * Frm	2.82	0.76	.863	0.12	0.17
Mem * Hem	L	Mem	2.83	2.28	.140	0.10	0.51
	R	Mem	2.83	0.86	.824	-0.20	0.19
	Ver	Hem	2.83	2.25	.148	0.43	0.51
	Spa	Hem	2.83	0.47	.962	0.57	0.11
		Mem * Hem	2.83	1.36	.534	0.58	0.31
Frm * Hem	L	Frm	2.76	3.30	.016	0.30	0.74
	R	Frm	2.76	0.78	.867	-0.33	0.17
	Std	Hem	2.76	2.15	.166	0.28	0.49
	Hyb	Hem	2.76	0.28	.991	0.75	0.06
		Frm * Hem	2.76	1.80	.297	0.68	0.45
Mem *Frm * Hem	Std / L	Mem	3.33	1.72	.672	0.10	0.39
	Std / R	Mem	3.33	1.55	.776	-0.05	0.35
	Hyb / L	Mem	3.33	1.81	.615	0.03	0.41
	Hyb / R	Mem	3.33	-0.41	.999	0.11	-0.10
	Ver / L	Frm	3.33	2.42	.278	0.37	0.54

Ver / R	Frm	3.33	2.12	.420	0.07	0.48
Spa / L	Frm	3.33	2.28	.341	0.16	0.52
Spa / R	Frm	3.33	-0.27	.999	-0.25	-0.06
Ver / Std	Hem	3.33	1.49	.805	0.37	0.33
Ver / Hyb	Hem	3.33	2.13	.416	0.50	0.48
Spa / Std	Hem	3.33	1.91	.552	0.50	0.46
Spa / Hyb	Hem	3.33	-1.57	.765	0.74	-0.35
Std	Mem * Hem	3.33	-0.37	.999	0.58	-0.09
Hyb	Mem * Hem	3.33	2.36	.302	0.57	0.53
Ver	Frm * Hem	3.33	-0.11	.999	0.42	-0.02
Spa	Frm * Hem	3.33	2.49	.248	0.72	0.63

Rep = Repetition (Old - New); Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); L = Left; R = Right; Std = Standard; Hyb = Hybrid; *M* = mean; CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval; $t_{critical}$ = critical *t*-value derived from permutation method; *t* = observed *t*-statistic; p_p = permutation significance test (10000x repetitions); *r* = correlation coefficient between tested means; *d* = effect size.

Supplementary Table 6a.
Descriptive and test statistics for theta (500 to 1500 ms) mean amplitude

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			2.88	-3.51	9.28
	Spa			-3.35	-10.04	3.34
Frm		Std		-1.08	-7.19	5.04
		Hyb		0.61	-6.23	7.45
Hem			L	2.01	-3.51	7.52
			R	-2.47	-9.17	4.23
Mem * Frm	Ver	Std		2.49	-3.69	8.66
		Hyb		3.28	-5.10	11.66
	Spa	Std		-4.64	-13.09	3.81
		Hyb		-2.06	-8.58	4.47
Mem * Hem	Ver		L	4.73	-1.19	10.65
			R	1.04	-6.22	8.30
	Spa		L	-0.72	-7.19	5.75
			R	-5.98	-13.16	1.20
Frm * Hem		Std	L	1.36	0.00	7.08
			R	-3.51	-10.20	3.19
		Hyb	L	2.65	-3.75	9.06
			R	-1.43	-9.00	6.13
Mem * Frm * Hem	Ver	Std	L	4.55	-1.31	10.42
			R	0.42	-6.37	7.21
		Hyb	L	4.91	-2.67	12.48
			R	1.66	-8.06	11.37
	Spa	Std	L	-1.84	-9.94	6.25
			R	-7.43	-16.55	1.68
		Hyb	L	0.40	-6.35	7.15
			R	-4.52	-11.18	2.15

6b.

ANOVA Factor	*F*(1,19)	*p*	η_p^2
Mem	6.26	.022	.25
Frm	0.52	.480	.03
Hem	13.87	.001	.42

Mem * Frm	0.13	.721	.01
Mem * Hem	0.80	.383	.04
Frm * Hem	0.57	.461	.03
Mem * Frm * Hem	0.01	.943	.00

6c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mem * Frm	Std	Mem	2.68	1.79	.290	0.38	0.41
	Hyb	Mem	2.68	1.81	.281	0.68	0.42
	Ver	Frm	2.68	-0.23	.996	0.54	-0.05
	Spa	Frm	2.68	-0.77	.857	0.59	-0.18
		Mem * Frm	2.68	0.36	.984	0.01	0.08
Mem * Hem	L	Mem	2.76	2.02	.201	0.59	0.45
	R	Mem	2.76	2.72	.054	0.72	0.61
	Ver	Hem	2.76	2.27	.129	0.89	0.55
	Spa	Hem	2.76	3.94	.005	0.92	0.91
		Mem * Hem	2.76	-0.89	.786	0.78	-0.20
Frm * Hem	L	Frm	2.78	-0.54	.946	0.66	-0.12
	R	Frm	2.78	-0.87	.809	0.76	-0.20
	Std	Hem	2.78	4.22	.003	0.94	1.03
	Hyb	Hem	2.78	2.83	.045	0.92	0.68
		Frm * Hem	2.78	0.75	.869	0.91	0.17
Mem *Frm * Hem	Std / L	Mem	3.26	1.62	.694	0.33	0.37
	Std / R	Mem	3.26	1.85	.548	0.40	0.42
	Hyb / L	Mem	3.26	1.45	.785	0.60	0.33
	Hyb / R	Mem	3.26	1.85	.544	0.70	0.45
	Ver / L	Frm	3.26	-0.11	.999	0.54	-0.03
	Ver / R	Frm	3.26	-0.31	.999	0.53	-0.07
	Spa / L	Frm	3.26	-0.64	.996	0.52	-0.14
	Spa / R	Frm	3.26	-0.87	.980	0.65	-0.21
	Ver / Std	Hem	3.26	2.98	.085	0.91	0.70
	Ver / Hyb	Hem	3.26	1.42	.803	0.88	0.35
	Spa / Std	Hem	3.26	3.40	.037	0.93	0.80
	Spa / Hyb	Hem	3.26	3.31	.045	0.89	0.74
	Std	Mem * Hem	3.26	-0.74	.990	0.89	-0.17
	Hyb	Mem * Hem	3.26	-0.65	.995	0.69	-0.15
	Ver	Frm * Hem	3.26	0.46	.999	0.88	0.11
	Spa	Frm * Hem	3.26	0.41	.999	0.89	0.09

Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); L = Left; R = Right; Std = Standard; Hyb = Hybrid; *M* = mean; CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval; $t_{critical}$ = critical *t*-value derived from permutation method; *t* = observed *t*-statistic; p_p = permutation significance test (10000x repetitions); *r* = correlation coefficient between tested means; *d* = effect size.

Supplementary Table 7a.

Descriptive and test statistics for theta (500 to 1500 ms) mean amplitude of repetition effects (old - new)

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			-3.96	-8.53	0.61
	Spa			0.43	-3.73	4.60
Frm		Std		0.66	-3.22	4.54
		Hyb		-4.19	-9.39	1.02

Hem			L	-0.91	-5.17	3.36
			R	-2.62	-6.41	1.17
Mem * Frm	Ver	Std		-3.12	-8.27	2.03
		Hyb		-4.80	-10.88	1.28
	Spa	Std		4.44	-1.07	9.95
		Hyb		-3.58	-10.28	3.13
Mem * Hem	Ver		L	-2.99	-7.77	1.78
			R	-4.92	-10.27	0.43
	Spa		L	1.18	-4.21	6.57
			R	-0.32	-4.51	3.88
Frm * Hem		Std	L	1.71	-3.08	6.49
			R	-0.38	-4.65	3.88
		Hyb	L	-3.52	-8.90	1.87
			R	-4.85	-10.81	1.10
Mem * Frm * Hem	Ver	Std	L	-3.29	-9.96	3.39
			R	-2.95	-8.31	2.41
		Hyb	L	-2.70	-7.78	2.38
			R	-6.89	-15.45	1.66
	Spa	Std	L	6.70	0.98	12.41
			R	2.18	-4.08	8.44
		Hyb	L	-4.33	-12.61	3.94
			R	-2.82	-9.56	3.93

7b.

ANOVA Factor	$F(1,19)$	p	η_p^2
Mem	3.56	.075	.16
Frm	3.27	.087	.15
Hem	1.04	.320	.05
Mem * Frm	1.42	.248	.07
Mem * Hem	0.02	.883	.00
Frm * Hem	0.07	.795	.00
Mem * Frm * Hem	3.16	.092	.14

7c.

	M	CI_{low}	CI_{upp}	t	p
Rep (grand average)	-1.76	-5.23	1.60	-1.02	.340

7d.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mem * Frm	Std	Mem	2.76	-2.16	.152	0.06	-0.48
	Hyb	Mem	2.76	-0.34	.982	0.32	-0.08
	Ver	Frm	2.76	0.53	.945	0.32	0.12
	Spa	Frm	2.76	1.86	.250	-0.08	0.42
		Mem * Frm	2.76	-1.19	.612	-0.13	-0.27
Mem * Hem	L	Mem	2.78	-1.57	.421	0.41	-0.35
	R	Mem	2.78	-1.63	.388	0.25	-0.37
	Ver	Hem	2.78	0.92	.795	0.63	0.21
	Spa	Hem	2.78	0.64	.916	0.50	0.15
		Mem * Hem	2.78	0.15	.999	0.44	0.03
Frm * Hem	L	Frm	2.82	1.96	.239	0.40	0.44

	R	Frm	2.82	1.33	.558	0.07	0.30
	Std	Hem	2.82	0.93	.790	0.47	0.21
	Hyb	Hem	2.82	0.62	.925	0.68	0.14
		Frm * Hem	2.82	0.26	.994	0.57	0.06
Mem *Frm * Hem	Std / L	Mem	3.28	-2.63	.182	0.19	-0.59
	Std / R	Mem	3.28	-1.35	.865	0.07	-0.30
	Hyb / L	Mem	3.28	0.40	.999	0.26	0.09
	Hyb / R	Mem	3.28	-0.87	.985	0.20	-0.20
	Ver / L	Frm	3.28	-0.17	.999	0.31	-0.04
	Ver / R	Frm	3.28	0.87	.985	0.14	0.20
	Spa / L	Frm	3.28	2.49	.237	0.16	0.57
	Spa / R	Frm	3.28	1.05	.957	-0.17	0.24
	Ver / Std	Hem	3.28	-0.11	.999	0.46	-0.03
	Ver / Hyb	Hem	3.28	1.24	.908	0.56	0.31
	Spa / Std	Hem	3.28	2.00	.491	0.69	0.45
	Spa / Hyb	Hem	3.28	-0.46	.999	0.59	-0.11
	Std	Mem * Hem	3.28	-1.65	.708	0.70	-0.37
	Hyb	Mem * Hem	3.28	1.12	.940	0.33	0.25
	Ver	Frm * Hem	3.28	-0.93	.979	0.26	-0.21
	Spa	Frm * Hem	3.28	1.89	.562	0.76	0.42

Rep = Repetition (Old - New); Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); L = Left; R = Right; Std = Standard; Hyb = Hybrid; *M* = mean; CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval; $t_{critical}$ = critical *t*-value derived from permutation method; *t* = observed *t*-statistic; p_p = permutation significance test (10000x repetitions); *r* = correlation coefficient between tested means; *d* = effect size.

Supplementary Table 8a.

Descriptive and test statistics for alpha (0 to 500 ms) mean amplitude

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			-14.45	-22.39	-6.51
	Spa			-18.79	-28.94	-8.63
Frm		Std		-15.16	-23.35	-6.97
		Hyb		-18.08	-27.59	-8.57
Hem			L	-13.41	-22.17	-4.65
			R	-19.83	-28.81	-10.85
Mem * Frm	Ver	Std		-11.44	-19.14	-3.74
		Hyb		-17.46	-27.05	-7.87
	Spa	Std		-18.87	-29.39	-8.35
		Hyb		-18.70	-29.37	-8.03
Mem * Hem	Ver		L	-11.55	-19.56	-3.54
			R	-17.35	-25.71	-8.99
	Spa		L	-15.26	-25.79	-4.73
			R	-22.31	-32.63	-11.99
Frm * Hem		Std	L	-11.68	-19.91	-3.45
			R	-18.64	-27.39	-9.88
		Hyb	L	-15.13	-24.98	-5.28
			R	-21.02	-30.57	-11.48
Mem * Frm * Hem	Ver	Std	L	-8.41	-16.54	-0.28
			R	-14.47	-22.65	-6.30
		Hyb	L	-14.69	-24.19	-5.19
			R	-20.23	-30.27	-10.18
	Spa	Std	L	-14.95	-25.53	-4.36
			R	-22.80	-33.99	-11.61
		Hyb	L	-15.58	-26.89	-4.27

				R	-21.82	-32.43	-11.22

8b.

ANOVA Factor	$F(1,19)$	p	η_p^2
Mem	2.56	.126	.12
Frm	2.52	.129	.12
Hem	12.57	.002	.40
Mem * Frm	1.48	.240	.07
Mem * Hem	0.38	.547	.02
Frm * Hem	0.44	.516	.02
Mem * Frm * Hem	0.10	.759	.01

8c.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	t	p_p	r	d
Mem * Frm	Std	Mem	2.70	1.84	.254	0.61	0.43
	Hyb	Mem	2.70	0.37	.978	0.76	0.08
	Ver	Frm	2.70	1.77	.284	0.68	0.41
	Spa	Frm	2.70	-0.06	.999	0.84	-0.01
		Mem * Frm	2.70	1.21	.591	0.06	0.27
Mem * Hem	L	Mem	2.78	1.18	.594	0.78	0.28
	R	Mem	2.78	1.88	.246	0.85	0.45
	Ver	Hem	2.78	3.04	.027	0.88	0.68
	Spa	Hem	2.78	3.15	.022	0.90	0.71
		Mem * Hem	2.78	-0.61	.909	0.76	-0.14
Frm * Hem	L	Frm	2.76	1.53	.437	0.88	0.36
	R	Frm	2.76	1.39	.519	0.93	0.32
	Std	Hem	2.76	3.23	.018	0.86	0.73
	Hyb	Hem	2.76	3.27	.017	0.93	0.73
		Frm * Hem	2.76	0.66	.913	0.70	0.16
Mem *Frm * Hem	Std / L	Mem	3.28	1.48	.785	0.54	0.34
	Std / R	Mem	3.28	1.98	.489	0.62	0.46
	Hyb / L	Mem	3.28	0.27	.999	0.79	0.06
	Hyb / R	Mem	3.28	0.42	.999	0.71	0.09
	Ver / L	Frm	3.28	1.76	.624	0.65	0.40
	Ver / R	Frm	3.28	1.61	.708	0.68	0.37
	Spa / L	Frm	3.28	0.22	.999	0.85	0.05
	Spa / R	Frm	3.28	-0.29	.999	0.79	-0.07
	Ver / Std	Hem	3.28	2.38	.280	0.79	0.53
	Ver / Hyb	Hem	3.28	3.06	.079	0.93	0.69
	Spa / Std	Hem	3.28	2.92	.105	0.87	0.66
	Spa / Hyb	Hem	3.28	2.58	.200	0.89	0.58
	Std	Mem * Hem	3.28	-0.60	.998	0.76	-0.13
	Hyb	Mem * Hem	3.28	-0.31	.999	0.80	-0.07
	Ver	Frm * Hem	3.28	0.23	.999	0.80	0.05
	Spa	Frm * Hem	3.28	0.64	.997	0.69	0.15

Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); L = Left; R = Right; Std = Standard; Hyb = Hybrid; M = mean; CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval; $t_{critical}$ = critical t-value derived from permutation method; t = observed t-statistic; p_p = permutation significance test (10000x repetitions); r = correlation coefficient between tested means; d = effect size.

Supplementary Table 9a.
Descriptive and test statistics for alpha (0 to 500 ms) mean amplitude of repetition effects (old - new)

ANOVA Factor	Mem	Frm	Hem	*M*	CI_{low}	CI_{upp}
Mem	Ver			0.66	-3.75	5.06
	Spa			-1.55	-6.08	2.97
Frm		Std		1.16	-3.92	6.24
		Hyb		-2.06	-5.76	1.65
Hem			L	-1.54	-5.36	2.28
			R	0.64	-3.15	4.43
Mem * Frm	Ver	Std		1.17	-5.18	7.52
		Hyb		0.14	-6.09	6.37
	Spa	Std		1.15	-5.98	8.28
		Hyb		-4.25	-8.29	-0.22
Mem * Hem	Ver		L	-0.24	-4.97	4.50
			R	1.55	-3.74	6.84
	Spa		L	-2.84	-8.16	2.49
			R	-0.27	-5.47	4.94
Frm * Hem		Std	L	-1.24	-7.27	4.79
			R	3.56	-2.22	9.34
		Hyb	L	-1.83	-6.32	2.66
			R	-2.28	-6.52	1.97
Mem * Frm * Hem	Ver	Std	L	-0.10	-7.48	7.28
			R	2.44	-5.05	9.94
		Hyb	L	-0.37	-7.25	6.51
			R	0.66	-6.16	7.48
	Spa	Std	L	-2.38	-11.06	6.30
			R	4.68	-3.00	12.35
		Hyb	L	-3.30	-9.77	3.18
			R	-5.21	-10.31	-0.12

9b.

ANOVA Factor	$F(1,19)$	p	η_p^2
Mem	0.64	.434	.03
Frm	1.38	.255	.07
Hem	1.77	.199	.09
Mem * Frm	0.62	.440	.03
Mem * Hem	0.05	.832	.00
Frm * Hem	1.75	.202	.08
Mem * Frm * Hem	1.11	.306	.06

9c.

	M	CI_{low}	CI_{upp}	*t*	*p*
Rep (grand average)	-0.45	-3.60	2.85	-0.28	.790

9d.

Interaction contrasts	*Fixed*	*Tested*	$t_{critical}$	*t*	p_p	*r*	*d*
Mem * Frm	Std	Mem	2.82	0.01	.999	0.13	0.00
	Hyb	Mem	2.82	1.24	.584	0.00	0.28
	Ver	Frm	2.82	0.24	.994	-0.02	0.05
	Spa	Frm	2.82	1.56	.396	0.26	0.37

		Mem * Frm	2.82	-0.79	.841	0.00	-0.18
Mem * Hem	L	Mem	2.84	0.83	.818	0.15	0.19
	R	Mem	2.84	0.52	.946	0.04	0.12
	Ver	Hem	2.84	-0.78	.847	0.54	-0.17
	Spa	Hem	2.84	-1.00	.722	0.48	-0.22
		Mem * Hem	2.84	0.22	.996	0.40	0.05
Frm * Hem	L	Frm	2.82	0.17	.998	0.03	0.04
	R	Frm	2.82	1.82	.280	0.12	0.41
	Std	Hem	2.82	-1.67	.352	0.48	-0.37
	Hyb	Hem	2.82	0.20	.997	0.44	0.04
		Frm * Hem	2.82	-1.32	.548	0.31	-0.30
Mem *Frm * Hem	Std / L	Mem	3.27	0.45	.999	0.12	0.10
	Std / R	Mem	3.27	-0.48	.999	0.16	-0.11
	Hyb / L	Mem	3.27	0.62	.998	-0.10	0.14
	Hyb / R	Mem	3.27	1.44	.816	-0.01	0.33
	Ver / L	Frm	3.27	0.05	.999	-0.12	0.01
	Ver / R	Frm	3.27	0.39	.999	0.09	0.09
	Spa / L	Frm	3.27	0.17	.999	-0.03	0.04
	Spa / R	Frm	3.27	2.64	.182	0.30	0.61
	Ver / Std	Hem	3.27	-0.69	.997	0.46	-0.15
	Ver / Hyb	Hem	3.27	-0.38	.999	0.65	-0.08
	Spa / Std	Hem	3.27	-1.83	.599	0.52	-0.41
	Spa / Hyb	Hem	3.27	0.48	.999	-0.04	0.11
	Std	Mem * Hem	3.27	0.92	.977	0.50	0.21
	Hyb	Mem * Hem	3.27	-0.56	.998	0.30	-0.13
	Ver	Frm * Hem	3.27	-0.33	.999	0.56	-0.07
	Spa	Frm * Hem	3.27	-1.50	.785	0.15	-0.34

Rep = Repetition (Old - New); Mem = Memory (Verbal - Spatial); Frm = Form (Standard - Hybrid); L = Left; R = Right; Std = Standard; Hyb = Hybrid; *M* = mean; CI_{low}/CI_{upp} = lower/upper bounds of 95% confidence interval; $t_{critical}$ = critical *t*-value derived from permutation method; *t* = observed *t*-statistic; p_p = permutation significance test (10000x repetitions); *r* = correlation coefficient between tested means; *d* = effect size.

Chapter 7: General Discussion

The aim of this thesis was to investigate the impact of different factors on the lateralisation of memory functions to the right hemisphere of the brain. This thesis topic was inspired by the limitations of the dominant model of hemispheric lateralisation, material specificity, which predicts that the left hemisphere mediates memory for verbal material and the right hemisphere mediates memory for nonverbal material, which have led to significant challenges with the clinical assessment of the right temporal lobe. The main limitations of material specificity as discussed in Chapter 1 include the vagueness of the concept of nonverbal memory (e.g., Smith, Malec, & Ivnik, 1992), the ease of verbalisability of putatively nonverbal stimuli (e.g., Barr, 1997), and the poor clinical and experimental testing of material specific effects relative to other potential lateralising factors (e.g., Habib, Nyberg, & Tulving, 2003). The primary focus of this thesis was to examine the effect on lateralisation of three factors related to material specificity: i) the type of nonverbal stimulus (i.e., abstract designs, faces, spatial), ii) differences in task-related processing (e.g., encoding versus retrieval), and iii) potential lower-level stimulus confounds (i.e., memory versus perceptual processing). The eventual goal is to use these findings to help improve neuropsychological assessment of memory functions affected by pathology in the right hemisphere

1. Material type was the dominant lateralising influence

The results of this thesis suggested that memory for nonverbal material per se was consistently associated with right hemispheric function. While Chapter 3 showed interactions between material type, processing type and brain region, and Chapter 4 showed an independent effect of processing, overall this thesis showed that the influence of material on right-lateralisation was more reliable than the influence of type of memory processing. Furthermore, the association between right-lateralised brain activity and nonverbal memory function was shown to occur over and above the potentially confounding effects of perceptual processing. Supporting the notion of a unique association between nonverbal memory and the right hemisphere, the empirical chapters showed that brain activity during nonverbal memory

tasks never showed left-lateralisation relative to verbal memory tasks, while conversely the verbal memory tasks never showed right-lateralisation relative to the nonverbal memory tasks. Furthermore, the joint results of the meta-analysis and empirical chapters showed the association was consistent across clinical and healthy populations, whether published neuropsychological tests or experimental tests were used, and across different task demands including: different types of learning formats, delays before testing, and different processing demands.

2. Delineating the limitations of material specificity

The overall pattern of findings in this thesis suggests that, despite the limitation of the material specificity model, material type may be the primary factor influencing the right-lateralisation of memory function. This thesis revealed important limitations and caveats to this general pattern, however. The meta-analysis revealed that in presurgical temporal lobe epilepsy (TLE) patients while the capacity of clinical nonverbal memory tests to detect right- versus left-sided pathology was consistent the effects were uniformly small in size (*d*s ~ 0.2), regardless of the type of nonverbal stimulus or task demands. These small-sized effects reflect the notorious lack of reliability in using nonverbal memory tests to detect damage in the right temporal region (e.g., Baxendale, Thompson, & Duncan, 2008; Lee, Yip, & Jones-Gotman, 2002; Vaz, 2004). Therefore, more work is needed to determine the critical mechanisms underlying the right-lateralisation of memory abilities to better predict right temporal lobe pathology in presurgical TLE patients. As a group, spatial learning tests showed a marginally significant medium-sized effect in presurgical patients, suggesting they may hold the greatest promise and should therefore be the focus of future investigations.

The results in postsurgical TLE patients also highlighted another key weakness of the material specificity model, since tests of facial memory or spatial memory were more effective (medium-sized effects) than tests of abstract design memory (small-sized effects) at discriminating right- from left-resected patients. These findings suggest that the right hemisphere may be more specialised for remembering faces or spatial information than

designs, undermining the explanatory power of a nonverbal construct specifically and of the material specificity model more generally. The findings for face memory supported previous meta-analytic reviews (Sherman et al., 2011; Vaz, 2004), and the results for spatial memory extended previous findings with experimental spatial memory tests to clinical memory tests (e.g., Kessels et al., 2001). Conceivably, these patterns of results could be explained by the alternative spatial frequency model (Sergent, 1982), since both face and spatial stimuli require attention predominantly to low spatial frequency features, posited to be preferentially processed in the right hemisphere (e.g., Awasthi, Sowman, Friedman, & Williams, 2013; Peyrin et al., 2003), whereas abstract design stimuli (e.g., the Rey Complex Figure Test) typically involve a mixture of low and high frequency features which are processed in both hemispheres. Alternatively, the results could be explained by the fact that abstract design stimuli are easier to verbalise than facial/spatial stimuli, as suggested in previous studies (e.g., Golby et al., 2001), or there are correlated contributions of spatial frequency and verbalisability. Neither of these proposals could be systematically tested in the meta-analysis, however, and so remain speculative until explored in future studies.

While the experimental nonverbal memory tasks used in the empirical chapters produced consistent right-lateralisation of EEG measures, the verbal memory tasks did not show complementary left-lateralisation. Therefore, the results did not support the double dissociation of lateralisation by material type expected by material specificity. This overall pattern of findings contrasts with the majority of previous evidence that showed stronger support for the verbal, left hemispheric component of material specificity than for the nonverbal, right hemispheric component (e.g., Lee, Yip, & Jones-Gotman, 2002). The pseudowords and trigrams that were used as verbal stimuli lacked semantic content and it is possible this decreased the involvement of the left hemisphere, consistent with previous a study that showed lower left-lateralisation of the Blood Oxygen Level Dependent (BOLD) response within the medial temporal regions for meaningless than meaningful words (Martin et al., 1997).

An influential review of speech networks, however, has suggested that the semantic aspects of word processing are relatively bilaterally distributed while the articulatory aspects of speech are more left-lateralised (Hickok & Poeppel, 2007). Therefore, the fact that the verbal tasks were visual and not requiring the comprehension or production of speech is probably the most important difference between the experimental verbal memory tasks used and those used in the successful left-lateralisation of temporal lobe pathology in clinical studies (e.g., Alpherts et al., 2006). The use of meaningful words as verbal stimuli, however, would have resulted in confounding semantics (semantic versus non-semantic) and modality (auditory versus visual) with the material type and reduced the interpretability of the results. Therefore, while the verbal memory tasks fulfilled an important role as controls for the nonverbal memory tasks in the context of each experiment, the trade-off was that they were not designed to maximise the degree of left-lateralisation. In general, this suggests that the specific type of stimuli, whether concerning memory for nonverbal or verbal materials, has a very strong impact on the degree and direction of the lateralisation observed.

In the empirical chapters, only one type of nonverbal memory task was used, involving memory for spatial patterns within irregularly arranged positions without a grid. This task required memory for precise distances and positional inter-relationships, a very specific type of spatial information, with minimal variation across the two empirical studies. This task does not necessarily reflect those used in experimental studies which more commonly involve object-location or navigational paradigms (e.g., Kessels et al., 2001; Kuhn & Gallinat, 2014). The experimental task was also unlike most clinical nonverbal memory tests, including tests of spatial memory (cf. the 7/24 Spatial Learning test, for example). It was arguably most similar to the Brown Location Test (Brown et al., 2010), which interestingly showed a strong capacity (d = 1.56) to discriminate right from left presurgical TLE patients in the meta-analysis (Chapter 2).

The experimental spatial memory tasks were also resistant to verbalisation, as shown by lower ratings of verbalisation compared to the verbal memory tasks. This supports a range

of studies indicating the importance of using tasks with low verbalisability to maximise their sensitivity to right hemispheric processing (e.g., Hampstead et al., 2010), and suggests this factor may have contributed to the strong and consistent pattern of right-lateralisation produced by these specific tasks. As these tasks were only compared to verbal stimuli however, it is not clear whether they have a low level of verbalisability compared to other types of nonverbal stimuli (e.g., abstract designs). Other studies have shown that novel patterns were less verbalisable and more right-lateralised than scenes or faces, and that 3D spatial "towers" made of blocks were less verbalisable and more efficient at identifying right temporal lobe pathology than colour-colour association tasks, so it is conceivable that this would be the case for the very novel and spatial stimuli (Hampstead et al., 2010; Golby et al., 2001).

In sum, while the experimental task and its variants showed consistent right-lateralisation they were not necessarily representative of nonverbal memory tasks more generally. Therefore, with respect to understanding the mechanisms underlying the right-lateralisation of memory, the results strongly suggest that memory for precise distances and positional inter-relationships are an important factor, but cannot necessarily be extrapolated to support the use of any and all types of nonverbal memory tasks in clinical settings.

3. Processing-specific lateralisation

3.1 Task demands in clinical nonverbal memory tests had no effect on right-lateralisation

The meta-analysis examined whether task demands had an impact on the degree to which nonverbal memory tests could predict right- versus left -lateralised pathology in TLE patients. The task demands that were examined primarily included whether the memory tasks i) had single or multiple learning trials, and ii) tested memory immediately after learning, during learning, or after a long delay. The results strongly indicated these task demands had highly inconsistent effects on the lateralising capacity of nonverbal memory tests, supporting some previous findings (Barr et al., 1997; Vaz, 2004), but not supporting other evidence in favour of using multiple, repeated learning trials rather than single learning trials (e.g., Jones-

Gotman, Harnadek, & Kubu, 2000), and findings showing that delayed spatial memory is more right-lateralised than memory tested immediately after learning (Kuhn & Gallinat, 2014).

Despite the overall lack of consistent findings, it remains possible that the lateralising effects of stimulus type and task demands may interact in a complex manner. For example, differences in favour of immediate over delayed memory testing for face stimuli contrasted with an advantage of delayed over immediate memory for spatial stimuli. It is unclear why this may be the case. Due to the small number of studies involved in this pattern of findings, however, it may reflect the disproportionate effects of specific memory tests more than a generalised pattern. Taken together, these findings of the meta-analysis concerning task demands provide a novel contribution to the clinical literature as there had been no previous synthesis regarding their effects on lateralisation.

3.2 Evidence for processing-related lateralisation and interactions with material type and brain region

In contrast to the findings of the meta-analysis, the experimental study in Chapter 3 showed effects of processing type on lateralisation that were independent of and interacted with those due to the type of material. Nonverbal material was consistently associated with right-lateralisation of ERP peaks during both encoding and retrieval, in the frontal and parietal regions, and for each individual combination of process type and brain region. The type of processing also had an effect in frontal regions, with greater left-lateralisation during encoding (N270 peak) and greater right-lateralisation during retrieval (VPP, vertex positive potential), supporting the hemispheric encoding retrieval hypothesis of lateralisation (e.g., Habib et al., 2003). In parietal regions, by contrast, the results showed the opposite pattern to HERA for nonverbal material, with encoding showing greater right lateralisation than retrieval (N170), or showed no effect of processing type (P300).

The findings of this study support previous evidence of differences in processing type exhibit stronger effects on lateralisation in the anterior brain region (focused on the prefrontal

cortex) than in posterior regions (Nyberg et al., 2000). The region-dependent interaction between processing type and material could suggest, in parallel to the material specificity model, the HERA model explains the pattern of processing-specific lateralisation more effectively for verbal material better than it does for nonverbal material. Alternatively, the HERA model may simply only apply in frontal regions. These are exciting possibilities that could be explored further.

The study also suggests that expanding the scope of investigation beyond the use of PET/fMRI methods focused on the prefrontal cortex may yield important insights about processing-related lateralisation. There may even be potential clinical implications for patients with unilateral TLE, as suggested by one fMRI study which showed independent effects of material and processing within medial temporal lobe structures (Kennepohl, Sziklas, Garver, Wagner, & Jones-Gotman, 2007). The pattern of results also suggests that rather than either material specificity or HERA needing to predominate over the other, both may contribute to lateralisation during memory tasks, supporting previous arguments by the proponents of HERA (Habib et al., 2003). Unlike many neuroimaging studies, the study was designed in a way that adequately tested both theories, rather than only testing one within the context of the other (an in-depth of discussion of this issue is presented by Habib et al., 2003).

The use of ERP measures also permitted an original perspective of the relative timing of memory-related lateralisation effects, and importantly is the first known study using this technique to directly compare material specificity to HERA. In terms of the timing of the lateralisation effects, this study suggests they occurred within the first 350 ms after a stimulus is presented, including within the earliest time window of the N170 peak (140 to 220 ms). This finding supports previous reports of memory effects within this time period in theta-frequency power (e.g., Klimesch, Doppelmayr, Pachinger, & Russegger, 1997) and suggests that ERP measures could be sensitive to early aspects of memory processing that may not be detected using PET/fMRI measures with lower temporal resolution.

These findings were interpreted cautiously given the novelty of our experimental

method compared to previous studies, and since the same effect was not replicated in full by the EEG frequency measures in Chapter 4. Nonetheless, these findings do suggest a way to reconcile studies that support material specificity over HERA (e.g., Wagner et al., 1998) and those showing support for both proposals (e.g., Kennepohl et al., 2007), by using more temporally precise measures of brain lateralisation. Due to the dense anatomical interconnectivity between the prefrontal cortex, the focus of the HERA model, and the medial temporal lobe, the focus of the material specificity model, it is conceivable that the lateralising influences of material and processing interact in a spatiotemporally dynamic manner that is not captured by either EEG or PET/fMRI methods alone.

The lack of similar findings from the meta-analysis is most likely due to multiple methodological differences, including its specific emphasis on the temporal lobe of epilepsy patients in contrast to the broader areas of the brain measured using electroencephalographic recordings in the empirical studies. The design of the meta-analysis also necessarily involved a post-hoc grouping of test measures with generally similar processing demands from studies which usually did not design comparisons to detect processing effects, while material effects were more often the focus of study. The empirical studies by comparison involved highly specific comparisons of well-defined encoding and retrieval tasks in a within-subject context. In summary, it is possible the design of the empirical studies was more sensitive to detecting the processing effects than was the meta-analysis. Yet both kinds of study are considered to offer valuable complementary sources of information on when and how processing-related lateralisation effects may occur.

3.3 Summary of processing-specific lateralisation

Taken together, there was evidence both for and against the idea that different processing demands affect hemispheric lateralisation. While the meta-analysis of clinical patients produced negative results, the empirical studies uncovered evidence that lateralisation in the frontal brain regions was affected by processing in a manner that was independent of material type and consistent with the HERA model, and additionally that lateralisation in

anterior brain regions involved an interaction between material and processing type. The lack of consensus across meta-analytic and empirical methods is likely due to the emphasis on the temporal lobe in the former and broader brain regions including the frontal lobe in the latter. The novelty of the findings from the empirical studies warrants further investigation.

4. Perceptual processing and verbalisation

Investigations of material specific lateralisation have typically confounded material type with stimulus modality or response type. For example, clinical tests of verbal memory typically involve auditory stimuli and responses, such as listening to and repeating back a list of words, while tests of nonverbal memory usually involve presentation of visual stimuli and a pointed response. Experimental studies are less likely to confound material and modality but nonetheless do not frequently match stimulus size, colour, or spatial frequency (cf. e.g., Bellgowan et al., 2009). In Chapters 3 and 4 there were potential confounds of spatial frequency and stimulus size between these stimuli, which are very relevant to studies of lateralisation since both have been associated with right-lateralisation of early neural activity (e.g., Martinez et al., 2001; Sergent, 1982; van der Ham, Postma, & Laeng, 2014). Chapters 5 and 6 explored the effects of these stimulus attributes compared to the to-be-remembered material.

Chapter 5 demonstrated that with appropriate experimental controls, spatial memory and spatial perceptual form can be shown to independent contribute to the right-lateralisation of the N170 ERP peak. Importantly, the right-lateralisation of the N170 peak to spatial memory did not depend on differences in spatial perceptual form, as the effect was significant whether the perceptual form of the stimuli was matched or not. This is of crucial importance since it suggests that previous findings showing early right-lateralisation to spatial memory, in both this thesis and in other studies in general, are not necessarily due merely to task-irrelevant perceptual processing. The pattern of results is inconsistent with a clear temporal distinction between memory and perceptually based lateralisation (cf. Maillard et al., 2011) but rather suggest a high degree of temporal overlap at the early stages of processing. More

broadly the findings validate previous evidence across neuropsychological, neuroimaging, and ERP methodologies for an association between spatial memory and right medial temporal lobe function (Baker & Holroyd, 2013; Bellgowan, Buffalo, Bodurka, & Martin, 2009; Bohbot et al., 1998; Diaz-Asper, Dopkins, Potolicchio, & Caputy, 2006; Kessels et al., 2002).

The same lateralisation effects were not observed in frequency-specific EEG power, instead showing a near-universal pattern of right-lateralisation. In retrospect the time windows used to measure EEG power (0 to 500 ms, 500 to 1500 ms) were possibly too wide to discriminate the effects which, in the ERP study in Chapter 5, not only occurred very early but also within the same time window (140 to 230 ms). Alternatively, or in addition, the tasks had very closely matched requirements for precise visual and spatial processing demands and such general visual-spatial attentional processing could explain the near-universal pattern of right-lateralisation in this study (e.g., Corbetta & Shulman, 2011; Langner & Eickhoff, 2013; van der Ham, Postma, & Laeng, 2014). By contrast, Chapter 4 showed lateralisation effects due to material and processing but there was less precise matching of the stimuli and tasks involved. The design of the verbal memory tasks may have encouraged strategies similar to letter-by-letter reading which have been associated with the right hemisphere (e.g., see Ellis et al., 2004, for a review).

While not the primary focus of this thesis, the role of verbalisation was also considered in Chapters 5 and 6. The results confirmed previous demonstrations that the right-lateralisation of memory processing is broadly correlated with the ease of verbalisation (Hampstead et al., 2010). Additionally, perceptual form also moderated the level of verbalisation such that hybrid verbal-spatial forms were equally verbalisable despite varying memory tasks (verbal versus nonverbal), suggesting that both memory and perceptual form affected the encoding strategies of participants. It was concluded that the effect of verbalisation on hemispheric lateralisation was relatively subtle as it was prone to interference by the type of perceptual form and greater verbalisation did not result in outright left-lateralisation of the verbal memory tasks in either ERP or EEG power measures. Therefore,

these findings demonstrate that it is critical to consider perceptually-mediated lateralisation effects and stimulus verbalisability when interpreting lateralisation differences in verbal and nonverbal memory tasks.

5. Future research directions

The findings of this thesis suggest many possible areas of future research. Among these are the use of additional imaging methods or stimulation techniques to investigate the causal relationship between lateralised brain structures and types of memory deficit, the use of different kinds of memory task to disentangle different accounts of hippocampal function, and an exploration of nonverbal memory in the auditory domain.

While the empirical studies used EEG methods in order to improve upon the temporal resolution of fMRI studies, the use of magnetoencephalography (MEG) or a combined EEG-fMRI or MEG-fMRI design would allow the precise spatial localisation of transient effects in EEG measures within particular participants. This would help build upon and clarify the complex interactions between material, processing, brain region, and timing of the neural response found in Chapter 4. For example, MEG has allowed the precise spatiotemporal tracking of material specific memory effects from visual areas (within the first 200 ms) to the hippocampal regions (200 to 800 ms) at the level of the individual participant: Memory for kaleidoscope pictures showed right-lateralisation and memory for abstract nouns showed left-lateralisation (Papanicoloau et al., 2002). More generally, validation of the experimental effects in Chapters 3 to 6 in unilateral temporal lobe epilepsy patients would also help bridge the gap between cognitive neuroscience and clinical findings.

The majority of clinical and experimental investigations of material specific lateralisation have not investigated whether lower-level stimulus attributes may contribute to putatively memory-based lateralisation effects (see Bellgowan, Buffalo, Bodurka, & Martin, 2009 for an exception). The findings of Chapter 5 suggest the importance of stimulus factors and could be taken up by researchers in all fields to improve the quality of the data interpretation. This is especially important since recent studies have suggested that the medial

temporal lobe itself may be critical in performing complex perceptual tasks such as discriminating specific associations of features (e.g., colour x shape x pattern) that do not depend on long-term memory (see Graham, Barense, & Lee, 2010 for a review). Hence researchers interested in the complex perception and memory of different materials should exercise great caution in the design and interpretation of experiments designed to elicit lateralised medial temporal activity.

The use of repetitive transcranial magnetic stimulation (rTMS) to stimulate the brain in healthy participants or TLE patients is a potentially powerful method to explore the causal relationship between time-frequency measures and right-lateralisation of memory function. Few studies have explored this option. In one study the use of repetitive TMS at the dominant alpha frequency of each participant was found to improve performance on a mental rotation task (Klimesch, Sauseng, & Gerlof, 2003). Similarly, stimulation in the gamma frequency (50 Hz) in the right perirhinal cortex of a presurgical TLE patient resulted in recollection of vivid memories and produced a widely distributed discharge within the theta frequency (Barbeau et al., 2005). A combined rTMS-EEG method could be particularly useful to separate cause from effect with respect to the role of the right hemisphere in nonverbal memory function.

The expansion of the empirical studies in this thesis to include memory tasks requiring explicit association between spatial stimuli would help determine whether the associative or the spatial map theory of hippocampal function best explains the observed patterns of lateralisation (Eichenbaum, Otto, & Cohen, 1994; O'Keefe & Nadel, 1978). While Chapters 5 and 6 compared the effects of memory and perceptual form on lateralisation by merely controlling for each, more in-depth manipulation of spatial frequencies may help compare the explanatory power of the spatial frequency model to that of material specificity. One possible design could involve continuously varying the spatial frequency of stimuli while comparing memory tasks that require attention to high or low spatial frequencies. Ideally, this design could be combined with EEG to measure peaks using the steady state visual evoked response (SSVR; see e.g., Ales, Farzin, Rossion, & Norcia, 2012; Liu-Shuang, Norcia, & Rossion,

2014) that could elicit differential responses corresponding to perceptual and memory-related processing with an extremely high signal-to-noise ratio and hence reliability.

This thesis focused on the pattern of lateralisation associated with visual nonverbal memory tasks, in line with the vast majority of studies of this type. There is a need, however, for further investigation of lateralisation of auditory memory. Tests of musical memory, for example, could provide a valuable alternative clinical test when visual methods of testing cannot be conducted, such as when a patient has visual impairment or spatial neglect, or simply when expert musical memory skills may be threatened by right temporal lobe surgery (e.g., Peretz, Champod, & Hyde, 2003). The generalisability of the spatial frequency model of lateralisation to auditory stimuli could also be explored. There have been findings suggesting hemispheric dissociation between temporal and spectral aspects of auditory analysis that may generalise across speech and music (see Zatorre, Belin, & Penhune, 2002, for a review). Investigating the potential overlap between the visual spatial frequency model and the auditory temporal/spectral model concerning hemispheric lateralisation is a tantalising proposal; while ambitious, it is eminently testable given the ease with which Fourier analysis could create appropriate stimuli.

6. Clinical ramifications and further clinical research

The findings of the meta-analysis in Chapter 2 suggest that while there is no single category of nonverbal memory test that is clearly superior in assessing the risk of surgery in presurgical patients, particular individual tests stand out with large effect sizes. These include the Dade Face Learning Test, Denman Facial Recognition Test, Austin Maze, Route Learning Test, Brown Location Test, Design Learning from the AMIPB, and the Doors Test. The utility of these tests in detecting right TLE pathology urgently needs further validation to advance clinical practice in this area. In assessing the presence of memory decline following surgery for intractable TLE, tests of face memory such as the subtest of the Warrington Recognition Memory Test have the greatest clinical utility in distinguishing right TLE impairment. Further studies are required, however, to validate whether these tests are equally effective with

increasingly popular and more tailored surgeries such as selective amygdalohippocampectomy, since the majority of the studies in Chapter 2 involved standard anterior temporal lobectomy which may remove lateral temporal areas involved in face perception.

The experimental spatial memory tasks employed in Chapters 3 to 6 could be potentially validated in a clinical setting. More research is needed with these tasks to determine their psychometric properties, and whether adding different demands such as delayed recognition impact on the degree of right-lateralisation. The methodology used in Chapters 5 and 6 suggested that the use of perceptually identical stimuli with differing memory demands (and vice versa) may be a convenient way of separating perceptual from memory related impairment in patients with right-lateralised brain pathology.

7. Final remarks

This thesis has shown that multiple factors affect right hemisphere memory function. The factor that most consistently predicted right-lateralisation was the use of nonverbal stimulus material. The type of nonverbal stimulus also had an important effect, however, with meta-analysis showing that memory for facial and spatial stimuli has greater capacity to discriminate the impact of right versus temporal lobe resection than memory for abstract design stimuli. EEG measures were also used to show independent and interactive effects of material specific and processing specific lateralisation in healthy participants, with material effects occurring regardless of the brain region while processing effects were limited to the frontal brain region. In a separate EEG study, spatial memory and spatial perceptual form showed separable effects on right-lateralisation, while the degree of verbalisation had a subtle effect which was modified by both memory and perceptual demands.

In conclusion, the findings confirm that while material type is the most powerful influence on lateralisation to the right hemisphere, there are important limitations and caveats to this general material specific pattern. The type of processing engaged in during memory and the perceptual form of the to-be-remembered stimulus also impact on lateralisation, and

considering the impact of each factor has potential clinical relevance. Further investigations might include the use of stimulation or imaging approaches that complement EEG to further delineate the relationship between aspects of nonverbal memory and right hemisphere brain function.

References

Ales, J. M., Farzin, F., Rossion, B., & Norcia, A. M. (2012). An objective method for measuring face detection thresholds using the sweep steady-state visual evoked response. *Journal of Vision, 12*(10), 18-18. doi:10.1167/12.10.18

Alpherts, W. C. J., Vermeulen, J., van Rijen, P. C., da Silva, F. H. L., van Veelen, C. W. M., & Dutch Collaborative Epilepsy, S. (2006). Verbal memory decline after temporal epilepsy surgery? A 6-year multiple assessments follow-up study. *Neurology, 67*(4), 626-631. doi:10.1212/01.wnl.0000230139.45304.eb

Awasthi, B., Friedman, J., & Williams, M. A. (2011). Faster, stronger, lateralized: Low spatial frequency information supports face processing. *Neuropsychologia, 49*(13), 3583-3590. doi:10.1016/j.neuropsychologia.2011.08.027

Baker, T. E., & Holroyd, C. B. (2013). The topographical N170: Electrophysiological evidence of a neural mechanism for human spatial navigation. *Biological Psychology, 94*(1), 90-105.

Barbeau, E. J., Taylor, M. J., Regis, J., Marquis, P., Chauvel, P., & Liégeois-Chauvel, C. (2008). Spatio temporal dynamics of face recognition. *Cerebral Cortex, 18*(5), 997-1009. doi:10.1093/cercor/bhm140

Barr, W. B. (1997). Examining the right temporal lobe's role in nonverbal memory. *Brain and Cognition, 35*(1), 26-41.

Barr, W. B., Chelune, G. J., Hermann, B. P., Loring, D. W., Perrine, K., Strauss, E., . . . Westerveld, M. (1997). The use of figural reproduction tests as measures of nonverbal memory in epilepsy surgery candidates. *Journal of the International Neuropsychological Society, 3*(5), 435-443.

Baxendale, S., Thompson, P. J., & Duncan, J. S. (2008). The role of the Wada test in the surgical treatment of temporal lobe epilepsy: An international survey. *Epilepsia, 49*(4), 715-720. doi:10.1111/j.1528-1167.2007.01515_1.x

Bellgowan, P. S. F., Buffalo, E. A., Bodurka, J., & Martin, A. (2009). Lateralized spatial and object memory encoding in entorhinal and perirhinal cortices. *Learning & Memory, 16*(7), 433-438. doi:10.1101/lm.1357309

Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia, 36*(11), 1217-1238.

Brown, F. C., Tuttle, E., Westerveld, M., Ferraro, F. R., Chmielowiec, T., Vandemore, M., . . . Spencer, S. S. (2010). Visual memory in patients after anterior right temporal lobectomy and adult normative data for the Brown Location Test. *Epilepsy & Behavior, 17*(2), 215-220. doi:10.1016/j.yebeh.2009.11.026

Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. In S. E. Hyman, T. M. Jessell, C. J. Shatz, C. F. Stevens, & H. Y. Zoghbi (Eds.), *Annual Review of Neuroscience, Vol 34* (Vol. 34, pp. 569-599).

Diaz-Asper, C. M., Dopkins, S., Potolicchio, S. J., & Caputy, A. (2006). Spatial memory following temporal lobe resection. *Journal of Clinical and Experimental Neuropsychology, 28*(8), 1462-1481. doi:10.1080/13803390500434359

Eichenbaum, H., Otto, T., & Cohen, N. J. (1994). Two functional components of the hippocampal memory system. *Behavioral and Brain Sciences, 17*(3), 449-472.

Ellis, N. C., Natsume, M., Stavropoulou, K., Hoxhallari, L., Daal, V. H., Polyzoe, N., . . . Petalas, M. (2004). The effects of orthographic depth on learning to read alphabetic, syllabic, and logographic scripts. *Reading Research Quarterly, 39*(4), 438-468.

Golby, A. J., Poldrack, R. A., Brewer, J. B., Spencer, D., Desmond, J. E., Aron, A. P., & Gabrieli, J. D. E. (2001). Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. *Brain, 124*, 1841-1854. doi:10.1093/brain/124.9.1841

Graham, K. S., Barense, M. D., & Lee, A. C. H. (2010). Going beyond LTM in the MTL: A synthesis of neuropsychological and neuroimaging findings on the role of the medial

temporal lobe in memory and perception. *Neuropsychologia, 48*(4), 831-853. doi:10.1016/j.neuropsychologia.2010.01.001

Habib, R., Nyberg, L., & Tulving, E. (2003). Hemispheric asymmetries of memory: the HERA model revisited. *Trends in Cognitive Sciences, 7*(6), 241-245. doi:10.1016/s1364-6613(03)00110-4

Hampstead, B. M., Lacey, S., Ali, S., Phillips, P. A., Stringer, A. Y., & Sathian, K. (2010). Use of complex three-dimensional objects to assess visuospatial memory in healthy individuals and patients with unilateral amygdalohippocampectomy. *Epilepsy and Behavior, 18*(1-2), 54-60.

Hickok, G., & Poeppel, D. (2007). Opinion - The cortical organization of speech processing. *Nature Reviews Neuroscience, 8*(5), 393-402. doi:10.1038/nrn2113

Jones-Gotman, M., Harnadek, M. C. S., & Kubu, C. S. (2000). Neuropsychological assessment for temporal lobe epilepsy surgery. *Canadian Journal of Neurological Sciences, 27*, S39-S43.

Kennepohl, S., Sziklas, V., Garver, K. E., Wagner, D. D., & Jones-Gotman, M. (2007). Memory and the medial temporal lobe: Hemispheric specialization reconsidered. *Neuroimage, 36*(3), 969-978. doi:10.1016/j.neuroimage.2007.03.049

Kessels, R. P. C., de Haan, E. H. F., Kappelle, L. J., & Postma, A. (2001). Varieties of human spatial memory: a meta-analysis on the effects of hippocampal lesions. *Brain Research Reviews, 35*(3), 295-303.

Kessels, R. P. C., Kappelle, L. J., de Haan, E. H. F., & Postma, A. (2002). Lateralization of spatial-memory processes: evidence on spatial span, maze learning, and memory for object locations. *Neuropsychologia, 40*(8), 1465-1473.

Klimesch, W., Doppelmayr, M., Pachinger, T., & Russegger, H. (1997). Event-related desynchronization in the alpha band and the processing of semantic information. *Cognitive Brain Research, 6*(2), 83-94. doi:10.1016/s0926-6410(97)00018-9

Klimesch, W., Sauseng, P., & Gerloff, C. (2003). Enhancing cognitive performance with repetitive transcranial magnetic stimulation at human individual alpha frequency. *European Journal of Neuroscience, 17*(5), 1129-1133. doi:10.1046/j.1460-9568.2003.02517.x

Kuhn, S., & Gallinat, J. (2014). Segregating Cognitive Functions Within Hippocampal Formation: A Quantitative Meta-analysis on Spatial Navigation and Episodic Memory. *Human Brain Mapping, 35*(4), 1129-1142. doi:10.1002/hbm.22239

Langner, R., & Eickhoff, S. B. (2013). Sustaining Attention to Simple Tasks: A Meta-Analytic Review of the Neural Mechanisms of Vigilant Attention. *Psychological Bulletin, 139*(4), 870-900. doi:10.1037/a0030694

Lee, T. M. C., Yip, J. T. H., & Jones-Gotman, M. (2002). Memory deficits after resection from left or right anterior temporal lobe in humans: A meta-analytic review. *Epilepsia, 43*(3), 283-291.

Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2014). An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. *Neuropsychologia, 52*, 57-72. doi:10.1016/j.neuropsychologia.2013.10.022

Maillard, L., Barbeau, E. J., Baumann, C., Koessler, L., Benar, C., Chauvel, P., & Liegeois-Chauvel, C. (2011). From Perception to Recognition Memory: Time Course and Lateralization of Neural Substrates of Word and Abstract Picture Processing. *Journal of Cognitive Neuroscience, 23*(4), 782-800. doi:10.1162/jocn.2010.21434

Martin, A., Wiggs, C. L., & Weisberg, J. (1997). Modulation of human medial temporal lobe activity by form, meaning, and experience. *Hippocampus, 7*(6), 587-593. doi:10.1002/(sici)1098-1063(1997)7:6<587::aid-hipo1>3.0.co;2-c

Martinez, A., Di Russo, F., Anllo-Vento, L., & Hillyard, S. A. (2001). Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies. *Clinical Neurophysiology, 112*(11), 1980-1998.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map* (Vol. 3): Clarendon Press Oxford.

Papanicolaou, A. C., Simos, P. G., Castillo, E. M., Breier, J. I., Katz, J. S., & Wright, A. A. (2002). The hippocampus and memory of verbal and pictorial material. *Learning & Memory, 9*(3), 99-104. doi:10.1101/lm.44302

Peretz, I., Champod, A. S., & Hyde, K. (2003). Varieties of musical disorders. *Annals of the New York Academy of Sciences, 999*(1), 58-75.

Peyrin, C., Chauvin, A., Chokron, S., & Marendaz, C. (2003). Hemispheric specialization for spatial frequency processing in the analysis of natural scenes. *Brain and Cognition, 53*(2), 278-282. doi:10.1016/s0278-2626(03)00126-x

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation. *Journal of Experimental Psychology-Human Perception and Performance, 8*(2), 253-272. doi:10.1037/0096-1523.8.2.253

Sherman, E. M. S., Wiebe, S., Fay-McClymont, T. B., Tellez-Zenteno, J., Metcalfe, A., Hernandez-Ronquillo, L., . . . Jette, N. (2011). Neuropsychological outcomes after epilepsy surgery: Systematic review and pooled estimates. *Epilepsia, 52*(5), 857-869. doi:10.1111/j.1528-1167.2011.03022.x

Smith, G. E., Malec, J. F., & Ivnik, R. J. (1992). Validity of the construct of nonverbal memory: A factor-analytic study in a normal elderly sample. *Journal of Clinical and Experimental Neuropsychology, 14*(2), 211-221. doi:10.1080/01688639208402824

van der Ham, I. J. M., Postma, A., & Laeng, B. (2014). Lateralized perception: The role of attention in spatial relation processing. *Neuroscience and Biobehavioral Reviews, 45*, 142-148. doi:10.1016/j.neubiorev.2014.05.006

Vaz, S. A. M. (2004). Nonverbal memory functioning following right anterior temporal lobectomy: a meta-analytic review. *Seizure-European Journal of Epilepsy, 13*(7), 446-452. doi:10.1016/j.seizure.2003.12.004

Wagner, A. D., Poldrack, R. A., Eldridge, L. L., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. *Neuroreport, 9*(16), 3711-3717.

Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: music and speech. *Trends in Cognitive Sciences, 6*(1), 37-46. doi:10.1016/s1364-6613(00)01816-7

Final Approval- Ethics application reference-5201100342

Reply

Ethics Secretariat to A/Prof, A/Prof, me show details May 18 (12 days a go)

Dear A/Prof Savage

Re: "Nonverbal memory and perception in the right hemisphere" (Ethics Ref: 5201100342)

Thank you for your recent correspondence. Your response has addressed the issues raised by the Human Research Ethics Committee and you may now commence your research.

The following personnel are authorised to conduct this research:

A/Prof Greg Savage- Chief Investigator/Supervisor
A/Prof Genevieve McArthur & Mr Adam Craig Bentvelzen- Co-Investigators

NB. STUDENTS: IT IS YOUR RESPONSIBILITY TO KEEP A COPY OF THIS APPROV AL
EMAIL TO SUBMIT WITH YOUR THESIS.

Please note the following standard requirements of approval:

1. The approval of this project is conditional upon your continuing compliance with the National Statement on Ethical Conduct in Human Research (2007).

2. Approval will be for a period of five (5) years subject to the provision of annual reports. Your first progress report is due on 18 May 2012.

If you complete the work earlier than you had planned you must submit a Final Report as soon as the work is completed. If the project has been discontinued or not commenced for any reason, you are also required to submit a Final Report for the project.

Progress reports and Final Reports are available at the following website:

http://www.research.mq.edu.au/for/researchers/how_to_obtain_ethics_approval/human_research_ethics/forms

3. If the project has run for more than five (5) years you cannot renew approval for the project. You will need to complete and submit a Final Report and submit a new application for the project. (The five year limit on renewal of approvals allows the Committee to fully re-review research in an environment where legislation, guidelines and requirements are continually changing, for example, new child protection and privacy laws).

4. All amendments to the project must be reviewed and approved by the Committee before implementation. Please complete and submit a Request for Amendment Form available at the following website:

http://www.research.mq.edu.au/for/researchers/how_to_obtain_ethics_approval/human_research_ethics/forms

5. Please notify the Committee immediately in the event of any adverse effects on participants or of any unforeseen events that affect the continued ethical acceptability of the project.

6. At all times you are responsible for the ethical conduct of your research in accordance with the guidelines established by the University. This information is available at the following websites:

http://www.mq.edu.au/policy/

http://www.research.mq.edu.au/for/researchers/how_to_obtain_ethics_approval/human_research_ethics/policy

If you will be applying for or have applied for internal or external funding for the above project it is your responsibility to provide the Macquarie University's Research Grants Management Assistant with a copy of this email as soon as possible. Internal and External funding agencies will not be informed that you have final approval for your project and funds will not be released until the Research Grants Management Assistant has received a copy of this email.

If you need to provide a hard copy letter of Final Approval to an external organisation as evidence that you have Final Approval, please do not hesitate to contact the Ethics Secretariat at the address below.

Please retain a copy of this email as this is your official notification of final ethics approval.

Yours sincerely
Dr Karolyn White
Director of Research Ethics
Chair, Human Research Ethics Committee